FIRE-GRAZING INTERACTION:

AN ECOLOGICAL PROCESS

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Abstract: The ecological interactions between fire and grazing are widespread throughout fire-prone ecosystems. It is an ecological process that drives ecosystem structure and function, influencing broad, landscape level events to fine, localized processes. The fire-grazing interaction occurs when spatially distinct fires are are present across a landscape and move through time, forcing grazing animals to choose among burned and unburned areas. The mechanisms of this interaction occur at multiple levels. At broad, landscape level scales, animals are attracted to and focus their grazing on recently burned areas. This attraction decreases as the amount of time since fire progresses. For bison (*Bison bison*) and cattle (*Bos taurus*) in tallgrass prairie of North America, the influence of time since fire supersedes most landscape features (e.g., distance to water, topography, etc.), indicative of the overall strength of the fire-grazing interaction.

Mechanisms of the fire-grazing interaction are also present at finer, patch level scales. Forage quality and quantity differences between burned areas are responsible for preferential grazing of burned areas. Forage quality is inversely related to time since fire, so that recently burned areas are greatest in quality, while areas with greater time since fire are significantly lower. The opposite relationship is present with forage quantity, with burned areas having small amounts of quantity compared to areas with greater time since fire. Tradeoffs between forage quality and quantity emerge and influence the attraction of grazing animals to burned areas.

The light environment at finer, plot level scales is also determined by the amount of time since fire within the fire-grazing interaction. The preferential grazing of recently burned areas maintain high light environments throughout the growing season. These areas differ from that of fire alone, where light limitations quickly return after fire. The high light environment allows for increased photosynthetic rate of dominant prairie plants, but at the expense of low leaf area through continual preferential grazing by animals. As a result, total carbon gain by plants is reduced compared to areas with greater time since fire. These results feedback and affect forage quality and quantity.

TABLE OF CONTENTS

LIST OF TABLES

Chapter 1 Page

Chapter 2 Page

Chapter 4 Page

LIST OF FIGURES

Chapter 1 Page

Chapter 2 Page

Chapter 3 Page

Chapter 4 Page

CHAPTER I

The role of herbivores in Great Plains conservation: comparative ecology of bison and cattle

The role of herbivores in Great Plains conservation: comparative ecology of bison and cattle

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Abstract

The Great Plains of North America evolved with significant influence from bison (*Bison bison*), but is presently dominated by cattle (*Bos taurus*). While there are a variety of opinions concerning differences between these two species, there is a lack of scientific comparisons, including those that incorporate important ecological variation. We developed a framework to study and compare the grazing behavior and effects of bison and cattle within grassland ecosystems. Environmental (e.g., resource distribution, disturbance) and animal (e.g., number, social organization) factors play a critical role in determining grazing effects and should be incorporated into discussions that compare the effects of bison and cattle. Using this framework we specifically compare the grazing behavior of both species in tallgrass prairie and discuss the implications of these differences in the context of conservation. We collared bison and cattle with global positioning systems and used resource selection functions to estimate the importance of various environmental factors on site selection. Both species preferred recently burned areas and avoided steeper slopes. Cattle selected areas that were closer to water, while bison were not limited by distance to water; cattle also preferred areas with woody vegetation, while bison avoided them. Incorporating broad scale environmental complexity allows for an effective comparison of ecological differences between bison and cattle. While there are similarities and differences in these species, a comprehensive analysis of all conditions and scenarios is not possible. It is clear, however, that the greatest differences between these species will likely be evident from broad scale studies across complex landscapes. In addition to species, conservation and land managers need to consider other environmental factors that are critical to grazing effects and overall conservation.

Keywords

Fire; grassland; grazing; herbivory; restoration; species comparisons; tallgrass prairie.

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Introduction

The role of herbivores in grassland ecosystems has been an important topic debated by ecologists and ecosystem managers for more than a century. The Great Plains of North America are central to this discussion as most flora and fauna evolved with significant impact from large herbivores and other disturbances (Axelrod 1985, Anderson 2006). Until their near extirpation in the late 1800s, American Bison (*Bison bison*) were keystone herbivores within the Great Plains, sharing complex landscapes with other herbivores and predators for nearly 10,000 years (Knapp et al. 1999, Anderson 2006). Since their near extinction, the vast and complex landscapes that contained the roaming herds have been replaced by fragmented agricultural lands where domestic cattle are the dominant grazers. Restoration and conservation of bison has been pursued by private citizens, conservation organizations, and government agencies with a primary goal of conserving the species and restoring critical ecosystem processes and functions.

Grazing by large herbivores can affect a system in many different ways (Milchunas et al. 1988, Augustine and McNaughton 1998, Anderson et al. 2006). The effects of grazing are often viewed in isolation of each other, removing all complexity and variation besides that of grazing. Such work has enhanced the understanding and management of grasslands. The evolutionary effects of grazing, however, are much more complex than traditional, small scale experimental designs can replicate (Levin 1992, Fuhlendorf et al. 2009). Grazing is a dynamic process that interacts with complex landscapes to form disturbance patterns that are critical to many ecosystem functions, including biodiversity (Collins et al. 1998, Tews et al. 2004). Because of this, the effects of grazing are influenced by many factors, including those associated with animals and the environment.

The species of animal alone is not the only determinant of grazing effects. Age, sex, number, and social organization of animals contribute to altering behavior and ecological influences. In addition to the structure of the grazer community, environmental factors (e.g. disturbances, climate, predation, resources) will also contribute to grazing effects. When discussing grazing or grazing behavior, a traditional reductionist approach is to focus on one factor without considering the complexity of other factors. In the Great Plains of North America, ecologists, conservation biologists, and land managers have studied and debated the effects of grazing by bison and domestic cattle (*Bos taurus*), often without including other interacting factors (Hartnett et al. 1997, Steuter and Hidinger 1999). Common managerial differences associated with bison and cattle also confound differences in effects between the two species (Towne et al. 2005). Cattle herds are often associated with ranches that are based on commodity production, where animals are commonly separated for most of the year based on sex or age (e.g. cows and calves, bulls). In the Great Plains of North America, cattle are rarely, if ever, managed as wildlife or with a conservation focus. Bison, on the other hand, may be managed as either production or conservation herds.

While similarities and differences between cattle and bison are widely discussed and debated, the peer reviewed literature comparing the two is largely inconclusive. For example, in popular press, government reports, and scientific literature, it is often stated that bison spend less time near water or riparian areas than cattle (Manning 1995, Hartnett et al. 1997, Fritz et al. 1999, Reynolds et al. 2003, National Park Service 2009). Indeed, van Vuren (1982) found a greater percentage of observations of cattle closer to water than bison. Unfortunately, it is apparent that the confounding management strategies of the two species were not taken into account, specifically with regard to stocking rate or animal density: “a herd of about 300 wild bison … shares its summer range with several hundred range cattle” (van Vuren 1982). With no clear definition of how many animals were present or specific management plans for each species, a reliable conclusion cannot be made. Direct comparisons of foraging ecology or behavior between bison and cattle have also been minimal. Plumb and Dodd (1993) found that in general, bison spent less time feeding with shorter grazing bouts than cattle, but had greater number of bouts per day.

We argue that recognizing ecological differences between bison and cattle would be best studied on large, complex landscapes that do not limit behavior to finer scales (Holland et al. 2004, Boyce 2006, Bowyer and Kie 2006). Incorporating landscape variability will allow for a more effective comparison of grazing behavior and effects between bison and cattle, as animals can interact with environmental factors that contribute to grazing effects. We describe the design, results, and limitations of a current study comparing bison and cattle behavior on complex landscapes that include other disturbances (e.g. fire). We then develop a conceptual model to facilitate the discussion of the conservation value of reintroducing bison within human dominated landscapes of the Great Plains.

Methods

The Tallgrass Prairie Preserve: a model for experimental design

The Nature Conservancy Tallgrass Prairie Preserve, located in northeast Oklahoma, USA, is a 16,000 ha natural area that is managed for biodiversity and heterogeneity (Hamilton 2007). The preserve lies at the southern end of the Flint Hills of the Great Plains. Vegetation is classified as tallgrass prairie, with small patches of cross timbers forest. Dominant grasses include *Andropogon gerardii* Vitman, *Schizachyrium scoparium* (Michx.) Nash, *Panicum virgatum* L., and *Sorghastrum nutans* (L.) Nash. Crosstimbers vegetation is dominated by *Quercus stellata* Wang. and *Q. marilandica* Münchh. Precipitation and various climate measurements are measured on site by an Oklahoma Mesonet station (Brock et al. 1995). Total precipitation for April through September for 2009 and 2010 (time period of study) was 64.7 and 72.5 cm, respectively. Long term mean total for April through September is 62.2 cm (14.94 standard deviation).

Within the site, there is one large bison unit (9532 ha) and seven smaller cattle units (430-980 ha) (Fig. 1). Only perimeter fences are present and animals are free to roam within their respective units. There is minimal handling of both bison and cattle with no supplemental feeding. Bison are maintained in their respective unit all year; herd size is approximately 2,300 animals. Sex ratio of the bison herd is approximately seven females per male; ages of females range from 0-10 years, while males are 0-6 years. Cattle units are stocked with stocker steers approximately one year old (mixed European breeds); cattle are only present April through September. Cattle herds vary with each unit, ranging from 169 to 463 animals. Bison and cattle units are stocked with similar moderate stocking rates (bison: 2.1 AUM/ha; cattle: 2.4 AUM/ha). The entire preserve is managed extensively with fire and in such way that fire and grazing are allowed to interact (Hamilton 2007, Fuhlendorf et al. 2009). Bison and cattle units are shifting mosaics with fire occurring in discrete portions of the landscape (Fig. 1). Fire-grazing interactions become present as animals select between recently burned areas and those with greater time since fire (Archibald et al. 2005, Fuhlendorf et al. 2009).

To specifically examine herbivore site selection, we deployed global positioning system (GPS) collars on seven female bison (four to six years in age) from November 2008 through November 2010 and seven cattle (steers, one year in age; one per unit) from April through September of 2009 and 2010. For bison, GPS batteries were replaced and new animals chosen in November 2009; for cattle, new animals were chosen and new batteries used in April 2010. We recorded location information of animals at two different frequencies, alternately weekly from 12 minutes to one hour. Schedule of GPS fixes was equal for bison and cattle. We imported all GPS location data into a spatially enabled database (PostgreSQL/PostGIS) and reduced bison data to match that of cattle (April - September). We mapped treatment unit perimeters, fire histories, and water sources (ponds and streams) with handheld GPS units, aerial photographs, and United States Geological Survey 7.5 minute topographic maps. Slope and aspect were calculated from digital elevation models for the area (United States Geological Survey; 10 m resolution). We transformed aspect data by simple trigonometric functions; two variables were created, northing = cosine(aspect) and easting = sin(aspect). Herbaceous and woody vegetation was determined for the site using a GeoEye-1 satellite image acquired September 20, 2009.

We compared similarity of units by randomly placing 1,000 sampling points within each unit. At each sampling point, distance to water, distance to patch edge, distance to woody vegetation, slope, northing, and easting were calculated. Measured characteristics among animal units were compared individually using analysis of variance and did not differ between units ($P > 0.05$). We used Ivlev electivity indices (Ivlev 1961, Jacobs 1974) to evaluate the use of riparian areas by bison and cattle. Riparian areas were defined by putting a 20 and 40 m buffer around all mapped water sources. We calculated electivity indices using the formula $E_i = (r_i - p_i)/(r_i + p_i)$ where r_i is the fraction of GPS locations recorded in a riparian area by animal i and p_i is the fraction of area enclosed by the sum of buffers available to animal i. A value of +1 indicates complete preference to riparian areas, while a value of -1 indicates complete avoidance. Indices were calculated for each collared bison and cattle individual, separating water sources into ponds, streams, and pond/stream combination. Indices between bison and cattle were compared for each size riparian area (i.e. 20 and 40 m) using a *t*-test. We also used Ivlev electivity indices to compare bison and cattle preferences for recently burned areas (six months or less since fire). We calculated indices for each collared animal based upon recently burned area available; we compared indices using a *t*-test.

To examine the influence of environmental factors on the grazing behavior of bison and cattle, we estimated resource selection functions using mixed-effect logistic regression models (used/available design; Boyce et al. 2002, Manly et al. 2002). To depict available habitat, we created five random locations for each observed location. We calculated the amount of time since fire, distance to water, distance to fire patch edge, slope, northing, and easting for all locations. We also classified each location as herbaceous or woody vegetation. To determine if the presence of woody vegetation is confounded with water sources (i.e., the presence of woody vegetation is primarily near water sources), we quantified the distribution of woody vegetation around water sources. The percentage of woody vegetation within 20 and 40 m of water sources across the site was 3% and 7%, respectively. Furthermore, we examined variables for collinearity and found none ($r^2 < 0.27$ for all variable combinations), indicating that variables are not confounding with one another (i.e., woody vegetation is not limited near water sources). To account for variation among individual animals within resource selection functions, individuals were included as a random intercept within logistic regressions. To account for fire availability among units and potential response variation to fire, time since fire and its interaction with other variables (e.g., time since fire × distance to water; see below) were included as random slopes within logistic regressions (Gillies et al. 2006).

We created models using various combinations of environmental factors; as the influence of time since fire is likely to be highly influential (Vinton et al. 1993, Fuhlendorf and Engle 2004, Archibald et al. 2005), we included interaction terms for this variable with all others individually (i.e., time since fire × distance to water, time since fire × slope, etc.). In all models with interaction terms, main effects of both variables were included. To allow for comparison of environmental factors and to more easily interpret interaction terms, we standardized variables by subtracting the mean and dividing by the standard deviation (Gelman and Hill 2007). We compared and ranked models using Akaike information criterion (AIC; Burnham and Anderson 2002). We used bootstrapping procedures to further estimate the precision of resource selection coefficients of the top ranked model. We calculated 95% confidence intervals of coefficients after 1,000 iterations of randomly sampled datasets. To further examine variation among individual animal behavior, we calculated resource selection functions for each animal per year (28 animals total) using top ranked models. We performed all analyses in R (R Development Core Team 2009) with additional use of the *lme4* (Bates and Maechler 2010), *doMPI* (Weston 2009), *foreach* (Revolution Computing 2009) and *Rmpi* (Yu 2010) packages.

Results

Of bison locations, 9 and 15% fell within riparian areas of size 20 and 40 m, respectively (ponds and streams combined). Of cattle locations, 13 and 20% fell within riparian areas of size 20 and 40 m, respectively. Mean Ivlev electivity indices of riparian areas varied significantly between bison and cattle with all water sources and riparian area sizes ($P < 0.01$; Fig. 2). Cattle had a greater preference for ponds (Fig. 2A), while bison avoided streams (Fig. 2B). When ponds and streams were combined, bison had a small avoidance of water, while cattle had a greater preference for it (Fig. 2C). These data show the difference between bison and cattle in their use of water and riparian areas, in similar fire-managed landscapes with abundant water.

Bison and cattle strongly preferred recently burned patches (Table 1). Mean percentages of GPS locations in areas with six months or less since fire did not vary between bison and cattle (*P* = 0.11) With bison, 68% of locations were found in recently burned areas (less than six months), while cattle were 58%. The amount of area burned within six months was approximately 25% of the landscape in both bison and cattle units. Bison and cattle were nearly three times likely to be in a burned area than by random chance alone. Mean Ivlev electivity indices of recently burned areas were 0.57 (0.01) and 0.43 (0.15) for bison and cattle, respectively (standard deviations in parentheses); indices did not differ between species (*P* = 0.12).

Estimation of resource selection functions permitted a detailed examination of environmental factors that influence selection behavior. Of models examined, the combination of interaction terms of time since fire with all variables (less northing and easting) appeared to have the best fit for both bison and cattle (Table 2). Resource selection functions for bison revealed that time since fire had the strongest influence in determining site selection. Furthermore, bison tended to avoid steeper slopes and wooded areas. Distance to water did not influence selection (Table 3). Interactions of time since fire with other environmental factors indicates the connectedness of fire with grazing behavior. The influence of time since fire increased as slope and distance to patch edge increased; conversely, the influence of time since fire decreased as woody vegetation and distance to water increased. This decrease is minimal due to the initial strong influence of fire. The probability of selection for bison, based upon time since fire, distance to water, and the interaction of those two factors, is displayed in Figure 3. In recently burned areas, bison avoid water slightly; in areas with greater time since fire, bison are not influenced by water.

Similar to bison, cattle also selected recently burned areas and avoided steeper slopes. Unlike bison, however, the most influential environmental factor was the preference of woody vegetation. Moreover, cattle appeared to minimize distance to water, opposite that of bison (Table 3). Interactions of time since fire with other variables further shows the importance of fire to understanding grazing within these ecosystems. As distance to water and patch edge increase, so does the influence of time since fire; the presence of woody vegetation, however, decreases the influence of time since fire. The probability of selection for cattle, based upon time since fire, distance to water, and the interaction of the two, is displayed in Figure 4. Cattle minimize their distance to water in both recently burned areas and areas with greater time since fire.

Resource selection functions for individual animals revealed variation in site selection (Table 4). Though individual animals generally followed trends indicated by the population model, cattle tended to be more variable in their response to environmental factors. Individual bison and cattle still strongly preferred recently burned areas (minimizing the amount of time since fire), but the response of cattle varied considerably among individuals. All individual cattle minimized their distance to water, while only three bison did so. Other factors, including interactions with time since fire, varied among animals. Because different animals were chosen each year, we cannot separate the variation among animals and the variation between years.

Discussion

The design of this study more effectively permits comparisons between bison and cattle, both in examining grazing behavior differences between the species (results presented here) and their ecological effects (e.g. plant response, water quality, etc; data not collected). Our design incorporates more of the variability found in complex landscapes than previous studies, allowing animals to interact and respond to variation and complexity across the landscape. Bison and cattle had similarities in some aspects of their behavior. Both species had a strong preference for recently burned areas, similar to separate studies of the individual species (Coppedge et al. 1998, Fuhlendorf and Engle 2004). Along with similarities we also identified two key differences. Cattle preferred areas with woody vegetation, while bison avoided them. This likely plays a critical role in thermal regulation, with woody canopy cover providing shade from solar radiation. Detailed mapping of the thermal environment is required to determine the influence of heat on the grazing behavior of bison and cattle. Additionally, because location information obtained by the GPS does not differentiate between grazing or resting, it is unclear if the preference for woody vegetation is a result of grazing or resting behavior.

It does show, however, behavioral preferences and differences that are likely to influence both selection and grazing decisions, especially when studying behavior at large spatial scales.

Selection for sites closer to water was also greater in cattle than bison; bison appeared to maximize their distance to water while cattle minimized it. These differences occurred in a well watered landscape and may be even more important in lands with greater distance between water sources. Though water included ponds and streams, ephemeral water sources were not included due to difficulty in measuring them at this spatial scale. Differences in use of ephemeral water between bison and cattle may explain measured differences. Additionally, both bison and cattle distribution and behavior may be influenced by precipitation patterns (Lott 2002, McAllister et al. 2006). At broader scales such as the Tallgrass Prairie Preserve, variability in spatial precipitation patterns may exist (Augustine 2010). Though not quantified, spatial variability in precipitation would likely influence animal distribution indirectly through vegetation responses and ephemeral water sources.

Although we did not collect data on ecological implications of grazing, it is likely that distribution differences between bison and cattle would result in contrasting effects. The preference or focusing of grazing in a particular area (large or small) will influence vegetation community and characteristics. The continued attraction of both bison and cattle to recently burned areas alters vegetation structure which affects biodiversity

(Fuhlendorf et al. 2006), fire behavior (Leonard et al. 2010), invasive species populations (Cummings et al. 2007), invertebrate populations and communities (Engle et al. 2008), and nutrient cycling and distribution (Anderson et al. 2006). The preference of riparian and woody vegetation areas by cattle will also likely result in vegetation and system changes. Reduced herbaceous cover, biomass, and productivity generally result from cattle grazing within riparian areas (Kauffman et al. 1983, Clary 1995, Belsky et al. 1999). Preference for water sources may also affect stream bank morphology, hydrology, and water quality (Kauffman and Krueger 1984, Trimble and Mendel 1995, Belsky and Blumenthal 1997). Concentration of livestock around ponds and streams may also likely increase nutrient concentrations (Schepers and Francis 1982, Belsky et al. 1999). We note, however, that direct comparisons of bison and cattle grazing effects on riparian processes are largely lacking.

It is difficult to account for the many factors that may create differences or similarities between bison and cattle, and like all studies of processes on complex landscapes, this study is not without limitations. Though stocking rates were similar between bison and cattle units, cattle were only present during the growing season (April – September), while bison remained throughout the year. Differences in the social and temporal organizations of cattle and bison herds may also confound differences. The bison herd was a mixture of males and females of various ages grazing together, while cattle herds were yearling stocker steers. A yearlong, cow-calf cattle operation would permit even better comparisons between the two species, particularly with regard to ecological effects. Though treatment units were large and incorporated landscape complexity, they were not of equal size. We could expect that animal behavior would be sensitive to and vary with available area. Smaller units would limit animal movement and behavior, restricting selection and interaction with other environmental factors. Available area would be important particularly regarding cattle preference for water, as smaller units would constrain animals closer to water. While cattle units within the Tallgrass Prairie Preserve are smaller than the bison unit, they are larger than the majority of land holdings within the Great Plains; size likely did not limit the distance to water. This study also compared bison to European cattle breeds that are typical for livestock production objectives on tallgrass prairies. Other breeds of cattle are likely to respond differently (Rook et al. 2004, VanWagoner et al. 2006). Brahman or Texas longhorn breeds, for example, are likely to be adapted to more arid environments where water is limiting and may behave more similarly to bison.

In the Great Plains of North America, bison are reintroduced for primarily two objectives: species conservation and restoration of ecosystem processes. Reintroduction to conservation areas, development of private herds, and recent efforts in identifying pure herds to conserve genetics have been successful in restoring wild bison populations to many areas. Conservation of this species is a unique success story that deserves acknowledgement. Bison are also reintroduced to restore keystone effects (Knapp et al. 1999). Conservation groups as well as government agencies reintroduce bison to both small prairie remnants and large landscapes to restore historical disturbance patterns. In most cases, this is done without considering the many other factors that influence grazing behavior or effects. While the first objective for reintroduction can be accomplished by building up bison herds throughout the Great Plains, the second objective is not possible without the consideration or reintroduction of other environmental or animal factors. For example, we show that both of these herbivores have a strong preference for recently burned areas. This may suggest that the reintroduction of bison, or the evaluation of differences between these species, may be largely irrelevant unless fire and other complexities are incorporated (Fuhlendorf et al. 2009). It is likely true that other factors, such as predators, would also greatly alter animal behavior and grazing effects (Ripple and Beschta 2003).

Conservation efforts regarding bison reintroduction should be evaluated to not only see if specific objectives are met, but how efforts contribute to overall conservation. We developed a conceptual model to evaluate the conservation value of different options regarding bison reintroduction (Fig. 5). We define conservation value as the contribution to regional conservation efforts, including promotion of native plants, animals, and ecosystem processes. The model is based on two primary factors that influence grazing behavior and effects, primarily complexity of grazers and the environment. Complexity of grazers refers to factors such as species, diversity, and social organization that contribute to the overall conservation value. Although this study examined only differences between two species, increasing species diversity with multiple species will add additional complexity to system and alter the effects of grazing (du Toit and Cumming 1999, Hooper et al. 2005, Burns et al. 2009). Other native species in North American grasslands, such as prairie dogs (*Cynomys* spp.) are also important components of the system; as an example, incorporating prairie dogs will increase conservation value (Coppock et al. 1983).

The social organization of ungulates, particularly age and sex ratios, also contribute to ecosystem functioning, complexity, and conservation (Sheldon and West 2004, Gordon et al. 2004, Milner et al. 2007). Variation in animal factors will also contribute to interactions with the environment. For example, the body size of animals (also related to age and sex) influences preferences for burned areas, playing an important role in spatiotemporal heterogeneity (Wilsey 1996, Sensenig et al. 2010). Simple social organization, such as the yearling stocker steers within cattle units of this study, limit variability and decrease conservation value. With particular regard to livestock production, complexity of grazers may be improved by increasing individual variation or combing differing breeds or species (VanWagoner et al. 2006, Searle et al. 2010). Historically, bison were a keystone species, but their impacts were dependent upon how they interacted with the environment, disturbances, and other herbivores. Increasing the complexity of grazers (more species diversity, more wild herbivores, etc.) increases the conservation value, but this value is also dependent upon environmental factors. The simple replacement of domestic cattle with bison may contribute to bison conservation, but may have minimal impact on the broader conservation value of ecosystems. In an extreme example, replacing cattle with bison in a small, intensively managed, and simplified livestock production operation (e.g. a feedlot or small pasture) has little conservation value. Restoring other important processes such as fire, predation, etc. are just as important as the large herbivore upon the landscape (Ripple and Beschta 2003, Fuhlendorf et al. 2009).

Conservation value is also dependent upon the environmental complexity of the area. The majority of these factors are independent of the species of herbivore. In mesic grasslands of the Great Plains (tallgrass and mixed grass prairies), fire-grazing interactions have been shown to be a dominant driver of animal distribution and integral ecosystem process (Fuhlendorf and Engle 2004, Vermeire et al. 2004, Anderson et al. 2006). Similar to the example given above, the simple replacement of cattle with bison without a restoration of fire regimes will not result in disturbance patterns that are critical for conservation and biodiversity. In our study, time since fire was a primary driver in bison and cattle grazing behavior. The suppression of fire or the simplification of fire-grazing interactions within fire prone systems will limit conservation value, regardless of the herbivore species. Environmental factors that are critical to grazing effects and other ecosystem processes need to be accounted for in study designs that evaluate the role of grazing in conservation efforts. In North American grasslands, key environmental factors include fire regimes (Wright and Bailey 1982, Knapp et al. 1998, Brockway et al. 2002), landscape complexity and size (Herkert 1994, With et al. 2008), water distribution (Bailey et al. 1996, Augustine 2010), and woody vegetation (Archer et al. 1995, Briggs et al. 2002). These do not only influence grazing and the resulting effects, but play a broader role in ecosystem functioning. On lands with minimal environmental complexity, any differences between bison and cattle will likely contribute little to conservation value.

Grasslands are endangered worldwide (Hoekstra et al. 2005). While propositions to restore or conserve grasslands regularly focus on native herbivores (e.g. Sanderson et al. 2008), it is often overlooked that the majority of grasslands are privately owned and used for domestic livestock production (particularly true in the Great Plains of North America; Samson and Knopf 1994). Low and high conservation values can be achieved with bison or cattle. Though bison are the iconic symbol of the Great Plains of North America, and it is critical that we conserve the species, there are not enough data to confidently state that landscapes with bison are inherently better than landscapes with cattle for overall conservation or biodiversity. Both species can be mismanaged and cause degradation of habitat as well as ecological processes. Using domestic cattle to achieve some conservation objectives may be more practical or relevant, as cattle currently make up the vast majority of herbivores in many grasslands. Conservation value of productions cattle herds can be improved by increasing the size and complexity of landscape available. Allowing cattle to move at broader spatial scales and to interact with biotic and abiotic factors, may increase conservation value substantially, perhaps more so than replacing cattle with bison at finer scales. Popular management strategies that constrain animal movement and behavior (through use of fencing and rotation) may prevent many important interactions between the animal and environment, potentially reducing conservation value. As more studies effectively and appropriately compare grazing behavior and effects at broad and fine spatial scales, additional reliable conclusions will be made that may change conservation efforts or directions.

We argue that for future studies and comparisons between bison and cattle (as well as other species) it is critical that we limit our extrapolation with discussions of the abiotic and biotic environment in which these studies occur. Though it is unlikely that we will be able to conduct studies that encompass all possibilities in environmental and herbivore complexity, we must begin to contextualize our discussions and limit our inferences. From a conservation perspective it is important to understand the ecological effects of cattle grazing for livestock production, and explore approaches to alter these patterns to more effectively achieve conservation objectives. It is not productive to look for differences or similarities between bison and cattle to justify certain management objectives or agenda. In the face of the vast variability and complexity in which these species are nested within, generalizations are limited and over inferences likely.

Conservation of bison is important as an iconic species and a keystone herbivore (Knapp et al. 1999). From a broad context, however, conservation efforts need to recognize that cattle will continue to be a dominant feature on the Great Plains and grasslands worldwide, and that some conservation objectives may be met using cattle. It is critical to understand grazing behavior and ecological effects of both species in simple and complex landscapes relevant to conservation. There is an important place for species comparisons, but this is just one aspect of grassland conservation and may not be the most important for future conservation of biodiversity.

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Tables

Table 1

Percentage of individual bison and cattle locations, annual means, and confidence intervals (95%) in recently burned areas (six months or less) at the Tallgrass Prairie Preserve, OK, USA, April through September 2009 and 2010.

	Percentage of locations			
	Bison 2009	Bison 2010	Cattle 2009	Cattle 2010
	68.3	64.1	78.6	42.4
	71.5	59.1	55.7	88.7
	69.1	66.9	77.5	100.0†
	68.8	67.8	60.8	73.2
	75.3	69.0	25.0	55.0
	66.2	65.2	100.0†	37.4
	75.1	75.1	67.6	40.6
Mean (CI)	70.6 (2.6)	66.7 (3.6)	60.9 (15.8)	56.2 (16.5)

†Due to fire patch design; not included in mean or confidence interval calculation.

Table 2

The difference in Akaike information criterion (ΔAIC) and the number of parameters (K) for varying models of resource selection for bison and cattle at the Tallgrass Prairie Preserve, OK, USA; model parameters include distance to water (*water*; m), distance to patch edge (*edge*; m), slope (*slope*; degrees), northing (*north*; degrees), easting (*east*; degrees), wooded area (*wood*), and time since fire (*tsf*; days).

	K	ΔAIC
Bison		
tsf×water + tsf×slope + tsf×edge + tsf×wood + tsf×north + tsf×east	15	1.8
tsf×water + tsf×slope + tsf×edge + tsf×wood + north + east	13	0.00
tsf×water + tsf×slope + tsf×edge + tsf×wood	10	2.7
tsf×water + tsf×slope + tsf×edge + wood	11	3.8
tsf×water + tsf×slope + edge + tsf×wood	10	4006.4
tsf×water + slope + tsf×edge + tsf×wood	10	882.4
water + tsf×slope + tsf×edge + tsf×wood	10	505.7
tsf + water + slope + edge + wood	7	6328.7
Cattle		
tsf×water + tsf×slope + tsf×edge + tsf×wood + tsf×north + tsf×east	15	3.26
tsf×water + tsf×slope + tsf×edge + tsf×wood + north + east	13	0.00
tsf×water + tsf×slope + tsf×edge + tsf×wood	10	2.71
tsf×water + tsf×slope + tsf×edge + wood	11	15.89
tsf×water + tsf×slope + edge + tsf×wood	10	126.34
tsf×water + slope + tsf×edge + tsf×wood	10	42.78
water + tsf×slope + tsf×edge + tsf×wood	10	329.18
tsf + water + slope + edge + wood	7	451.37

Notes: We included main effects in all models with interaction terms. Interaction terms represented with ×.

Table 3

Estimated resource selection function coefficients of the top ranked model for bison and cattle at the Tallgrass Prairie Preserve, OK, USA; model parameters include distance to water (water; m), distance to patch edge (edge; m), slope (slope; degrees), northing (north; degrees), easting (east; degrees), wooded area (wood), and time since fire (tsf; days).

	Estimate†	SE	Z value	*P*	CI‡
Bison					
intercept	-1.8460	0.120	-15.34	< 0.01	(-1.8513, -1.8384)
time since fire	-1.5521	0.353	-4.40	< 0.01	(-1.5538, -1.5509)
distance to water	0.0324	0.007	4.51	< 0.01	(0.0316, 0.0328)
slope	-0.5785	0.011	-49.59	< 0.01	(-0.5793, -0.5778)
distance to patch edge	-0.3351	0.009	-35.87	< 0.01	(-0.3360, -0.3344)
woody vegetation	-1.9116	0.077	-24.53	< 0.01	(-1.9164, -1.9092)
northing	-0.0117	0.005	-2.33	0.02	(-0.0120, -0.0115)
easting	0.0246	0.005	4.87	< 0.01	(0.0242, 0.0251)
time since fire × distance to water	0.1548	0.007	19.48	< 0.01	(0.1543, 0.1550)
time since fire × slope	-0.3814	0.013	-28.23	< 0.01	(-0.3818, -0.3809)
time since fire × distance to patch edge	-0.5412	0.011	-48.86	< 0.01	(-0.5420, -0.5408)
time since fire × woody vegetation	0.0509	0.041	1.24	0.21	(0.0478, 0.0549)
Cattle					
intercept	-0.8892	0.644	-1.38	0.16	(-0.8963, -0.8824)
time since fire	-1.2611	0.313	-4.03	<0.01	(-1.2621, -1.2602)
distance to water	-0.0768	0.006	-11.11	<0.01	(-0.0785, -0.0755)
slope	-0.1696	0.007	-21.50	<0.01	(-0.1699, -0.1691)
distance to patch edge	-0.5019	0.011	-42.44	<0.01	(-0.5025, -0.5015)
woody vegetation	1.4398	0.053	27.16	<0.01	(1.4390, 1.4404)
northing	-0.0044	0.005	-0.84	0.40	(-0.0048, -0.0040)
easting	-0.0109	0.005	-2.08	0.03	(-0.0112, -0.0107)
time since fire × distance to water	-0.0514	0.059	-2.08	0.03	(-0.0520, -0.0511)
time since fire × slope	0.0199	0.049	0.40	0.68	(-0.0210, -0.0190)
time since fire × distance to patch edge	-0.2667	0.219	1.22	0.22	(-0.2692, -0.2648)
time since fire × woody vegetation	0.4213	0.382	1.10	0.27	(0.4201, 0.4219)

†Standardized variables are shown for coefficient comparison and interaction term interpretation.

‡Confidence interval (95%) calculated from bootstrapping procedures (1,000 iterations).

Table 4

Estimated resource selection function coefficients[†] of the top ranked model for individual bison and cattle at the Tallgrass Prairie Preserve, OK, USA each year of study (2009 and 2010); model parameters include distance to water (water; m), distance to patch edge (edge; m), slope (slope; degrees), northing (north; degrees), easting (east; degrees), wooded area (woody), and time since fire (tsf; days).

Year	tsf	water	slope	edge	woody	north	east	tsf × wtr	tsf × slp	tsf × edge	tsf × wdy
Bison											
2009	-1.69	-0.01	-0.72	-0.55	-2.44	0.01	0.06	0.12	-0.48	-0.78	-1.85
2009	-1.29	0.20	-0.48	-0.12	-2.45	0.00	0.03	0.31	-0.22	-0.34	-1.64
2009	-1.74	0.19	-0.61	-0.50	-1.22	0.01	-0.01	-0.05	-0.35	-0.78	-0.47
2009	-1.16	0.00	-0.63	-0.43	-1.55	-0.03	0.06	0.15	-0.58	-0.59	-0.93
2009	-1.91	0.23	-0.45	-0.40	-2.45	-0.03	0.02	0.30	-0.31	-0.64	-2.38
2009	-1.35	-0.02	-0.62	-0.14	-2.59	-0.02	0.02	0.11	-0.37	-0.39	-2.23
2009	-1.57	0.10	-0.56	-0.36	-1.46	-0.03	0.00	0.00	-0.37	-0.43	-1.19
2010	-1.38	0.13	-0.51	-0.07	-1.38	0.03	0.00	0.20	-0.08	-0.26	0.30
2010	-1.16	0.13	-0.49	-0.14	-1.35	0.00	-0.03	0.10	-0.16	-0.22	0.27
2010	-1.37	0.06	-0.54	-0.25	-0.82	0.01	0.01	0.14	-0.17	-0.37	0.40
2010	-1.52	0.11	-0.51	-0.06	-0.71	0.01	-0.02	0.19	-0.16	-0.20	0.32
2010	-1.46	0.06	-0.57	-0.14	-0.40	0.04	-0.02	0.07	-0.07	-0.38	1.16
2010	-1.38	0.00	-0.79	-0.13	-1.59	0.02	0.00	-0.02	-0.30	-0.33	-0.11
2010	-1.79	-0.15	-0.43	-0.17	-1.21	-0.02	0.03	-0.08	-0.08	-0.32	0.11
Variation[‡]	0.23	0.10	0.10	0.17	0.70	0.02	0.03	0.12	0.16	0.19	1.12
Cattle											
2009	-1.70	-0.05	-0.46	-0.81	-1.66	0.04	-0.01	-0.19	-0.32	-1.20	-1.68
2009	-1.44	-0.33	-0.11	-0.87	2.74	-0.06	-0.02	0.26	0.05	-1.78	-0.23
2009	-1.16	-0.30	-0.02	-0.28	2.37	0.00	-0.01	-0.19	0.18	-0.94	0.18
2009	-0.37	-0.03	-0.15	-0.69	1.61	-0.01	0.01	-0.23	0.00	0.53	-0.47
2009	-0.36	-0.11	-0.25	-0.18	1.42	0.02	0.01	-0.09	-0.12	0.08	0.10
2009	-0.79	-0.22	-0.28	-0.12	1.24	0.00	0.00	-0.25	-0.08	0.03	0.40
2009	-3.35	-0.62	-0.15	-0.61	1.49	0.00	-0.04	-0.95	-0.04	-0.97	0.43
2010	-0.37	-0.09	-0.27	-0.07	1.60	0.01	0.00	-0.81	-0.01	0.00	0.04
2010	-2.72	-0.45	-0.42	-0.82	3.66	0.04	-0.02	-0.55	-0.47	-0.99	1.44
2010	-1.24	-0.38	-0.12	-0.37	1.86	0.05	-0.04	-0.56	0.14	-0.41	-0.72
2010	-1.59	-0.17	-0.02	-0.43	1.24	0.00	0.01	-0.39	-0.10	-0.38	-0.41
2010	-0.48	-0.29	-0.24	-0.32	2.79	-0.05	0.04	-0.44	-0.33	0.18	-0.50
2010	-2.09	-0.21	0.04	-1.18	1.31	-0.03	-0.01	-0.79	-0.03	-0.55	0.44
2010	-1.16	-0.13	-0.40	-0.41	0.82	0.00	-0.01	-0.21	-0.42	-0.39	-0.24
Variation[‡]	0.91	0.17	0.16	0.33	1.22	0.03	0.02	0.33	0.2	0.63	0.71

[†] Standardized variables are shown for coefficient comparison and interaction term interpretation.

[‡] Variation measured by calculating the standard deviation of coefficients within species.

Figures

Figure 1

Map of prescribed fire and water distribution within bison and cattle units at The Nature Conservancy Tallgrass Prairie Preserve, OK, USA, September 2009. Solid orange lines represent perimeter fences and delineate units. Black interior lines and areas represent water sources. Gray areas inside bison unit represent inholdings which bison cannot access. The large southern unit is 9532 ha in size and contains bison year round. The northern units are 430-980 ha in size and contains mixed European breeds of cattle April-September. Differing colors represent season of burn for 2009 and illustrate the patchiness of fire. Patches from previous years are not shown, but vary from one to five years since fire. Grazing animals have free access to all burns within their respective units (no internal fences present).

Figure 2

Ivlev electivity indices for riparian areas, separated by bison and cattle at the Tallgrass Prairie Preserve, OK, USA. Bars are means (n=14; animals), error bars are one standard deviation. Potential values range from -1 (complete avoidance) to +1 (complete preference). Distance around water indicates the size of buffer placed around water sources. A) Ivlev electivity indices for ponds only, separated by bison and cattle. Cattle preferred riparian pond areas more than bison. B) Ivlev electivity indices for streams only, separated by bison and cattle. Cattle preferred riparian stream areas more than bison; bison demonstrated a small avoidance to riparian stream areas. C) Ivlev electivity indices for ponds and streams combined, separated by bison and cattle. Cattle preferred all riparian areas more than bison; bison demonstrated a small avoidance to all riparian areas. Mean electivity indices of riparian areas varied significantly between bison and cattle for all water sources and buffer sizes ($P < 0.01$).

Figure 3

Probability of selection for bison at the Tallgrass Prairie Preserve, OK, USA September 2009. Probabilities presented as a function of time since fire, distance to water, and their interaction. Black interior lines and areas represent water sources. Solid orange lines represent perimeter fences. Refer to Figure 1 for recently burned areas. Bison prefer recently burned areas and do not minimize their distance to water. Due to the preference of recently burned areas, probabilities will change as fire is applied and moved around the landscape.

Figure 4

Probability of selection for cattle at the Tallgrass Prairie Preserve, OK, USA September 2009. Probabilities presented as a function of time since fire, distance to water, and their interaction. Black interior lines and areas represent water sources. Solid orange lines represent perimeter fences. Refer to Figure 1 for recently burned areas. Cattle prefer recently burned areas and minimize their distance to water. Due to the preference of recently burned areas, probabilities will change as fire is applied and moved around the landscape.

Figure 5

Conceptual model to evaluate conservation value with respect to animal and environmental factors. Conservation value is defined as the contribution to regional conservation efforts, which includes the promotion of native plants, animals, and ecosystem processes. Species of animal alone does not automatically increase the value in regard to conservation; other factors play an important role in overall conservation value.

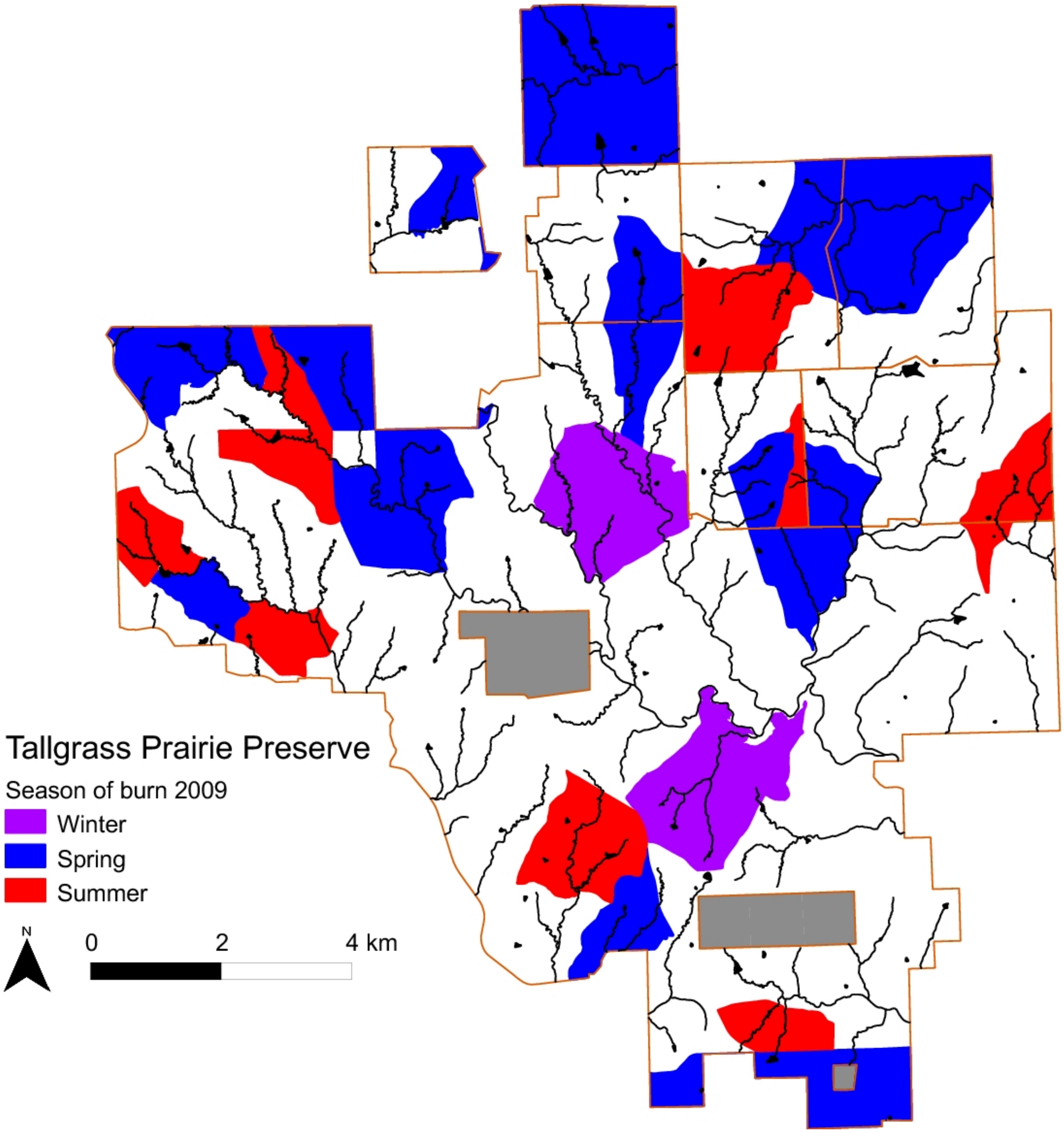
Tallgrass Prairie Preserve
Season of burn 2009
Winter
Spring
Summer
N
0
2
4 km

Figure 1

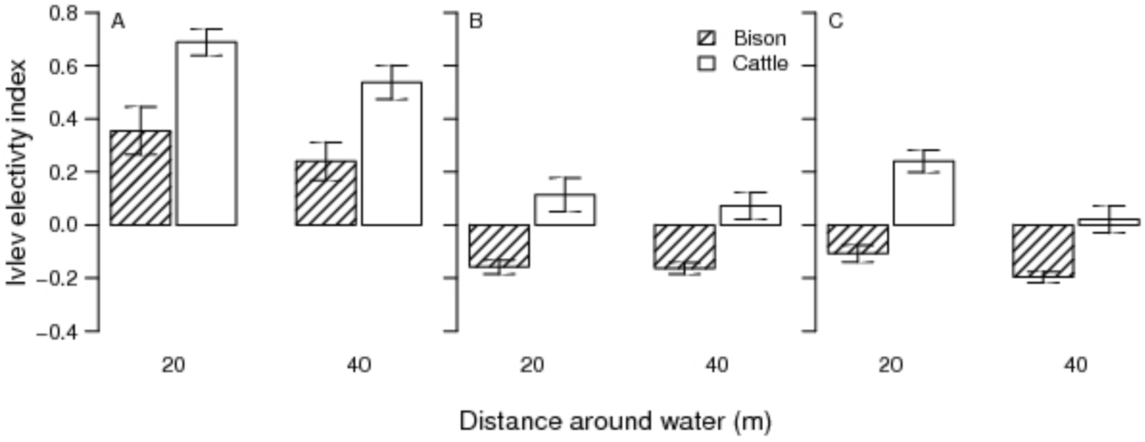
A
B
C
▨ Bison
☐ Cattle
Ivlev electivty index
0.8
0.6
0.4
0.2
0.0
−0.2
−0.4
20
40
20
40
20
40
Distance around water (m)

Figure 2

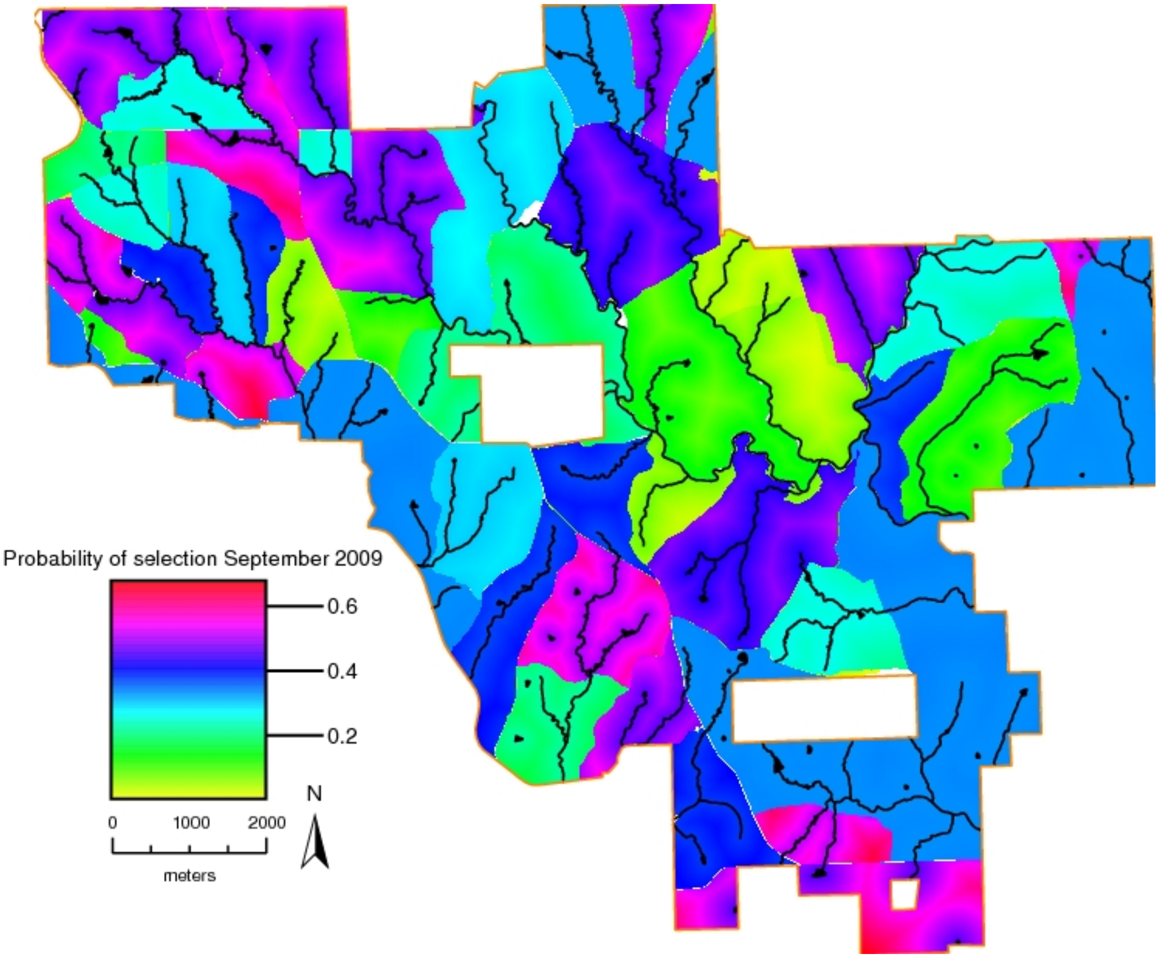
Probability of selection September 2009
0.6
0.4
0.2
0
1000
2000
meters
N

Figure 3

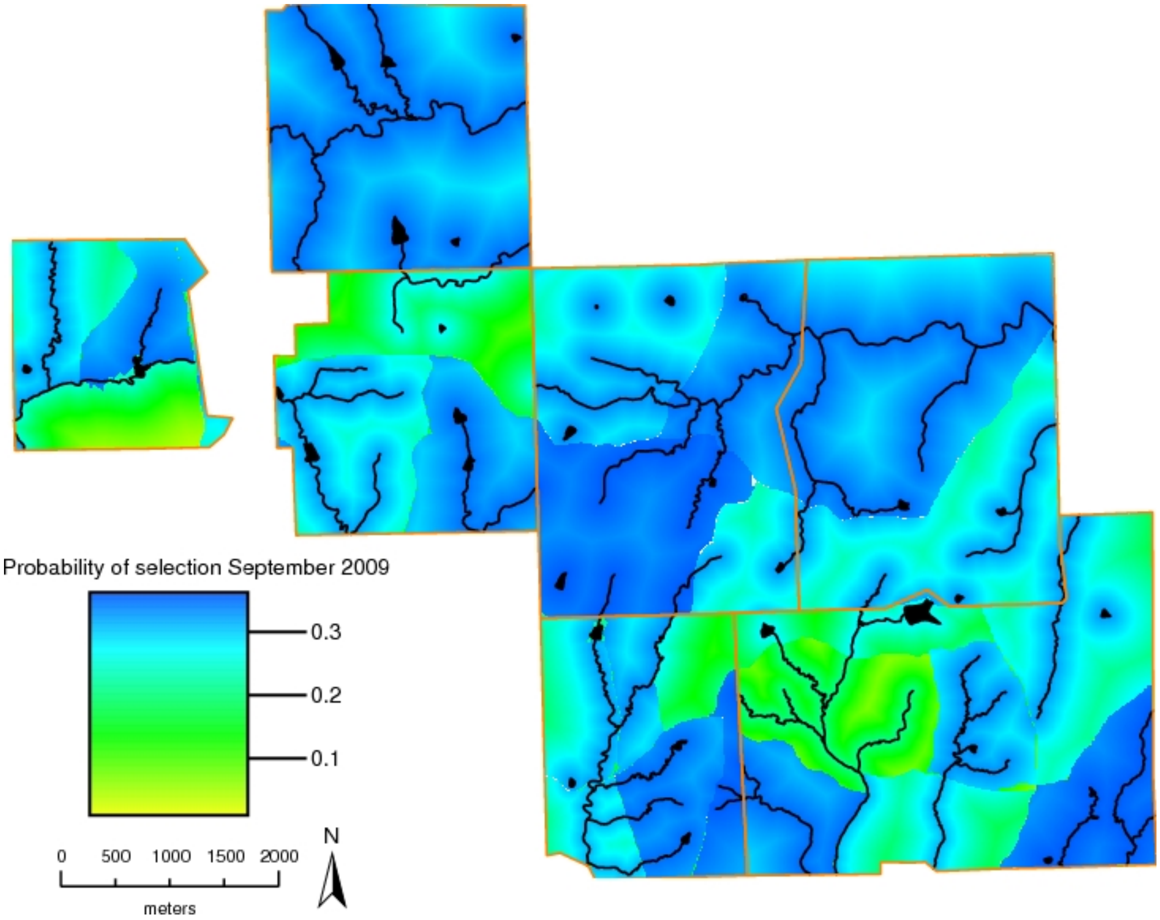
Probability of selection September 2009
0.3
0.2
0.1
0
500
1000
1500
2000
meters
N

Figure 4

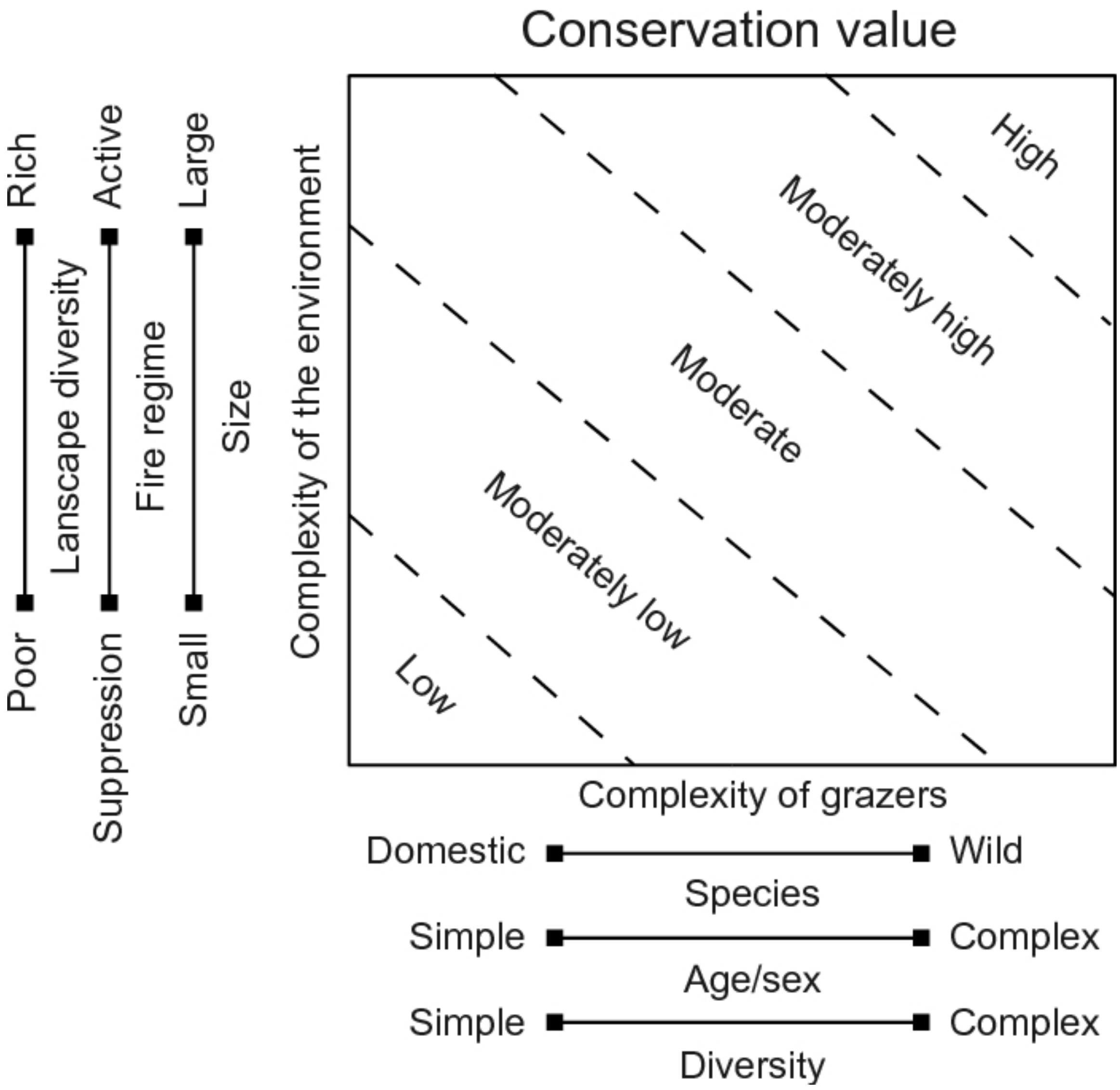
Conservation value
High
Moderately high
Moderate
Moderately low
Low
Complexity of the environment
Complexity of grazers
Rich
Poor
Lanscape diversity
Active
Suppression
Fire regime
Large
Small
Size
Domestic
Wild
Species
Simple
Complex
Age/sex
Simple
Complex
Diversity

Figure 5

CHAPTER II

Ungulate preference for burned patches reveals strength of fire-grazing interaction

Ungulate preference for burned patches reveals strength of fire-grazing interaction

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Abstract

The interactions between fire and grazing are widespread throughout fire dependent landscapes. The utilization of burned areas by grazing animals establishes the fire-grazing interaction, but the preference for recently burned areas relative to other influences (water, topography, etc.) is unknown. In this study we determine the strength of the fire-grazing interaction by quantifying the influence of fire on ungulate site selection. We compare the preference for recently burned patches relative to the influence of other environmental factors that contribute to site selection; compare that preference between native and introduced ungulates; test relationships between area burned and herbivore preference; and determine forage quality and quantity as mechanisms of site selection. We used two large ungulate species at two grassland locations within the southern Great Plains, USA. At each location, spatially distinct patches were burned within larger areas through time, allowing animals to select among burned and unburned areas. Using fine scale ungulate location data, we estimated resource selection functions to examine environmental factors in site selection. Ungulates preferred recently burned areas and avoided areas with greater time since fire, regardless of the size of landscape, herbivore species, or proportion of area burned.

Forage quality was inversely related to time since fire, while forage quantity was positively related. We show that fire is an important component of large ungulate behavior with a strong influence on site selection that drives the fire-grazing interaction. This interaction is an ecosystem process that supersedes fire and grazing as separate factors, shaping grassland landscapes. Inclusion of the fire-grazing interaction into ecological studies and conservation practices of fire prone systems will aid in better understanding and managing these systems.

Keywords

conservation, disturbance, grassland, behavior, heterogeneity, pyric herbivory, tallgrass prairie

Introduction

Fire and grazing affect a large proportion of the earth's ecosystems (Milchunas & Lauenroth 1993; Bond, Woodward, & Midgley 2005), playing a critical role in both establishment and maintenance of grasslands and savannas (Milchunas, Sala, & Lauenroth 1988; van Langevelde et al. 2003; Anderson 2006). While fire and grazing affect ecosystem processes independently, the interaction between them may be more ecologically important than their independent effects. This interaction has been proposed as a single disturbance, pyric herbivory, defined as grazing driven by fire (Fuhlendorf et al. 2009). The fire-grazing interaction is described by positive and negative feedbacks in a tightly coupled fire-grazing system, creating new states and effects not present when the two processes are examined independently (Fuhlendorf & Engle 2004; Archibald et al.

2005). When fire occurs in patches across a landscape, herbivores preferentially select recently burned areas over areas with greater time since fire (Vinton et al. 1993; Sensenig, Demment, & Laca 2010). Due to the dependence of fuel accumulation on grazing pressure, probability of fire and fire behavior respond correspondingly to variation in herbivory (Leonard, Kirkpatrick, & Marsden-Smedley 2010). These positive and negative feedbacks result in a complex disturbance interaction that is best expressed as spatiotemporal patterns across the landscape.

The fire-grazing interaction is dynamic in space and time, creating a shifting mosaic (Fuhlendorf & Engle 2004). This interaction shapes the landscape, creating heterogeneity at multiple scales (Fuhlendorf & Engle 2001; Archibald et al. 2005). Due to the complex spatiotemporal pattern, fire-grazing interactions are critical to grassland ecosystem structure and function. Variable vegetation structure associated with the fire-grazing interaction is important to biodiversity (Fuhlendorf et al. 2006), fire behavior (Kirkpatrick, Marsden-Smedley, & Leonard 2011; Kerby, Fuhlendorf, & Engle 2007), invasive species populations (Cummings, Fuhlendorf, & Engle 2007), animal populations and communities (Fuhlendorf et al. 2010; Parrini & Owen-Smith 2010), and ecosystem processes (Anderson, Fuhlendorf, & Engle 2006).

Referred to as the “magnet effect” by Archibald et al. (2005), burned areas attract grazing animals, resulting in heavy selection and use. This attraction to recently burned areas has been documented with numerous animal species throughout the globe (Pearson et al. 1995; Moe & Wegge 1997; Kramer, Groen, & van Wieren 2003; Klop, van Goethem, & de Iongh 2007; Murphy & Bowman 2007; Onodi et al. 2008). Although it is widely known that herbivores are attracted to burned areas, most large herbivore behavior studies do not include direct effects of fire, but focus instead on other abiotic (e.g. topography, temperature, climate, etc.) or biotic (e.g. forage quantity, predation, etc.) characteristics (e.g. Bailey et al. 1996; Fortin et al. 2003; de Knegt et al. 2007; Winnie, Cross, & Getz 2008; Beest et al. 2010). The influence of fire on site selection, in relation to other factors, is a key component of the fire-grazing interaction that is not well understood. While herbivore attraction to burned areas has been recognized, there is little work focused on the magnitude of the attraction as the context or mechanism of the fire-grazing interaction (but see Sensenig, Demment, & Laca 2010).

Our principal goal was to determine the strength of the fire-grazing interaction by examining the influence of fire on ungulate site selection across locations that varied in area and complexity, ranging from a large landscape with random fires to smaller landscapes with fixed fire patterns. To be clear, we do not directly assess the interaction itself (i.e., comparing systems with and without the interaction) but rather focus on understanding primary mechanisms of the fire-grazing interaction. The overall strength or significance of the fire-grazing interaction can be determined by examining how fire influences grazing behavior (the key link between fire and grazing). A pronounced and persistent influence will reveal a strong interaction, while a subtle or slight influence will indicate a weak interaction. Our specific objectives were to 1) compare ungulate preference for recently burned patches relative to the influence of other environmental factors, 2) compare that preference between native and introduced ungulate species, 3) test relationships between proportion of area burned and herbivore preference, and 4) determine forage quality and quantity as causal mechanisms of site selection. We show that fire is a primary driver in large herbivore behavior and that the fire-grazing interaction is an integral process within tallgrass prairies.

Methods

This study was conducted at two locations within the Southern Great Plains, USA: The Nature Conservancy Tallgrass Prairie Preserve, north of Pawhuska, OK, USA and the Oklahoma State University Research Range, southwest of Stillwater, OK, USA. The vegetation at both sites is classified as tallgrass prairie with small patches of cross timbers forest. Dominant grasses include *Andropogon gerardii* Vitman, *Schizachyrium scoparium* (Michx.) Nash, *Panicum virgatum* L., and *Sorghastrum nutans* (L.) Nash. Crosstimbers vegetation is dominated by *Quercus stellata* Wang. and *Q. marilandica* Münchh. Fire-grazing interactions are a dominant feature at both sites with spatially distinct patches burned within larger areas during both dormant and growing seasons (Fuhlendorf & Engle 2004; Hamilton 2007).

Experimental design

The Tallgrass Prairie Preserve contains one large unit (9532 ha) that is grazed by native bison (*Bison bison*) and five smaller units (430-980 ha) grazed by introduced cattle (*Bos taurus*). Bison and cattle have access to all areas within their respective units (i.e., there are no interior fences). Bison are maintained in their unit throughout the year; herd size is approximately 2,300 animals. Sex ratio of the bison herd is approximately seven females per male; ages of females range from 0-10 years, while males are 0-6 years. Herding and group sizes vary throughout the year; large, combined (bulls, cows, calves) groups are most common in summer months, while smaller, separated groups are present the rest of the year (Schuler et al. 2006). It is rare that female bison are found alone or grazing independently (B. Allred, personal observation). Cattle units are stocked with stocker steers approximately one year old (mixed European breeds); cattle are present April through September. Cattle numbers vary with unit, ranging from 169 to 463 steers. Cattle often congregate in herds, similar but smaller than that of bison (B. Allred, personal observation). Bison and cattle are minimally handled and provided with no supplemental feed. All units are stocked with similar moderate stocking rates (bison: 2.1 AUM ha^{-1}; cattle: 2.4 AUM ha^{-1}).

Approximately one third of the bison unit is burned annually. Burn patches vary in area (100-700 ha) and are located randomly across the landscape (non-contiguous, no fixed burn units; Fig. 1). About 80% of area burned occurs during the dormant season (40% in winter, 40% in late spring) and 20% during the growing season (Hamilton 2007). The variability in time since fire of patches ranges from zero to six years. We manipulated the proportion of area burned within cattle units to examine the influence of relative burned area available on ungulate site selection. We assigned each cattle unit a fire patch size of 50 (i.e., half the unit is burned), 33, 25, 17, or 12% (see Fig. S1 in Supporting Information). In contrast to randomly located burned patches within the bison unit, location of patches in cattle units is fixed and contiguous. Variability in time since fire of patches ranges from zero to four years, and is dependent upon proportion of area burned.

We fitted bison and cattle with global positioning systems (GPS; GPS7000MU & GPS3300L, Lotek Wireless). We deployed GPS collars on seven bison from November

2008 through November 2010 (batteries replaced and new animals chosen in November 2009) and five cattle (one per unit) from April through September of 2009 and 2010 (batteries replaced and new animals chosen April 2010). We recorded location information of each animal at frequencies ranging from 12 minutes to one hour.

To further understand the influence of fire on ungulate site selection at finer spatial scales, we used two units (65 ha each) grazed by cattle at the Oklahoma State University Research Range. As with the Tallgrass Prairie Preserve, only unit perimeter fences are present and animals are free to roam within their respective units. Units are equally stocked (3.0 AUM ha^{-1}) with cattle (European breeds, yearlong cow-calf operation). One sixth of each unit is burned in the late dormant season and an additional one sixth during the growing season (Fig. S1). Variability in time since fire ranges from zero to three years. We fitted cattle with GPS collars (GPS3300LR, Lotek Wireless); we deployed GPS collars on individual cattle (one per unit) from August 2007 through December 2009. We recorded location information at a frequency of five minutes. Collars were retrieved every six weeks to replace batteries. We omitted data from days in which animal behavior was influenced by human activity, e.g. general animal husbandry practices. Though smaller in size and animal numbers than other sites, cattle were often found congregated and grazing together (B. Allred, personal observation).

Spatial data

Animal location data were differentially corrected with stationary GPS data obtained from their respective location; corrected data were imported into a spatially enabled database (PostgreSQL/PostGIS). We mapped unit perimeter, fire history, water sources, and woody vegetation at all sites with handheld GPS units, aerial and satellite imagery, and United States Geological Survey 7.5 minute topographic maps. We obtained topography information (elevation, slope, aspect) from digital elevation models for each location. Aspect data were transformed with simple trigonometric functions by creating two variables, northing = cosine(aspect) and easting = sin(aspect). Variability of time since fire, elevation, water sources, and woody vegetation of the bison unit at the Tallgrass Prairie Preserve is shown in Figures S2-5. Variability of cattle units at the Tallgrass Prairie Preserve is similar to the bison unit; variability of cattle units at the Oklahoma State University Research Range is reduced due to smaller size.

Objective one

To compare the influence of time since fire relative to other environmental factors, we estimated resource selection functions (Boyce et al. 2002) for animals at each location. We established three random points for each observed location to provide estimates of available conditions across the landscape. We first tested whether animals used recently burned areas more than random; we compared the number of randomly placed points to recorded locations in areas that were six months since fire using a *t*-test. Distance to water, distance to fire patch edge, fire patch area, elevation, slope, northing, easting, and time since fire were associated with animal locations and established random points. We created resource selection functions using combinations of environmental factors for each site. Model parameter selection was based on knowledge of bison and cattle behavior and availability of data, either collected or remotely sensed. Crude protein and biomass data (discussed below) were not included in resource selection functions as they were sampled at only one site, within a narrower time frame and at a broader sampling frequency than animal location data. Although reviewers raised this concern, we show that using time since fire is satisfactory, as it is correlated with both crude protein and aboveground biomass. Because we were specifically interested in the influence of time since fire of burn patches, we included interaction terms for time since fire with all other variables (i.e., time since fire × distance to water, time since fire × slope, etc.). In all models with interaction terms, we included main effects of both variables. To compare influence of environmental factors, and to more easily interpret interaction terms, we standardized variables by subtracting their mean and dividing by their standard deviation (Gelman & Hill 2007). To account for correlation within an individual animal and among animals, individuals were included as a random intercept in logistic regressions; for cattle at the Tallgrass Prairie Preserve, individuals were also nested within their respective unit (Gillies et al. 2006). We compared and ranked various resource selection functions using Akaike information criterion (AIC; Burnham & Anderson 2002). We used bootstrapping procedures to estimate precision of resource selection coefficients and to test differences in influence of environmental factors within species at each research location. We compared coefficients after calculating confidence intervals (95%) from 1,000 iterations of randomly sampled datasets; coefficients were considered different if confidence intervals did not overlap.

Objective two

We used the bison and cattle units at the Tallgrass Prairie Preserve to compare preference for recently burned areas (as well other environmental factors) between native (bison) and introduced (cattle) ungulates in tallgrass prairie. To appropriately compare selection between the two, we reduced bison location data to match that of cattle (April – September, as well as frequency of GPS fix). We estimated separate resource selection functions for each species using top ranked models from objective one. We used bootstrapping procedures to estimate precision of resource selection coefficients and to test differences between species. We compared coefficients between species after calculating confidence intervals (95%) from 1,000 iterations of randomly sampled datasets; coefficients were considered different if confidence intervals did not overlap.

Objective three

We examined the influence of proportion of area burned on preference for recently burned patches using cattle units at the Tallgrass Prairie Preserve (varying from 50-12% burned). We estimated separate resource selection functions for each fire patch size, following procedures in objective one. We used linear regression to determine a relationship between proportion burned and herbivore preference for recently burned areas.

Objective four

We examined the response of forage quality and quantity to the fire-grazing interaction within cattle units of the Oklahoma State University Research Range. We harvested aboveground plant tissue (live and dead combined) from four randomly placed 0.10 m^2 plots in patches that varied in time since fire. We collected samples every two weeks from April through November 2009. After drying samples to a constant mass, we recorded the weight of each sample and determined percent crude protein using a dry combustion analyzer (LECO Corp., St. Joseph, MI, USA). We used linear regression to test relationships of crude protein and aboveground biomass to time since fire. We performed all analyses using R (R Development Core Team 2010) with additional use of the *lme4* package for mixed effects resource selection functions (Bates & Maechler 2010), and *doMPI* (Weston 2009), *foreach* (Revolution Computing 2009) and *Rmpi* (Yu 2010) packages for high performance computing.

Results

Animals at each research location used recently burned areas more than random ($P < 0.05$). Common environmental factors that influence ungulate site selection were of lesser influence than time since fire (objective one; Tables 1). Of resource selection functions examined for bison, the model that contained interaction terms of time since fire with all variables less northing and easting, had the best fit based on AIC criteria; (Table S1). Based on resource selection coefficients, primary drivers of bison site selection were time since fire (selecting recently burned areas) and avoiding woody vegetation (Table 1). Bison also avoided steeper slopes and larger fire patches. Bison selected areas closer to water and fire patch edge, but both had a small influence relative to other variables. Interactions of time since fire with other variables shows fire is critical to understanding most aspects of grazing behavior. The influence of time since fire increased as slope, distance to fire patch edge, fire patch area, and elevation increased. Conversely, the influence of time since fire decreased as distance to water increased and as woody vegetation became present. The probability of selection for bison at the

Tallgrass Prairie Preserve, based upon parameters in Table 1, is displayed in Figure 2.

Time since fire also was a primary driver in site selection by cattle at the Tallgrass Prairie Preserve (Table 1). The combination of interaction terms of time since fire with most other variables (less northing and easting) had the best fit based on AIC criteria (Table S2). Cattle selected recently burned patches, minimizing the amount of time since fire. In contrast to selection behavior of bison, however, cattle preferred woody vegetation over all other attractants. Cattle selected areas closer to water and patch edge, and avoided steeper slopes. Interactions of time since fire with other predictors again indicate the complexity of the influence of fire on site selection. At the Oklahoma State University Research Range, where unit size is smaller than other research locations, the preference for recently burned areas was also strong (Table 1). Of models examined, the combination of interaction terms of time since fire with most variables (less northing and easting) had the best fit based on AIC criteria similar to cattle in larger units (Table S3). Similar to other sites, cattle preferred recently burned areas. Cattle were also attracted to woody vegetation. As with other research locations described, the interactions of time since fire with other factors was present. Preference for recently burned areas was a primary driving force in site selection, with greater influence than other factors (objective one).

Comparison of bison and cattle selection revealed similar and contrasting preferences (Table 2). After appropriately matching data, most coefficients were similar in preference or avoidance (indicated by sign of coefficient, +/-) to population resource selection functions (created using full datasets, Table 1) but varied in magnitude. Selection changed for distance to water in bison (minimized distance to maximized distance) and cattle (minimized distance to maximize distance), and elevation (preferred higher elevations to avoided higher elevations) in cattle. While both species had strong preferences for recently burned areas, the magnitude of preference in native bison was greater than introduced cattle (objective two).

Resource selection functions for individual cattle units that varied in proportion and size of fire patch also displayed a strong influence of fire on site selection. Best fit models for cattle units varied by individual units, but consistently included interactions of time since fire with other variables (Table S4). Similar to the overall population model (in which cattle units were analyzed collectively), cattle primarily selected for recently burned and woody vegetation areas (Table 3). The proportion of area burned did not correlate with herbivore preference for burned areas. Coefficients for time since fire varied among cattle units, but there was no relationship with proportion burned ($P > 0.05$; objective three), i.e. preference for burned areas was not significantly altered if half or one eighth of the area was burned.

Forage quality and quantity of patches were dependent upon time since fire (objective four). Crude protein of patch vegetation was greatest in the most recently burned area regardless of season of burn (Fig. 3A-B). Forage quality decreased with time since fire ($P < 0.05$); at the end of sampling, forage quality within recently burned areas was nearly double that of other areas. In contrast to forage quality, forage quantity was lowest in recently burned areas and increased with time since fire (Fig. 4A-B; $P < 0.05$). A tradeoff between forage quality and quantity was present; areas with highest quality forage had the least quantities.

Discussion

The ecological interactions between fire and grazing are important and have a defining role across complex landscapes (Archibald et al. 2005; Leonard, Kirkpatrick, & Marsden-Smedley 2010; Sensenig, Demment, & Laca 2010). By specifically quantifying the influence of fire on ungulate site selection, we were able to measure the primary mechanism responsible for the fire-grazing interaction and better understand the role that fire and grazing play within these systems. The broad scale observational and experimental work in this study reveals that fire has a strong influence on animal behavior and that the interaction between fire and grazing itself is strong. The amount of time since a particular area has burned becomes the critical link between fire and grazing, as it is a driving force in site selection. We found that the simple presence of fire is less significant than the pattern or heterogeneity resulting from patch fires, which forms the mosaic that influences animal selection. If fire occurs homogeneously across the complete area available to grazing animals, the interactions between fire and grazing cannot occur.

For herbivores in our study, time since fire ultimately changed how animals distributed themselves, a key component to the fire-grazing interaction. Time since fire had a greater influence than slope or distance to water, two factors that have been shown to primarily determine site selection of bison and cattle (Bailey et al. 1996). Woody vegetation, on the other hand, appeared to be the primary determining factor of site selection, even greater than fire. Native bison avoided areas with trees, while domestic cattle preferred them. These dissimilarities may be attributed to differences in thermal regulation between the two species (Christopherson, Hudson, & Christophersen 1979), with woody canopy cover providing shade from solar radiation, particularly for cattle. It is often speculated that bison do not seek cover from solar radiation, as animals are adapted to temperature extremes of the Great Plains (Gogan et al. 2010). If true, there is likely little need for bison to select wooded areas, as vegetation is often different and reduced in quantity (Limb et al. 2010). Bison also preferred smaller burned patches over larger ones. As suggested by a reviewer, examining and incorporating other environmental variables deepens the definition and understanding of the fire-grazing interaction. It is not just the amount of time since fire that determines response but a suite of variables that influence one another. In particular, patch size contributes to grazing pressure (density of herbivores) of a recently burned patch, which can maintain vegetation characteristics to which grazers are attracted (high forage quality). Furthermore, by investigating the interaction of time since fire with other variables within resource selection functions, we show the complexity and connectedness of fire and grazing. For example, as time since fire increases, distance to patch edge becomes more important. Animals are more likely to stay closer to patch edges when in areas with greater time since fire, presumably to stay closer to preferred burned patches. Additionally, as slope increases, the magnitude of time since fire becomes greater. Animals will likely only select areas with steeper slopes if it has been recently burned. These interactions within selection decisions reinforce the ability of fire to modify behavior and the importance of studying the fire-grazing interaction.

The ability for fire to be a strong influence in herbivore behavior has many potential ecological consequences. The attraction to fire creates the fire-grazing interaction, which shapes the system, creates heterogeneity, influences ecosystem processes, and determines plant and animal populations and distributions (Archibald et al. 2005; Fuhlendorf et al. 2006; Leonard, Kirkpatrick, & Marsden-Smedley 2010). In addition to site selection, fire may alter other individual behavior characteristics not studied in this paper, such as residence time, movement tortuousity, or traveling velocity (Kerby 2002), changing how animals interact with and gather information from the landscape. Understanding the interaction of fire and grazing may also demonstrate evolutionary mechanisms and history. Differences in the attraction to fire have been shown between foregut and hindgut fermenters, the former more attracted to fire and becoming more dominant during increased fires prior to the Pleistocene (Sensenig, Demment, & Laca 2010). With so many far-reaching effects, the fire-grazing interaction is to be considered an integral process of fire prone systems.

The mechanisms of the fire-grazing interaction occur at multiple scales. At broad scales, fire and grazing must be present and able to influence one another (i.e., patchy fire; herbivores need to be able to select among burned and unburned areas). At finer scales, localized mechanisms attract animals to burned areas. Forage quality of plants in recently burned areas can be two to three times greater than areas with more time since fire (see also Sensenig, Demment, & Laca 2010). In tallgrass prairie, areas that were burned within a year had higher crude protein than areas with greater time since fire. As the growing season progressed, differences lessened and forage quality became more similar due to plant maturation. An additional fire in the middle of the growing season increased forage quality, and was again greater than other available areas. These spikes in nutritional content, created by fire and subsequent grazing, can be vital for the productivity of grazing animals within the system (Verweij et al. 2006; Parrini & Owen-

Smith 2010). With patch fires occurring regularly and throughout the landscape, high quality forage is readily available and maintained. Patch size will then play an important role in the maintenance of burned areas. Due simply to size, smaller patches will have greater grazing pressure (greater density of herbivores) and will be easier for animals to keep in a short developing state of high nutritional value, similar to grazing lawns (Waite 1963). This is the likely reason bison preferred smaller patches over larger ones. This maintenance of the burn patch is also shown by the preservation of higher forage quality and low biomass well past the growing season (December). The spatial heterogeneity of forage quality created by patchy fire and subsequent grazing is also primary mechanism of the fire-grazing interaction. The continual preference for burned areas is due to increased nutritional content in post fire regrowth (Hobbs et al. 1991; van de Vijver, Poot, & Prins 1999).

Along with site selection and other behavior attributes, the fire-grazing interaction may modify foraging strategies. Though high quality forage is readily available, grazing animals must also make decisions regarding the tradeoff between quality and quantity (Demment & van Soest 1985; Senft et al. 1987). In recently burned areas, where quantity is low, intake rates are constrained by plant cropping, whereas in areas with greater time since fire, intake rates become constrained by handling or processing (Spalinger & Hobbs 1992). Additionally, as plant biomass increases or matures, quality and digestibility decline (van Soest 1994). Such tradeoffs have been resolved by showing that grazing animals maximize energy intake by selecting for intermediate levels of vegetation quantity (Fryxell 1991; Mueller et al. 2008). Within the Serengeti, Wilmshurst et al. (1999) showed that wildebeest (*Connochaetes taurinus*) selected for intermediate biomass at broader landscapes scales, but not at finer local scales. In contrast, the findings presented here show that these grazing animals are primarily selecting recently burned patches, which contain the lowest amounts of biomass but highest amounts of protein. Decisions between forage quantity and quality will ultimately vary, depending upon the type of herbivore, resource availability, scale, etc. Due to metabolic requirements and animal physiology, larger herbivores may prefer both burned and unburned areas, while smaller animals may exclusively prefer burned areas (Wilsey 1996; van de Vijver, Poot, & Prins 1999; Sensenig, Demment, & Laca 2010).

The attraction of grazing animals to burned areas and the subsequent fire-grazing interaction are not phenomena restricted to North American grasslands, but are ecological processes which occur globally (Table S5). Magnitude of the attraction to burned areas and its establishment of the fire-grazing interaction can be expected to differ across systems and species (see Klop, van Goethem, & de Iongh 2007; Bleich et al. 2008). The influence of environmental variables on herbivore behavior will depend upon their distribution and complexity across the landscape, e.g. the influence of water is likely to be more influential in arid regions. Although predators are not present in the tallgrass prairie of this study, they would also play an important role in herbivore site selection. Herbivores may find refuge in recently burned areas, as visibility is increased and predators may be noticed more easily (Valeix et al. 2009; Eby 2010); but visibility of prey is also increased and may assist in predation. While the strength of the fire-grazing interaction may vary across systems, the interaction is likely to be present to some degree, influencing ecosystem structure and function.

Many fire dependent systems, particularly grasslands and savannas, are endangered worldwide (Hoekstra et al. 2005). While conservation goals within these systems frequently involve restoring critical ecosystem processes, including fire and grazing (Hutto 2008; Sanderson et al. 2008), the importance of fire is often underrepresented (Bowman et al. 2009). Our findings contribute to the importance of fire within the ecosystem and support that fire and grazing are a coupled or single disturbance; their interaction may be just as vital for the conservation of fire prone systems (Archibald et al. 2005; Fuhlendorf et al. 2009). Using knowledge from historical disturbance patterns, we can develop more effective land management and conservation strategies to preserve these endangered systems and their inherent processes. Furthermore, we show that the evolutionary disturbance patterns created by fire and grazing can be restored on working landscapes (domestic livestock production on small parcels). While there are differences between domestic and native or wild herbivores, using fire and grazing to manage livestock can help restore the defining role of these interactions, as well as critical processes that contribute to biodiversity and ecosystem function (Fuhlendorf & Engle 2001).

The fire-grazing interaction, however, is not simply a management tool for conservation, but an inherent ecological process of fire prone systems. Simplifying or overlooking this interaction leads to an incomplete understanding of the effects of fire and herbivory (Fuhlendorf et al. 2009). Our data show that the time since an area has burned is a primary driver of ungulate behavior. Animals selectively prefer recently burned areas and avoid areas with greater time since fire. This preference establishes the fire-grazing interaction, creating new conditions and effects that are not present when investigating fire or grazing independently. Though the magnitude of this preference was not as influential as woody vegetation, it is high and greater than other environmental predictors, indicating a strong interaction between fire and grazing. Incorporating and accounting for the fire-grazing interaction in ecological studies and conservation will continue to improve our knowledge of these disturbances. Further study of the mechanisms of this interaction, as well as its influence on other ecosystem processes (e.g., nutrient flow, trophic interactions, primary productivity, etc.) is necessary to better understand fire dependent landscapes.

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Tables

Table 1

Estimated resource selection function coefficients for bison and cattle at the Tallgrass Prairie Preserve, OK, USA and cattle at the Oklahoma State University Research Range, OK USA. Model parameters include distance to water (m), distance to fire patch edge (m), slope (%), elevation (m), fire patch area (ha), northing and easting (º; both derivatives of aspect), woody vegetation, and time since fire (days). Standardized variables shown for coefficient comparison. Letters indicate overlap in confidence interval (95%) within species and research location; confidence intervals calculated using bootstrapping procedures (1,000 iterations).

Bison, Tallgrass Prairie Preserve	Estimate	SE	Z value	*P*
intercept	-1.2901	0.0058	-220.34	< 0.01
time since fire	-0.7373	0.0033	-222.68	< 0.01
distance to water	-0.0100[a]	0.0023	-4.62	< 0.01
slope	-0.4370	0.0033	-130.67	< 0.01
distance to patch edge	-0.0133[a]	0.0027	-4.9	< 0.01
woody vegetation	-1.0759	0.0178	-60.33	< 0.01
elevation	0.1604	0.0025	62.42	< 0.01
patch area	-0.3460	0.0034	-100.85	< 0.01
time since fire × distance to water	0.0952	0.0024	38.83	< 0.01
time since fire × slope	-0.1523	0.0039	-38.15	< 0.01
time since fire × distance to patch edge	-0.1161	0.0031	-37.36	< 0.01
time since fire × woody	0.0521	0.0217	2.40	0.01
time since fire × elevation	-0.1356	0.0027	-49.09	< 0.01
time since fire × patch area	-0.5156	0.0054	-95.27	< 0.01

Cattle, Tallgrass Prairie Preserve	Estimate	SE	Z value	*P*
intercept	3.4719	0.4446	7.81	< 0.01
time since fire	-0.6959	0.0041	-168.44	< 0.01
distance to water	-0.0214	0.0032	-6.68	< 0.01
slope	-0.2079	0.0034	-60.31	< 0.01
distance to patch edge	-0.0798	0.0030	-26.61	< 0.01
woody vegetation	0.9805	0.0190	51.53	< 0.01
elevation	0.0121	0.0037	3.27	< 0.01
northing	-0.0075[a]	0.0025	-2.97	< 0.01
easting	-0.0077[a]	0.0025	-3.04	< 0.01
time since fire × distance to water	-0.1661	0.0041	-39.94	< 0.01
time since fire × slope	-0.1800	0.0045	-39.28	< 0.01
time since fire × distance to patch edge	0.0317	0.0029	10.79	< 0.01
time since fire × woody	0.3297	0.0182	18.07	< 0.01
time since fire × elevation	-0.0558	0.0045	-12.25	< 0.01

Cattle, Research Range	Estimate	SE	Z value	*P*
intercept	-1.3277	0.0032	-413.47	< 0.01
time since fire	-0.7614	0.0033	-224.54	< 0.01
distance to water	0.1398	0.0028	48.69	< 0.01
slope	-0.1010	0.0030	-33.39	< 0.01
woody vegetation	0.5993	0.0081	-73.24	< 0.01
northing	0.0151[a]	0.0026	5.62	< 0.01
easting	0.0061[a]	0.0026	2.28	0.02
time since fire × distance to water	-0.0387[b]	0.0029	-13.05	< 0.01
time since fire × slope	-0.0292[b]	0.0033	-8.78	< 0.01
time since fire × woody	0.2355	0.0088	26.72	< 0.01

Table 2

Estimated resource selection function coefficients comparing native bison and introduced cattle at the Tallgrass Prairie Preserve, OK, USA. Data were reduced to the months of April – September and equal frequency sampling to appropriately compare selection between the two species. Model parameters include distance to water (m), distance to fire patch edge (m), slope (%), elevation (m), fire patch area (ha), northing and easting (°; both derivatives of aspect), woody vegetation, and time since fire (days). Standardized variables are shown for coefficient comparison. Letters indicate overlap in confidence interval (95%) between bison and cattle; confidence intervals calculated using bootstrapping procedures (1,000 iterations).

	Bison	Cattle
intercept	-1.8795	3.2734
time since fire	-1.6072	-0.7438
distance to water	0.0724	0.0075
slope	-0.5338	-0.2242
distance to patch edge	-0.0425	-0.0990
woody vegetation	-0.8216	1.1566
elevation	0.2095	-0.0531
patch area	-0.4735	-
northness	-	-0.0170
eastness	-	-0.0040
time since fire × distance to water	0.1656[a]	0.1534[a]
time since fire × slope	-0.2554	-0.2097
time since fire × distance to patch edge	-0.2004	0.0453
time since fire × woody	0.3705[b]	0.3690[b]
time since fire × elevation	-0.0446	-0.1096
time since fire × patch area	-0.7287	-

Table 3

Estimated resource selection function coefficients for cattle units that varied in proportion of area burned at the Tallgrass Prairie Preserve, OK, USA. Model parameters include distance to water (m), distance to fire patch edge (m), slope (%), elevation (m), northing and easting (º; both derivatives of aspect), woody vegetation, and time since fire (days). Standardized variables are shown for coefficient comparison.

Proportion burned	time since fire	water	slope	edge	woody	elevation	north	east
50	-0.8152	-0.1928	-0.2224	-0.1824	-0.2644	0.4938	-	-
33	-0.9401	0.1866	-0.0837	-0.2114	2.9839	0.0392	0.0182	-0.0171
25	-0.7408	0.0663	-0.1999	-0.1733	1.1045	-0.2263	-	-
17	-0.8191	-0.0493	-0.0155	-0.4602	2.5479	0.1785	-0.0466	-0.0192
12	-0.5010	-0.2257	-0.2363	-0.1436	1.1764	0.1511	-	-
Size		tsf × wtr	tsf × slp	tsf × edge	tsf × wdy	tsf × elev	tsf × north	tsf × east
50		-	-0.0874	-0.3173	-0.1095	0.1265	-	-
33		0.0391	0.0062	-0.3838	0.6220	-0.0375	-	-
25		-0.0716	-0.0267	-0.1980	0.2719	0.0282	-	-
17		-0.0531	-0.0232	-0.5955	-0.1584	0.1120	-0.0338	-0.0115
12		-0.1726	-0.0789	-0.1271	-0.3816	0.1483	-	-

Figures

Figure 1

Illustration of patchy fire within the bison unit (9532 ha) at the Tallgrass Prairie Preserve, OK, USA. Map displays fires applied in 2009 and 2010. Spatially distinct patches are burned within the bison unit in spring, summer, and winter. Burn locations are not fixed and vary by year and season. Only perimeter fences are present, allowing bison free access to all burns. The fire-grazing interaction occurs as bison select between recently burned and areas with greater time since fire.

Figure 2

Relative probability of site selection by bison at the Tallgrass Prairie Preserve, OK, USA, for September 2009 and 2010. Probabilities presented as a function of parameters in Table 1. Solid orange lines represent perimeter fences. Refer to Figure 1 for recently burned areas. Bison prefer recently burned areas; probabilities change as fire moves around the landscape.

Figure 3

Crude protein (%) of tallgrass prairie vegetation from April to December 2009 at the Oklahoma State University Research Range, OK, USA. Symbols are means (n=4) representing patches that vary in the amount of time since fire; error bars are one standard error. A) Crude protein shown by day of year. B) Crude protein as determined by the amount of time since fire (days).

Figure 4

Aboveground plant biomass (g 0.10 m^{-2}) of tallgrass prairie vegetation from April to December 2009 at the Oklahoma State University Research Range, OK, USA. Symbols are means (n=4) representing patches that vary in the amount of time since fire; error bars are one standard error. A) Aboveground plant biomass shown by day of year. B) Aboveground plant biomass as a function of time since fire (days).

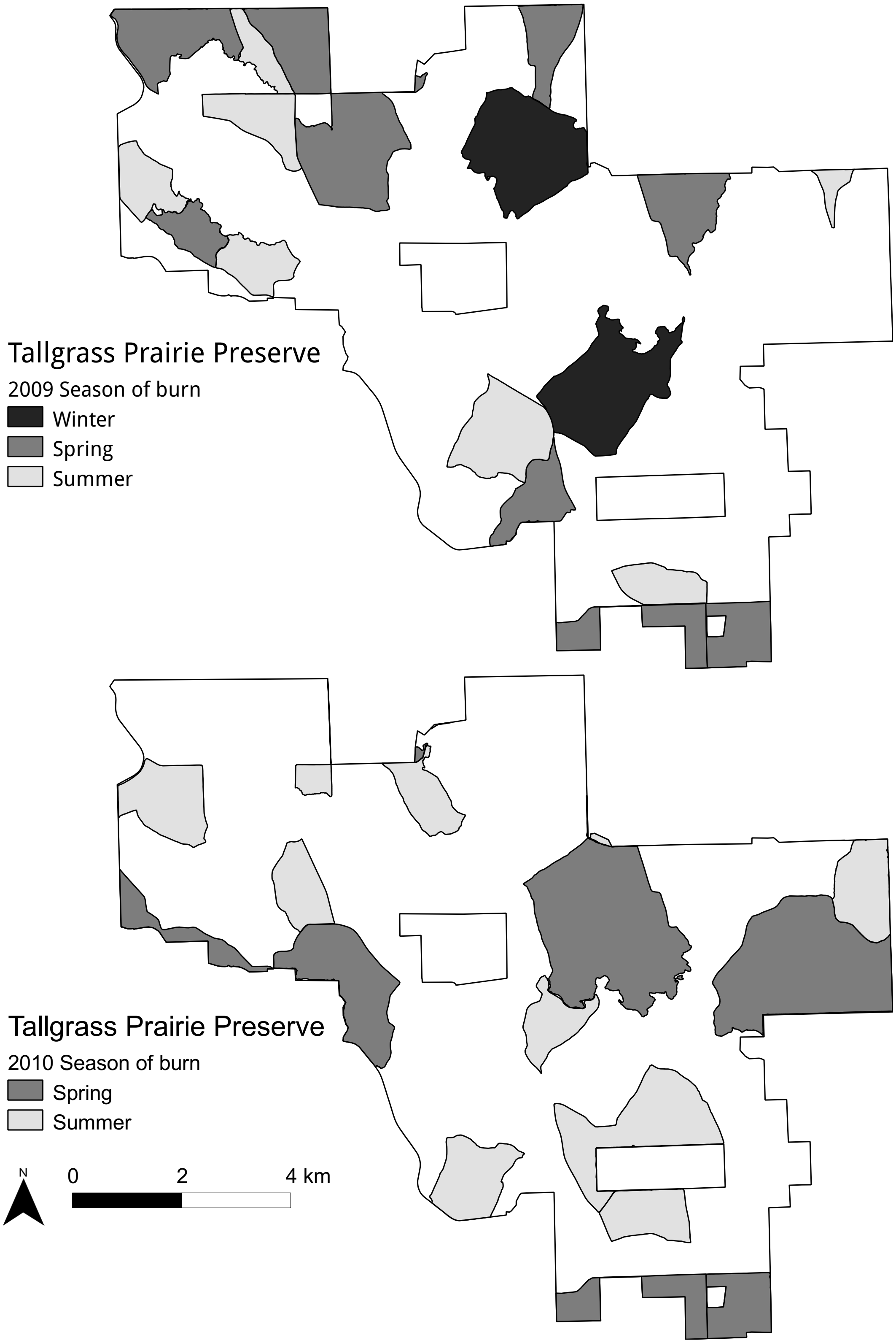
Tallgrass Prairie Preserve
2009 Season of burn
Winter
Spring
Summer
Tallgrass Prairie Preserve
2010 Season of burn
Spring
Summer
N
0
2
4 km

Figure 1

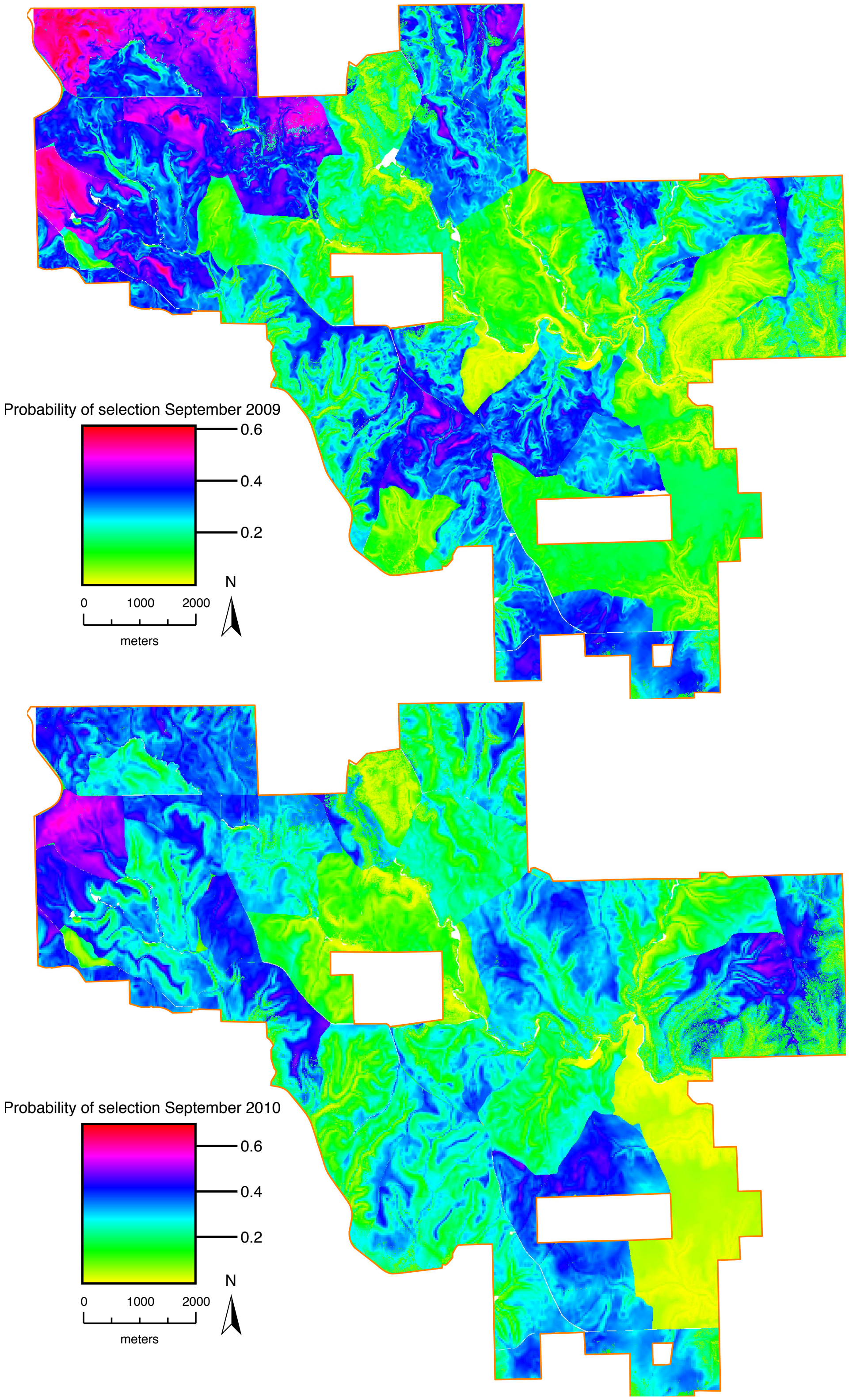
Probability of selection September 2009
0.6
0.4
0.2
0
1000
2000
meters
N
Probability of selection September 2010
0.6
0.4
0.2
0
1000
2000
meters
N

Figure 2

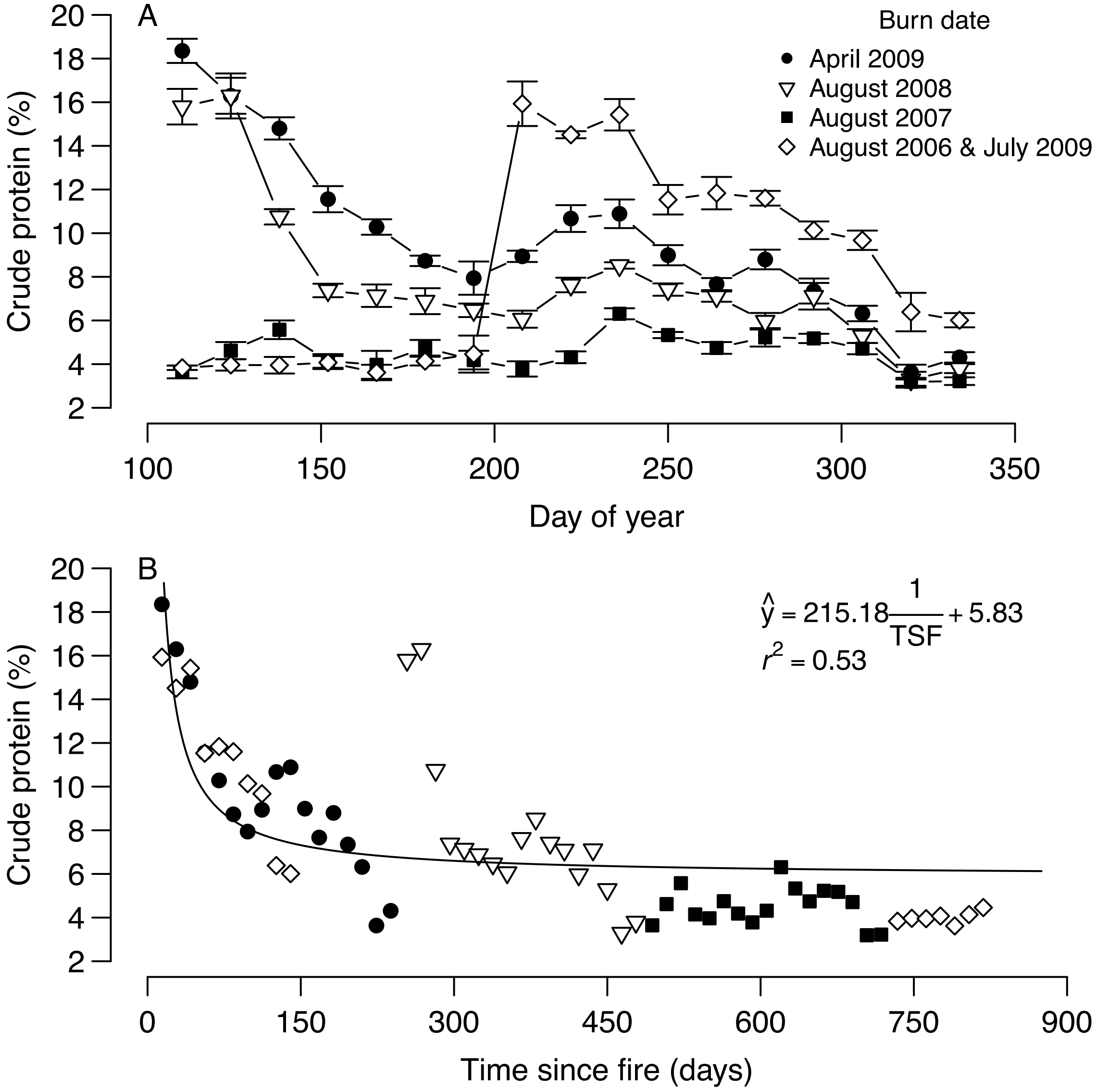
A
Burn date
April 2009
August 2008
August 2007
August 2006 & July 2009
Crude protein (%)
20
18
16
14
12
10
8
6
4
2
100
150
200
250
300
350
Day of year
B
$\hat{y} = 215.18\frac{1}{TSF} + 5.83$
$r^2 = 0.53$
Crude protein (%)
20
18
16
14
12
10
8
6
4
2
0
150
300
450
600
750
900
Time since fire (days)

Figure 3

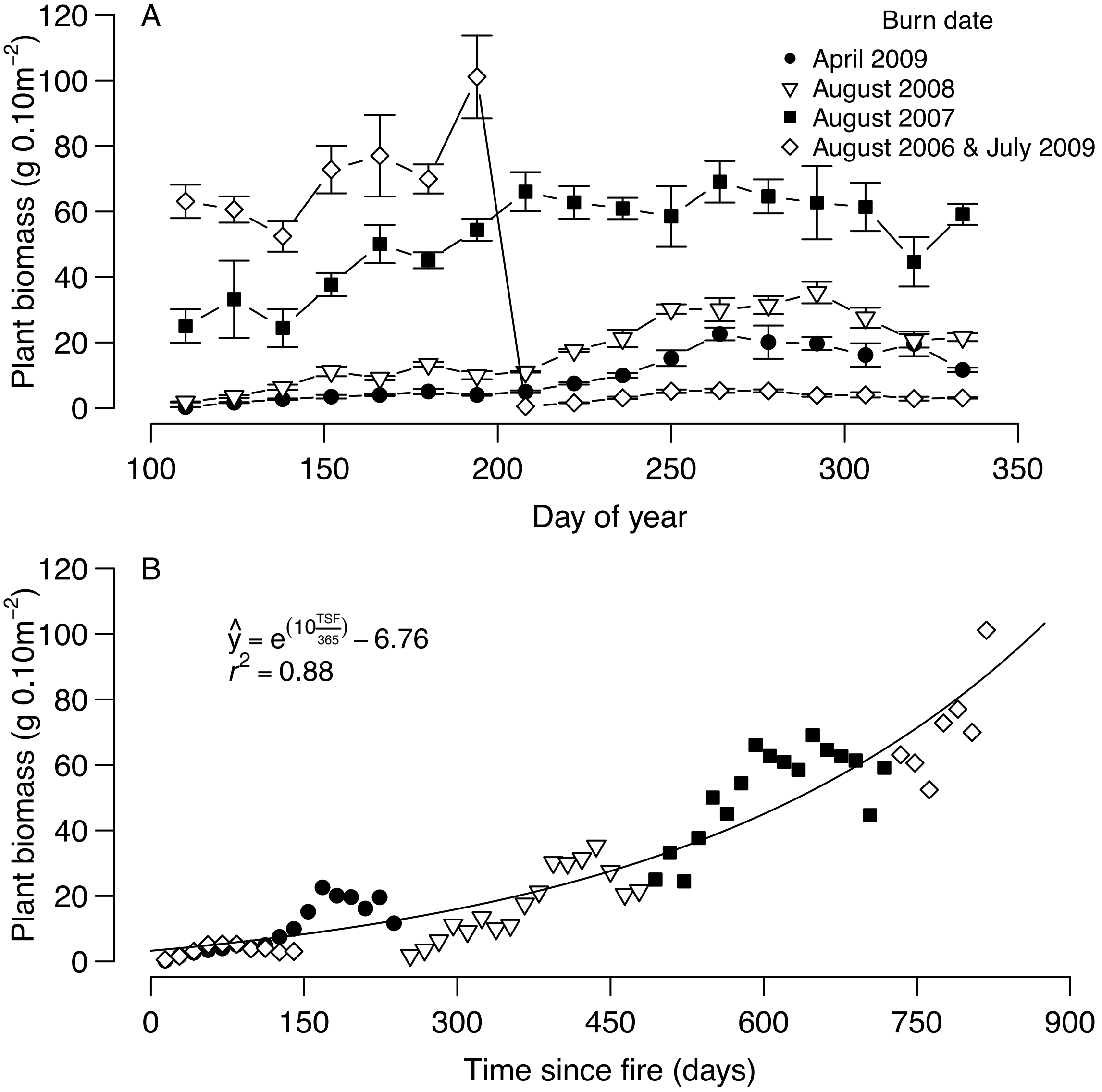
A
Plant biomass (g 0.10m^{-2})
120
100
80
60
40
20
0
Burn date
April 2009
August 2008
August 2007
August 2006 & July 2009
100
150
200
250
300
350
Day of year
B
Plant biomass (g 0.10m^{-2})
$\hat{y} = e^{\left(10\frac{TSF}{365}\right)} - 6.76$
$r^2 = 0.88$
0
150
300
450
600
750
900
Time since fire (days)

Figure 4

CHAPTER III

Interactive disturbance regulates aboveground resource in a fire prone grassland

Interactive disturbance regulates aboveground resource in a fire prone grassland

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Abstract

Aboveground and belowground resource dynamics contribute to patterns of ecosystem processes and vegetation in tallgrass prairie. Light, the primary aboveground resource in these mesic grasslands, can regulate photosynthesis and contribute to overall productivity and ecosystem function. Fire and grazing, dominant disturbances under which tallgrass prairies developed, independently modify both aboveground and belowground resource availabilities. The ecological interaction between fire and grazing, however, is an interactive disturbance that differs from fire and grazing alone, altering ecosystem structure and function in these disturbance adapted grasslands. To understand aboveground resources within the context of this interactive disturbance, we examine light dynamics and patterns of plant carbon assimilation resulting from the fire-grazing interaction and fire alone in tallgrass prairie of the southern Great Plains, USA.

Compared to fire alone, burned patches within grasslands subjected to the fire-grazing interaction experience less light limitation. Plant carbon assimilation increases with time since fire on patches within the fire-grazing interaction, so that carbon assimilation in recently burned patches was consistently lowest among all patches throughout the season. Reducing light limitation to plants can potentially alter interactions with belowground resources and productivity. The results of this study demonstrate that the fire-grazing interaction, specifically the gradient of time since fire, is a primary driver of tallgrass prairie and that it influences ecosystem processes at various levels.

Keywords

Andropogon gerardii, carbon assimilation, fire-grazing interaction, light, photosynthesis, pyric herbivory, resource limitation, tallgrass prairie

Introduction

Soil nutrients, solar radiation, and water are resources that globally constrain terrestrial primary productivity. In ecosystems where water is the primary limiting factor, belowground resources (i.e., soil nutrients) are often secondary constraints. In contrast, ecosystems with ample precipitation are primarily limited by aboveground resources (i.e., light; Lauenroth and Coffin 1992, Burke and others 1998). In tallgrass prairies of North America, where the abundance of water varies spatially and temporally, both belowground and aboveground resources drive vegetation and ecosystem patterns (Knapp and Seastedt 1986, Seastedt and others 1991, Briggs and Knapp 1995). Disturbance within prairies, however, often mediates resource dynamics and limitations (Seastedt and

Knapp 1993). Tallgrass prairies developed with fire and grazing, and these two disturbances influence resource and vegetation dynamics (Hobbs and others 1991, Ojima and others 1994, Hartnett and others 1996, Turner and others 1997).

In many productive grasslands, including tallgrass prairie, the primary aboveground resource is light. Light availability influences numerous ecophysiological responses including carbon assimilation, which sustains growth and reproduction necessary for ecosystem productivity and function (Owensby and others 1993, Knapp and others 1998). Accumulated detritus (litter) in these grasslands significantly limits the light energy available to plants and affects the entire ecosystem (Knapp and Seastedt 1986). While fire removes detritus and increases light availability in tallgrass prairies, light limitation quickly returns with plant regrowth after fire (Knapp 1984, 1985).

Whereas light is limiting aboveground, soil nitrogen is a belowground resource and is also largely influenced by fire and grazing; fire reduces plant-available nitrogen (Seastedt and others 1991, Ojima and others 1994, Blair 1997), but grazing often enhances plant-available nitrogen (McNaughton 1984, Holland and Detling 1990). Soil water also influences primary productivity dynamics, which varies inter and intra-annually with precipitation, topography, and the presence of fire or grazing (Briggs and Knapp 1995, Bremer and others 1998). Due to the variability of these aboveground and belowground resources in both space and time, and their response to dominant disturbances, tallgrass prairies are characterized as nonequilibrium ecosystems (Seastedt and Knapp 1993).

Though there are many studies examining fire and grazing independently within grasslands, the ecological interaction between them has received less attention. The fire-grazing interaction occurs when spatially distinct fires are present across a landscape and move through time, forcing grazing animals to choose among burned and unburned areas (Fuhlendorf and Engle 2001, Archibald and others 2005). Herbivores prefer recently burned areas and respond with heavy selection and use (Vinton and others 1993, Sensenig and others 2010, Allred and others 2011). Fuel accumulation is retarded with preferential grazing of burned patches, so the probability of fire responds negatively to preferential grazing (Kerby and others 2007, Leonard and others 2010). These interactions create a shifting mosaic landscape that influences biodiversity (Fuhlendorf and Engle 2001, Fuhlendorf and others 2006), fire behavior (Kirkpatrick and others 2011), wildlife populations (Churchwell and others 2008, Fuhlendorf and others 2010), and communities (Fuhlendorf and Engle 2004, Cummings and others 2007). The fire-grazing interaction is an ecosystem model that describes biodiversity, heterogeneity, and grassland structure and function, incorporating ecological interactions that historically shaped grasslands (Anderson 2006, Fuhlendorf and others 2009).

The dynamics and effects of aboveground and belowground resources are important to understanding ecosystem structure and function. Though widely studied as response variables to fire and grazing as independent disturbances, resource dynamics in the context of the fire-grazing interaction are less clear. The ability of the fire-grazing interaction to completely drive and shape the landscape is unique and will likely alter resource dynamics in a different manner compared to fire and grazing as independent disturbances. For example, Anderson and others (2006) examined belowground soil nitrogen dynamics within the framework of the fire-grazing interaction and found that nitrogen availability was greatest in recently burned areas and decreased with time, opposite of the effect present when fire occurs independent of grazing (Blair 1997). Aboveground resources in tallgrass prairie, primarily light dynamics and its influence on photosynthesis, might also deviate from dynamics previously demonstrated when fire and grazing are treated as non-interacting disturbances.

The main objective of this study was to examine aboveground resource dynamics of tallgrass prairie within the fire-grazing interaction. We focus on light dynamics and plant carbon assimilation, and we include temporal patterns of aboveground biomass. To appropriately characterize the fire-grazing interaction, we used small observation plots embedded within a large grassland landscape (Fuhlendorf and others 2009). We show that the fire-grazing interaction, specifically the amount of time since fire and subsequent grazing, regulates light dynamics and carbon assimilation in tallgrass prairie, further demonstrating the dominance of this ecosystem driver.

Methods

We investigated the fire-grazing interaction at the Oklahoma State University Research Range, southwest of Stillwater, OK, USA. Vegetation is tallgrass prairie, with patches of cross timbers forest. Dominant grasses include *Andropogon gerardii* Vitman, *Schizachyrium scoparium* (Michx.) Nash, *Panicum virgatum* L., and *Sorghastrum nutans* (L.) Nash. Crosstimbers vegetation is dominated by *Quercus stellata* Wang. and *Q. marilandica* Münchh.

The fire-grazing interaction is a dominant feature within the research site (Fuhlendorf and Engle 2004); spatially distinct patches (hereafter referred to as ‘patches’) are burned within larger units during both the dormant season (early spring) and growing season (summer; Figure 1). Only the perimeters of the units are fenced, giving grazing animals free access to the entire area. Units are stocked yearlong with European breed cattle; stocking rate was approximately 3.0 AUM ha^{-1}. Fire-grazing interactions occur as animals choose among patches that are recently burned and those with greater time since fire. To compare the fire-grazing interaction to that of fire alone, we performed measurements in patches of the fire-grazing interaction that varied in time since fire and in separate areas that had fire only (no grazing). Fire only areas were burned at the same time as the spring 2009 patches of the fire-grazing interaction, and had not burned for the previous two years. It is important to note that the range of time since fire is limited within fire only areas (0 to 30 weeks). With regard to patches of the fire-grazing interaction, time since fire refers to the amount of time since fire with subsequent grazing (due to grazing preferences); in fire only areas it refers to time since the 2009 fire event. All data were collected during the growing season of 2009.

Aboveground biomass

We harvested aboveground biomass from four randomly placed 0.10 m^2 plots in patches that varied in time since fire and in fire only areas. We collected samples every two weeks from April through October 2009. We dried samples to a constant mass and recorded the weight of each sample. We used regression to describe relationships of aboveground biomass to time since fire. We compared confidence intervals (95%) of slope coefficients to determine if biomass as a function of time since fire differed between patches of the fire-grazing interaction and fire only areas.

Light

We measured photosynthetically active radiation (PAR; μmol photons m^{-2} s^{-1}) within patches and fire only areas using a ceptometer (SunScan, Delta-T Devices). We recorded PAR monthly, May to October 2009, beginning six weeks after spring fires. Measurements were taken in full sunlight when sun angle was 15° or less from minimum zenith. We established three 1-m^2 plots in patches that varied in time since fire and in fire only areas. We oriented the ceptometer north-south and recorded PAR every 1.56 cm across the plot at 0, 20, 40, 60, 80, and 100 cm aboveground. To capture the variation in light across each plot, we performed this procedure five times at 10, 30, 50, 70, and 90 cm from the eastern edge of the plot. To eliminate horizontal edge effects, we removed all measurements located within the first and last 10 cm of the ceptometer. We averaged measurements at each height level within the plot and used regression to obtain predictive models of PAR relative to height aboveground. We also used regression to compare relationships of light at ground level with time since fire for patches of the fire-grazing interaction and fire only areas. We compared confidence intervals (95%) of slope coefficients to determine if relationships of light and time since fire differed between the fire-grazing interaction and fire only.

Gas exchange and carbon modeling

We measured leaf gas exchange characteristics of tallgrass dominant *Andropogon gerardii* at the same time we measured PAR (monthly May to October 2009) using a portable photosynthesis system (LI-6400, LI-COR) equipped with an artificial LED light source (LI-6400-02B, LI-COR). Within plots used to measure PAR, we measured the photosynthetic response of one representative *A. gerardii* leaf to varying PAR (2000, 1500, 1000, 500, 250, 125, 75, 25, and 0 μmol photons m^{-2} s^{-1}). During light response measurements, leaf chamber temperature and relative humidity were held constant at ambient conditions. CO_2 concentration and airflow within the leaf chamber were maintained at 380 μmol mol^{-1} and 500 μmol s^{-1}, respectively. To obtain predictive models of photosynthetic rate with available light, we fitted light response curves using a non-rectangular hyperbola (Thornley and Johnson 1990).

After taking photosynthetic measurements, we recorded leaf angles of *Andropogon gerardii* individuals at various points along each leaf. We clipped all plant individuals at ground level and transported them indoors. To obtain accurate measurements of leaf height, we laid plants horizontal and reconstructed leaf angles from original measurements. We measured leaf height (relative to the clipped stem, or ground level) and leaf width in one-cm intervals (hereafter referred to as ‘leaf segments’), starting from the ligule and moving toward the leaf tip. We then removed all leaves at the ligule and measured total leaf area using an optical scanner and image processing software (ImageJ; Abramoff and others 2004).

Using the height aboveground of each leaf segment and predictive models of PAR, we estimated the amount of light available to each leaf segment. It is important to note that this light estimate does not reflect complete light absorption, as it does not account for solar angle or leaf angle (which can change frequently due to wind), or the absorption differences between direct and diffuse sunlight (Anten and Hirose 2003). Accounting for such parameters would give a more accurate estimate of exact light absorption by leaf segments, but is out of the scope of this study. Using estimated available light, leaf metrics, and fitted photosynthetic light response curves, we calculated instant net photosynthesis for each leaf segment. We summed all leaf segments to estimate instantaneous carbon assimilation for each plant individual.

We examined relationships of maximum photosynthetic rate, leaf area, and plant carbon assimilation with time since fire using regression. We present data from fire only areas for visual comparison only. Photosynthetic rate varied with sampling period, so we analyzed separately data from each sampling period. We performed all analyses in R (R Development Core Team 2011).

Results

Aboveground biomass of recently burned patches increased with time since fire for both patches of the fire-grazing interaction and fire only areas ($P < 0.05$; Figure 2), but biomass increased more rapidly on fire only areas. Lower quantities of biomass in patches of the fire-grazing interaction are maintained through time as grazing animals preferentially select burned patches. As time since fire increases and new burned patches become available, grazing animals alter their selection preferences and biomass accumulates as grazing intensity lessens. In fire only areas, aboveground biomass accrues more quickly with time since fire. Biomass of fire only areas peaked at about 25 weeks compared to 90-100 weeks within the fire-grazing interaction. While the period of time since fire is limited within fire only areas (0 to 30 weeks), biomass accumulation is unlikely to slow to that of patches of the fire-grazing interaction, due to the lack of grazing animals and removal of biomass.

Available PAR at ground level decreased with time since fire for patches of the fire-grazing interaction and fire only areas ($P < 0.05$; Figure 3), but relationships differed between the two. Both patches of the fire-grazing interaction and fire only areas had large amounts of PAR after fire, but areas with fire only decreased more rapidly as time progressed. Again, the range of time since fire, as a treatment variable, is limited in fire only areas to 0 to 30 weeks, but it is unlikely that ground level PAR will increase with greater time, as there is no subsequent removal of vegetation (no grazing).

Within patches of the fire-grazing interaction, light attenuation from above the canopy to ground level was greatest in patches with 80+ weeks since fire. Light environments varied throughout the season, but the relationship with time since fire was consistent. Due to the interactions of fire and grazing (animals preferring recently burned areas) high light environments were present in recently burned patches (burned spring and summer 2009) through October (Appendix A in supplementary material). Photosynthetic active radiation was also more uniform within recently burned patches, both within and between specific heights aboveground (Appendix B in supplementary material).

Photosynthetic response curves of *Andropogon gerardii* followed typical responses; photosynthetic rates increased with light at lower intensities and plateaued at higher intensities (Appendix C in supplementary material). Photosynthetic rates of *A. gerardii* in patches of the fire-grazing interaction at maximum PAR (2000 μmol photons $m^{-2} s^{-1}$) were negatively correlated with time since fire ($P < 0.05$; Figure 4). Photosynthetic rate was always greatest in the recently burned patches of the fire-grazing interaction and appeared similar to or greater than that of fire alone at the same time since fire throughout the season (no statistical test performed).

Total leaf area of *Andropogon gerardii* within the fire-grazing interaction increased with time since fire ($P < 0.05$; Figure 5). Whole plant carbon assimilation of *A. gerardii* within the fire-grazing interaction also increased with time since fire, with plants in recently burned patches having the least amount of carbon assimilation ($P < 0.05$, less October; Figure 6). Trends disappeared in October when both photosynthesis and leaf area declined. Leaf area and carbon assimilation of *A. gerardii* within the fire-grazing interaction appeared less than that of plants in fire only areas (no statistical test performed).

Discussion

The fire-grazing interaction is a historically important, interactive disturbance that is present in grasslands and savannas worldwide (Moe and Wegge 1994, Pearson and others 1995, Salvatori and others 2001, Vandvik and others 2005, Kutt and Woinarski 2007, Waldram and others 2008). It shapes the landscape at various levels (Anderson and others 2006, Doxon and others 2011, Winter and others 2012), driving ecosystem structure and function of fire prone systems. In tallgrass prairie, the fire-grazing interaction regulates resource dynamics and acquisition. Light, a critical aboveground resource, becomes limiting as the amount of the time since fire increases. Though this is naturally intuitive for grassland ecosystems with fire, light dynamics of patches within the fire-grazing interaction differ from that of just fire alone, with high light environments of the interaction being extended for greater lengths of time. This change has far-reaching effects on individual plant carbon assimilation and productivity, as well as interactions with belowground resource availability.

The accumulation of detritus in grasslands limits light energy available for photosynthesis, which constrains productivity and other ecosystem processes (Knapp and Seastedt 1986). While a fire event removes detritus and light limitations, such an effect is often short lived as herbaceous vegetation is more productive and quickly regrows. Light limitations can be restored within a few weeks (see also Turner and Knapp 1996), limiting physiological processes and carbon assimilation as new growth develops in a decreased light environment (Knapp 1985). Contrasting this, recently burned patches of the fire-grazing interaction (spatially distinct fire with subsequent preferred grazing) maintain a higher light environment for a longer period of time. Fire removes detritus accumulation and light limitations, while the continuous attraction to and heavily utilization of burned patches by grazing animals prevents detritus accrual and sustains a high light environment in both the current and following growing season. In this study, light limitations begin to reappear in patches that were near two years since fire. Between two and three years, light becomes limited again as the patch returns to an unburned and ungrazed state. How quickly light limitations return after fire will ultimately vary and depend upon the attraction of animals to burned patches, animal densities, patch size, and general vegetation productivity (Allred and others 2011). It is important to note that light limitations are specific to spatially distinct patches. Within the fire-grazing interaction framework, multiple patches are present throughout the landscape and vary in time since fire. Aboveground limitations are therefore heterogeneously distributed across the landscape and are dependent upon number of patches and variability in time since fire.

The growth of plants, and therefore primary productivity of plant communities, ultimately depends upon resource availability, assimilation, and utilization. While tallgrass prairie light environments are increased and prolonged with the fire-grazing interaction, it is the ability of plants to capture light energy and use it for the photosynthesis that drives carbon assimilation. Many resources and plant characteristics will influence carbon assimilation, including light and moisture availability, leaf area, nitrogen (plant and soil), and net photosynthetic rate. Consistent with other studies, fire (with or without the interaction of grazing) increased photosynthetic rate of the dominant grass *Andropogon gerardii* when compared to plant individuals with greater time since fire. Within recently burned patches of the fire-grazing interaction, however, this increase came at the cost of reduced leaf area caused by preferential grazing.

The tradeoff of high photosynthetic rate and low leaf area, "the fundamental ecological dilemma" (Parsons and others 1983, Briske and Heitschmidt 1991), has direct implications for whole plant carbon assimilation and primary productivity. Carbon uptake after fire is limited by the continual lack of leaves. With fire only, this limitation is short lived as biomass and leaf area quickly recover; decreases in the photosynthetic rate of *Andropogon gerardii* with time are replaced by increases in leaf area, increasing carbon assimilation. The fire-grazing interaction, however, prolongs the high photosynthetic rate and low leaf area tradeoff due to the heavy utilization of burned areas by herbivores. Photosynthetic rate remains higher through time, relative to patches with greater time since fire, but reduced leaf area limits plant carbon uptake. The dynamics of carbon assimilation ultimately diverge from that of light energy. In recently burned patches, where light resources are high, total carbon gain of *A. gerardii* is reduced. This reduction of carbon assimilation is a potential mechanism for the temporal shifts in plant communities that occur with the fire-grazing interaction. As patches increase in time since fire, plant communities transition from being dominated by grasses to ruderal forbs, and then back to grasses (Fuhlendorf and Engle 2004, Winter and others 2012). The inability of grasses to immediately recover from heavy utilization post fire is likely impacted by the prolonged reduction in carbon assimilation. Though aboveground resources (i.e. light) are plentiful in recently burned patches, the ability of vegetation to utilize those resources is diminished by extended periods of reduced leaf area caused by the attraction of herbivores to burned areas.

While aboveground resources are essential to tallgrass prairie vegetation, it is often the interaction of both aboveground and belowground resources that shape ecosystem structure and function. In tallgrass prairie, light and soil nitrogen resources interact to influence vegetation and ecosystem patterns. The limitations of these resources have been shown to alternate through time with respect to fire. Blair (1997) demonstrated that with fire only (no grazing), soil nitrogen and mineralization were greatest in unburned sites and lowest after infrequent and frequent fire. Thus, when light energy is abundant after fire, soil nitrogen becomes limiting; when light energy is limiting, soil nitrogen is abundant. For a brief time after fire, the limitations of these two resources are released simultaneously and a pulse of productivity occurs (Seastedt and Knapp 1993, Blair 1997). The presence of an interactive disturbance, however, complicates the interactions and effects of aboveground and belowground resources. Though not quantified in this study, Anderson and others (2006) demonstrated that soil nitrogen availability within the fire-grazing interaction follows the same trend of light energy, higher in recently burned areas and decreasing with time. This pattern is similar to that caused by grazing lawns, where focal grazing increases N availability (McNaughton 1984). When examined at the scale of patches within the fire-grazing interaction, light and soil nitrogen dynamics do not alternate in limitations but mirror one another. As a result, releases from light and nitrogen limitations will occur concurrently, rather than alternating through time.

Compared to fire alone, the response of aboveground productivity of tallgrass prairie to the fire-grazing interaction is less clear, as the alternating limitations of light and soil nitrogen are absent, and biomass is continuously removed from burned patches. Light and soil nitrogen are more abundant in recently burned patches, suggesting that productivity would increase after fire and grazing. Plant carbon assimilation, however, is limited by the preferential grazing after fire. Though carbon gain is not a measure of productivity, it is important in both aboveground and belowground production (Owensby and others 1993), providing necessary components for growth and ecosystem function. If increases in plant growth and productivity were to occur in recently burned patches of the fire-grazing interaction, they would need to be the result of increased carbon utilization efficiency or belowground resources, as the ability to assimilate carbon is severely limited throughout the growing season. Due to the heavy and continuous consumption of biomass by herbivores after fire and the prolonged reduction in carbon assimilation, productivity may be greater in patches with longer time since fire. Further work examining productivity, as well as aboveground and belowground resources, is necessary to determine productivity responses within the fire-grazing interaction.

Conventional disturbance research often focuses on the effects of the disturbance as an independent force, limiting the interaction with other ecosystem components. Disturbance treatments are commonly uniformly applied to homogenous experimental units to minimize variation and more often than not, gradients of disturbance (e.g., none, light, moderate, and heavy grazing) are discarded for simpler binary responses, (e.g., grazed vs. ungrazed). While this has improved the understanding of single disturbances within grasslands, such an approach limits spatial and temporal interactions that naturally occur within the ecosystem. Incorporating and studying such interactions will often yield different results and a highly connected and interactive ecosystem. The fire-grazing interaction demonstrates this, as the gradient of time since fire becomes a primary driving force of the ecosystem, influencing broad, landscape level events and processes (e.g., grazing and fire behavior) to fine, localized processes (e.g., plant photosynthetic rates). This gradient of time since fire spans multiple patches, creating spatial and temporal heterogeneity in the processes and responses affected. In tallgrass prairie, this interactive disturbance regulates light energy and carbon assimilation, primary aboveground resources that shape ecosystem patterns and dynamics, providing further evidence that the fire-grazing interaction is a complex disturbance regime that shapes fire prone systems at multiple levels.

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Figures

Figure 1

Illustration of the fire-grazing interaction within a grazing unit at the Oklahoma State University Research Range. Each unit is 65 ha (bold perimeter line); spatially distinct patches (dashed lines) are burned within a unit. Only the perimeter of each unit is fenced, allowing grazing animals access to all patches. Text indicates burn sequence from summer 2007 through summer 2009. The fire-grazing interaction occurs as grazing animals choose among patches that are recently burned and patches with greater time since fire.

Figure 2

Mean aboveground plant biomass (g 0.10 m^{-2}; n=4) as a function of time since fire (TSF) for areas that were burned and not grazed (fire only) and for patches that were burned and grazed within the fire-grazing interaction ($P < 0.05$; no overlap between 95% confidence intervals of slope coefficients). Biomass accumulates more slowly within the fire-grazing interaction as grazing animals preferentially select burned patches, and more rapidly in fire only areas due to the lack of grazing animals.

Figure 3

Mean photosynthetic active radiation (PAR; µmol photons m^{-2} s^{-1}) at ground level as a function of time since fire (TSF) in areas with fire only and patches of the fire-grazing interaction ($P < 0.05$; no overlap between 95% confidence intervals of slope coefficients). High light environments of the fire-grazing interaction are prolonged because grazing animals preferentially select recently burned patches. High light environments of fire only areas quickly diminish as vegetation regrows after fire.

Figure 4

Maximum photosynthetic rate of *Andropogon gerardii* as a function of time since fire (TSF) in areas with fire only (open circles) and patches of the fire-grazing interaction (closed circles, solid line), May through October 2009. Maximum photosynthetic rate was highest in recently burned areas and decreased with time since fire. Fire only measurements are included for visual comparison only.

Figure 5

Total leaf area for *Andropogon gerardii* as a function of time since fire (TSF) in areas with fire only (open circles) and patches of the fire-grazing interaction (closed circles, solid line), May through October 2009. Due to grazing preferences, leaf area is lowest in recently burned patches and increases with time since fire. Fire only measurements are included for visual comparison only.

Figure 6

Carbon assimilation by *Andropogon gerardii* as a function of time since fire (TSF) in areas with fire only (open circles) and patches of the fire-grazing interaction (closed circles, solid line), May through October 2009. Each sample is an estimate of instantaneous whole plant carbon assimilation, calculated by predictive models that use PAR, light response curves, and leaf metrics as predictive variables. Carbon assimilation of plants within patches of the fire-grazing interaction reflects total leaf, with assimilation reduced in recently burned patches and increasing with time since fire. Fire only measurements are included for visual comparison only.

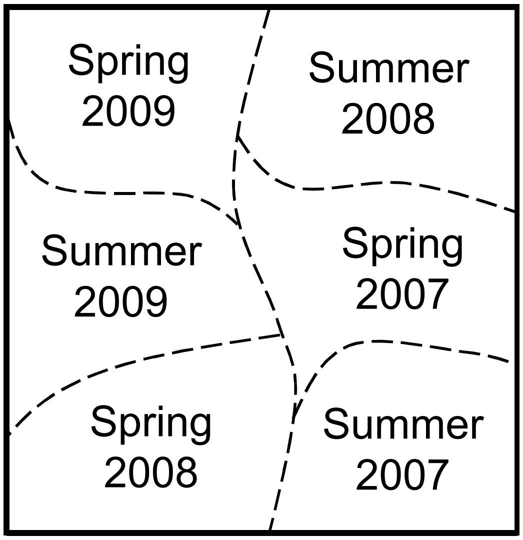
Spring 2009
Summer 2008
Summer 2009
Spring 2007
Spring 2008
Summer 2007

Figure 1

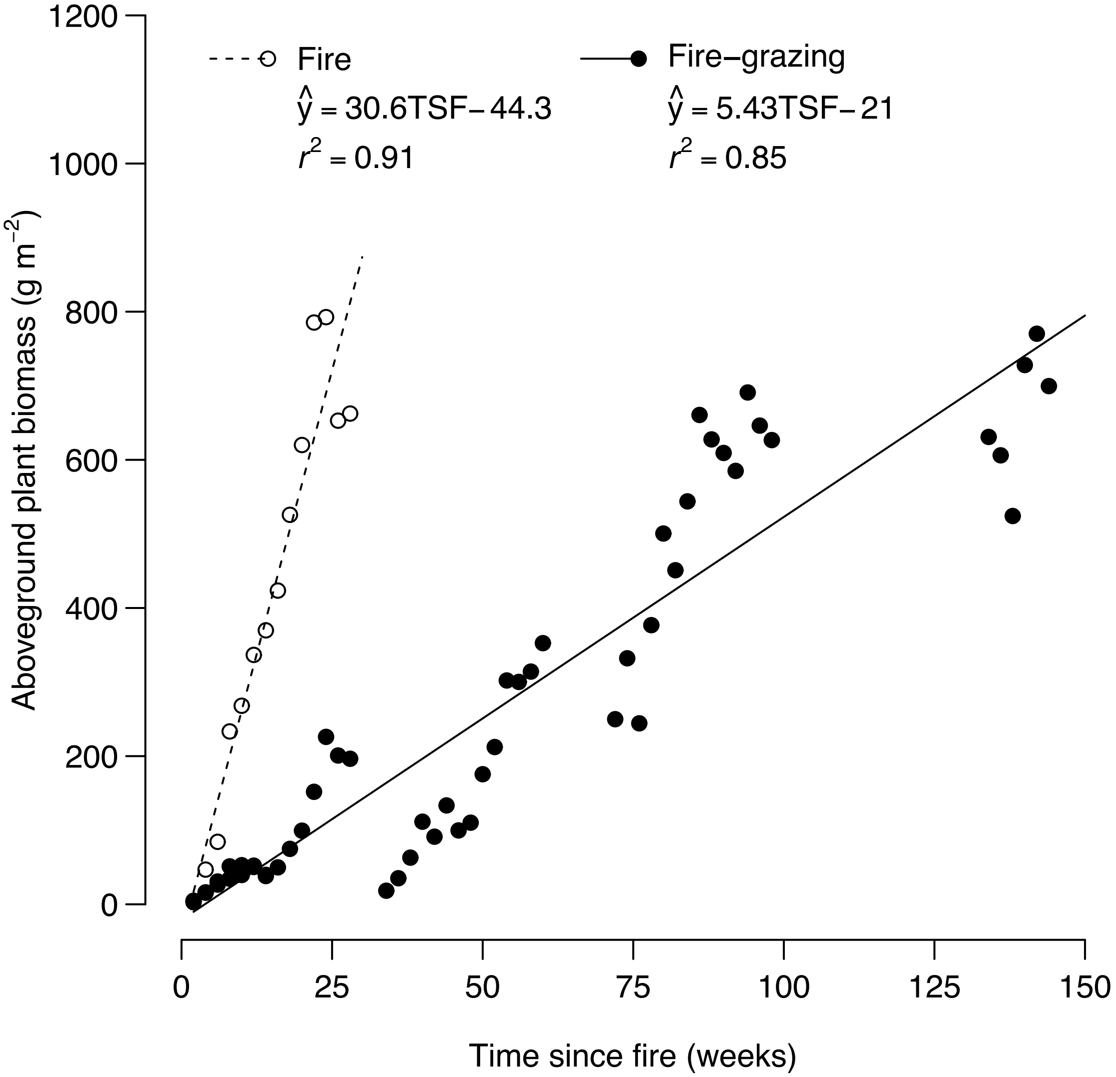
Fire
$\hat{y} = 30.6TSF - 44.3$
$r^2 = 0.91$
Fire−grazing
$\hat{y} = 5.43TSF - 21$
$r^2 = 0.85$
Aboveground plant biomass (g m^{-2})
0
200
400
600
800
1000
1200
0
25
50
75
100
125
150
Time since fire (weeks)

Figure 2

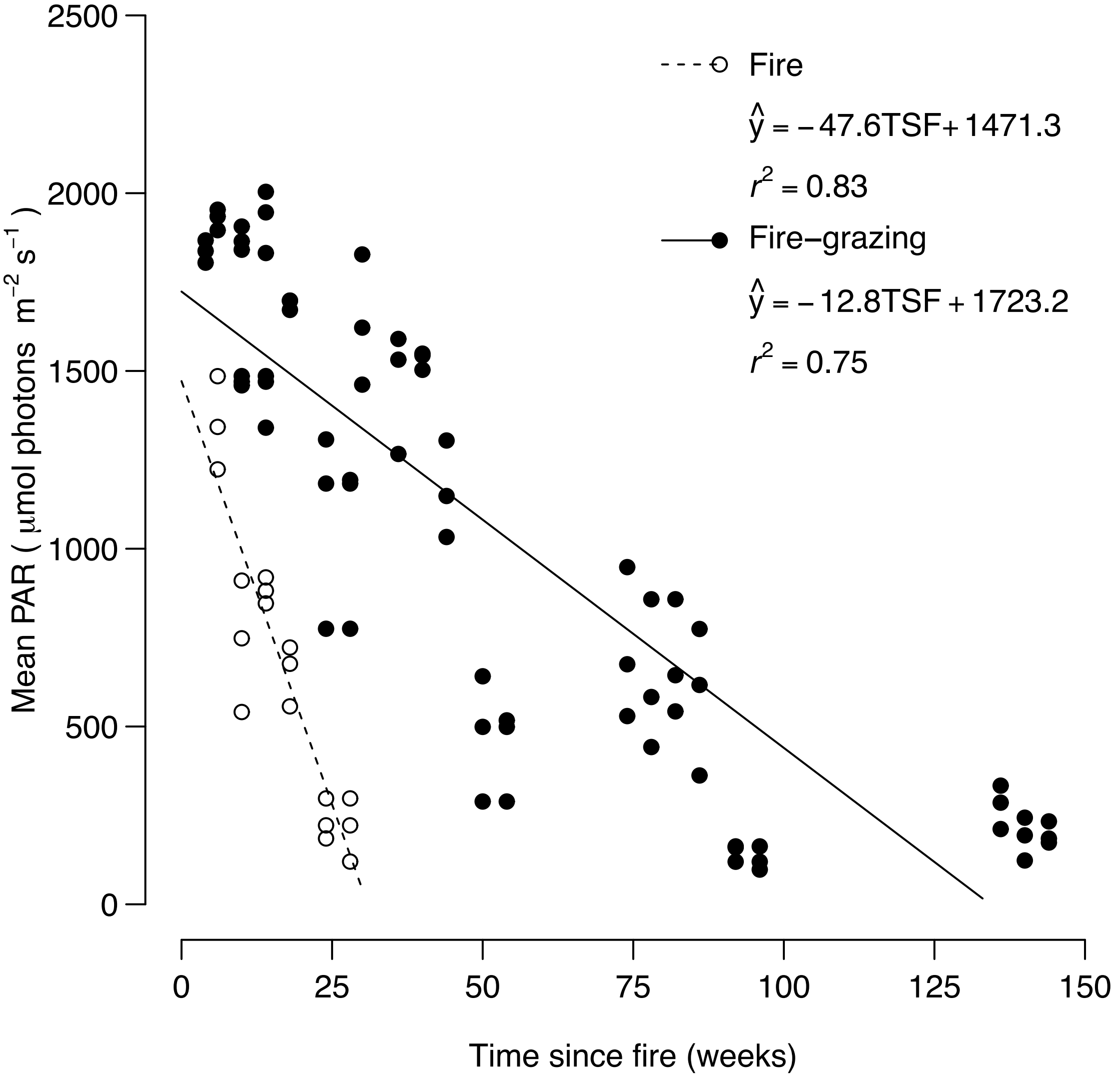
Fire
$\hat{y} = -47.6TSF + 1471.3$
$r^2 = 0.83$
Fire−grazing
$\hat{y} = -12.8TSF + 1723.2$
$r^2 = 0.75$
Mean PAR (µmol photons m^{-2} s^{-1})
2500
2000
1500
1000
500
0
0
25
50
75
100
125
150
Time since fire (weeks)

Figure 3

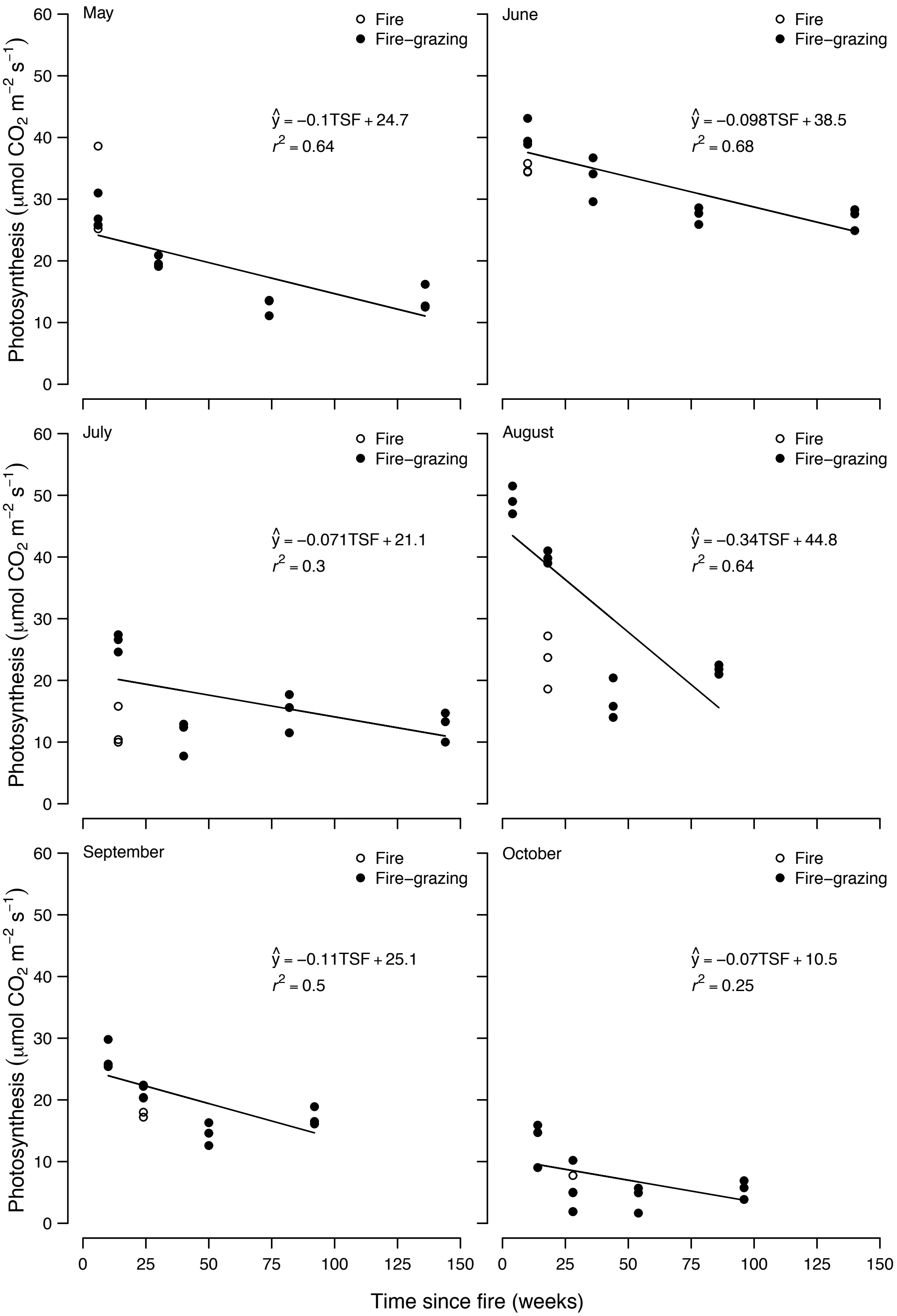
May
June
July
August
September
October
○ Fire
● Fire–grazing
$\hat{y} = -0.1\text{TSF} + 24.7$
$r^2 = 0.64$
$\hat{y} = -0.098\text{TSF} + 38.5$
$r^2 = 0.68$
$\hat{y} = -0.071\text{TSF} + 21.1$
$r^2 = 0.3$
$\hat{y} = -0.34\text{TSF} + 44.8$
$r^2 = 0.64$
$\hat{y} = -0.11\text{TSF} + 25.1$
$r^2 = 0.5$
$\hat{y} = -0.07\text{TSF} + 10.5$
$r^2 = 0.25$
Photosynthesis (μmol CO$_2$ m^{-2} s^{-1})
0
10
20
30
40
50
60
0
25
50
75
100
125
150
Time since fire (weeks)

Figure 4

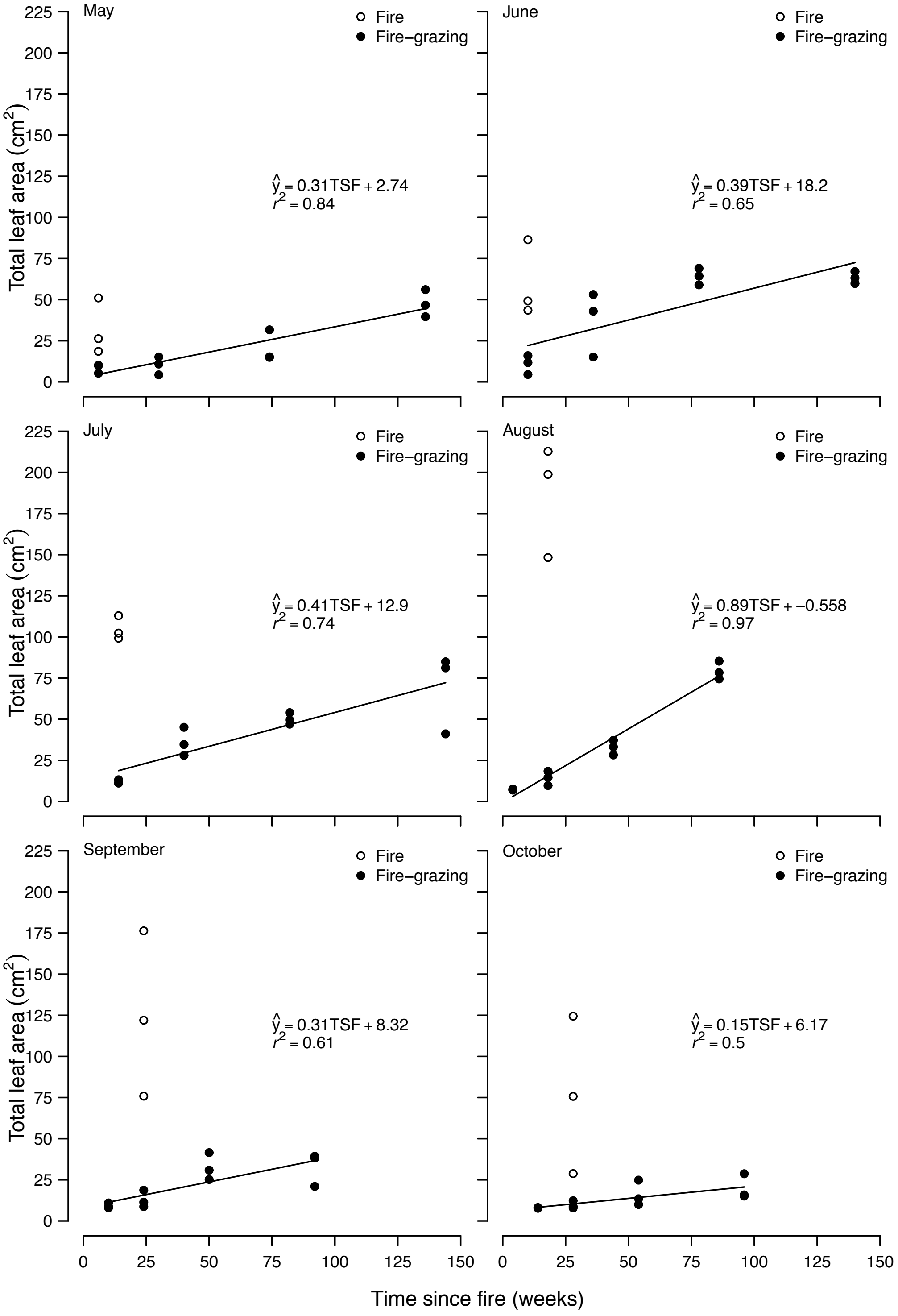
May
June
July
August
September
October
○ Fire
● Fire−grazing
$\hat{y} = 0.31TSF + 2.74$
$r^2 = 0.84$
$\hat{y} = 0.39TSF + 18.2$
$r^2 = 0.65$
$\hat{y} = 0.41TSF + 12.9$
$r^2 = 0.74$
$\hat{y} = 0.89TSF + -0.558$
$r^2 = 0.97$
$\hat{y} = 0.31TSF + 8.32$
$r^2 = 0.61$
$\hat{y} = 0.15TSF + 6.17$
$r^2 = 0.5$
Total leaf area (cm^2)
0
25
50
75
100
125
150
175
200
225
Time since fire (weeks)
0
25
50
75
100
125
150

Figure 5

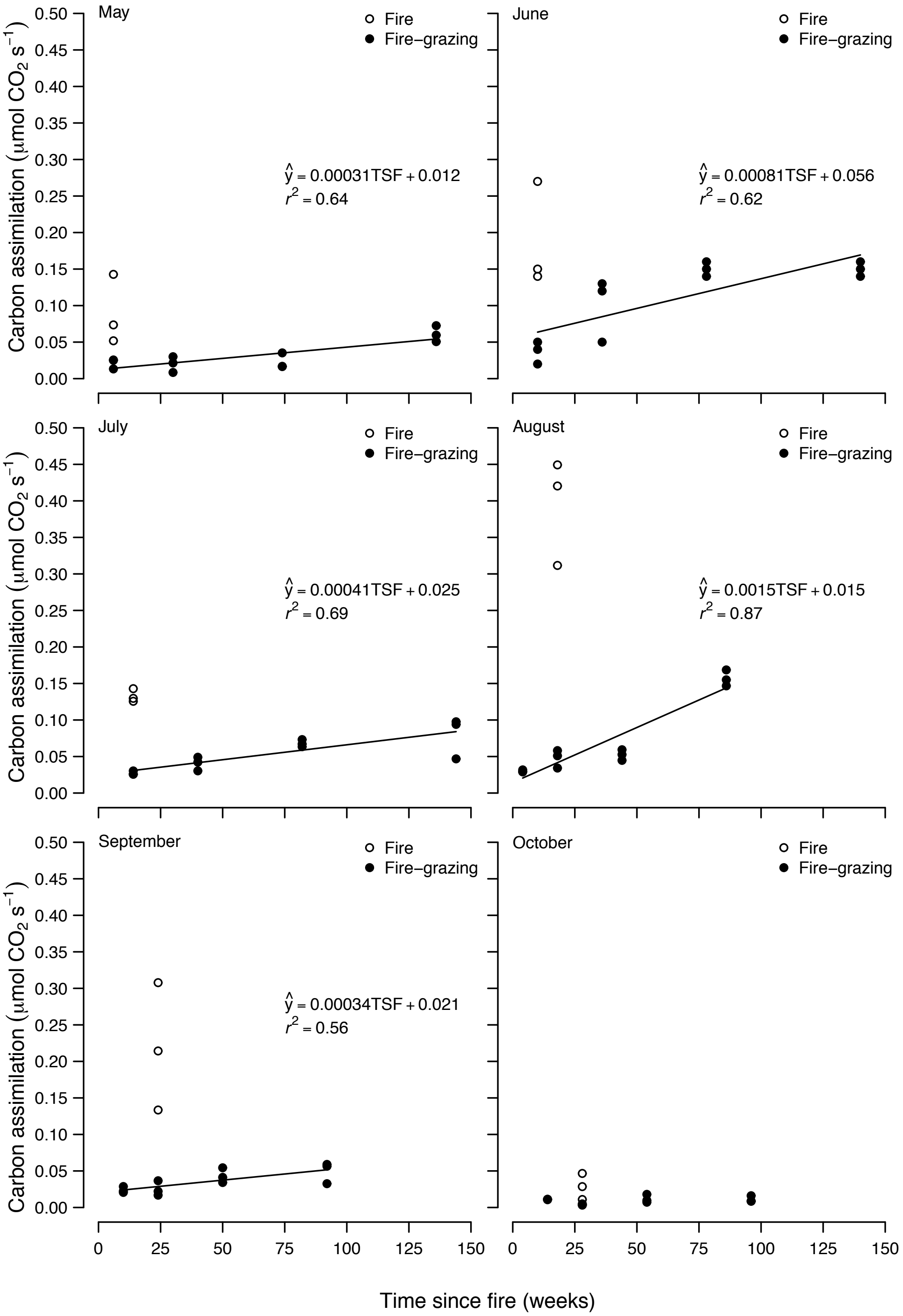
May
June
July
August
September
October
○ Fire
● Fire–grazing
$\hat{y} = 0.00031TSF + 0.012$
$r^2 = 0.64$
$\hat{y} = 0.00081TSF + 0.056$
$r^2 = 0.62$
$\hat{y} = 0.00041TSF + 0.025$
$r^2 = 0.69$
$\hat{y} = 0.0015TSF + 0.015$
$r^2 = 0.87$
$\hat{y} = 0.00034TSF + 0.021$
$r^2 = 0.56$
Carbon assimilation (μmol CO$_2$ s^{-1})
0.00
0.05
0.10
0.15
0.20
0.25
0.30
0.35
0.40
0.45
0.50
0
25
50
75
100
125
150
Time since fire (weeks)

Figure 6

CHAPTER IV

Conservation implications of native and introduced livestock in a changing climate

Conservation implications of native and introduced livestock in a changing climate

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Introduction

The Great Plains of North America developed with significant impact from large herbivores and other disturbances. After the megafaunal collapse near the end of the Pleistocene, bison, elk, and other herbivores became the primary grazers of these grasslands until pre-European settlement (Axelrod 1985; Potter et al. 2010). Due to their abundance, American Bison (*Bison bison*, as well as ancestors *B. antiquus* and *B. occidentalis*) influenced many processes within the ecosystem, altering ecosystem structure and function (Knapp et al. 1999; Anderson 2006). Much of the flora and fauna coevolved with and adapted to grazing by these and other herbivores (Axelrod 1985). Following European settlement, however, bison populations declined rapidly, driven primarily by hunting and competition from domestic livestock (Hornaday 1889; Potter et al. 2010). Bison numbers were estimated at less than 1,000 by the late 1800s (Hornaday 1889; Seton 1927). During the 20th century, the large and complex landscapes of which the bison occupied were converted to fragmented agricultural lands, supporting many private agricultural industries. Domestic livestock, primarily introduced European cattle (*Bos taurus*), replaced herds of bison and grew to become a successful economic enterprise. The 2010 estimate of cattle for meat production and their gross income within the United States was 93 million head and $51 billion, respectively, with approximately half or more of both estimates within the Great Plains (National Agricultural Statistics Service 2011).

During the same period of cattle and agricultural growth, the restoration of bison was pursued (and currently continues) by private citizens, government agencies, and conservation organizations for the purposes of species conservation and the restoration of ecosystem processes (Knapp et al. 1999). Bison numbers have increased from nearly extinct to approximately 20,000 in conservation herds and 400,000 in commercial livestock operations (Gates et al. 2010). Efforts to restore bison populations are considered a success, even though the number of animals is incomparable to that of introduced cattle. Indeed, bison restoration throughout the Great Plains cannot be fully separated from the cattle industry as nearly all rangeland is privately owned and used for livestock production (Samson & Knopf 1994).

The similarities and differences between bison and cattle are often discussed and debated between advocates, conservation biologists, ecologists, land managers, etc., and are often used to promote a specific agenda or ideology. For example, popular press, government agency reports, and scientific literature often maintain that bison spend less time near water than cattle (Manning 1995; Hartnett et al. 1997; Fritz et al. 1999; Reynolds et al. 2003; National Park Service 2009) and are therefore better suited for grazing in riparian systems or areas. Similar claims between bison and cattle abound though direct comparisons between them are minimal. Furthermore, statements often focus on the species of animal as the sole determinant of grazing effects, ignoring other important factors such as animal or landscape diversity, animal demography, disturbance regimes, or management practices. Recognizing ecological differences, as well as effects, between native and introduced livestock is important for better understanding and improved livestock management, but these differences are best studied in broad, complex landscapes in which animals are not limited in their environmental interactions (Allred et al. 2011b).

Climate is an important part of the structure and function of grazed ecosystems, and influences large herbivore behavior and grazing effects accordingly. Increased anthropogenic activity has resulted in changes in temperature and rainfall patterns at broad scales and current climate models predict a continued warming trend (IPCC 2007). While studies have examined the potential effects of climate change on livestock and the ecosystems in which they graze, many are focused on the response of quantity and quality of forage produced (Shaw et al. 2002; Craine et al. 2010), sustainability of livestock grazing (Hanson et al. 1993; Lohmann et al. 2012), or the interactive effects of grazing and climate change within ecosystems (most often with simulated grazing; Wan et al. 2002). The response of grazing behavior to climate change is equally important, as it drives overall grazing effects. How a herbivore modifies its behavior and adapts to climatic changes will influence the spatial distribution and intensity of grazing and ultimately alter ecosystem response. Understanding the differences between native and introduced herbivore behavior will aid in recognizing current ecosystem structure and function as well as ecosystem management and livestock production in a changing climate.

We evaluated the effect of temperature on the behavior of native bison and introduced cattle in tallgrass prairie. In particular, we address the following questions: i) How does the thermal environment of tallgrass prairie vary across the landscape? ii) Do bison and cattle alter selection behavior with increasing temperature? If so, how? iii) Does animal productivity vary with temperature?

Methods

We examined herbivore behavior at The Nature Conservancy Tallgrass Prairie Preserve, located in northeast Oklahoma, USA within the southern Great Plains. The preserve is a 16,000 ha natural area that is managed for biodiversity and heterogeneity. Vegetation is tallgrass prairie, with small patches of cross timbers forest. Dominant grasses include *Andropogon gerardii* Vitman, *Schizachyrium scoparium* (Michx.) Nash, *Panicum virgatum* L., and *Sorghastrum nutans* (L.) Nash. Crosstimbers vegetation is dominated by *Quercus stellata* Wang. and *Q. marilandica* Münchh. Air temperature, precipitation, and various climate measurements are measured on site every five minutes by an Oklahoma Mesonet station (Brock et al. 1995; McPherson et al. 2007).

There is one large bison unit (9,532 ha) and seven smaller cattle units (430-980 ha) within the preserve. Only perimeter fences are present and animals are free to roam within their respective units. There is minimal handling of both bison and cattle with no supplemental feeding. Bison are maintained in their respective unit all year; herd size is approximately 2,300 animals. Sex ratio of the bison herd is approximately seven females per male; ages of females range from 0-10 years, while males are 0-6 years. Cattle units are stocked with stocker steers approximately one year old (mixed European breeds); cattle are only present April through September. Cattle herds vary with each unit, ranging from 169 to 463 animals. Bison and cattle units are stocked with similar moderate stocking rates (bison: 2.1 AUM/ha; cattle: 2.4 AUM/ha). The entire preserve is managed extensively with fire and in such way that fire and grazing are allowed to interact (Hamilton 2007; Fuhlendorf et al. 2009). Fire-grazing interactions become present as animals select between recently burned areas and those with greater time since fire (Archibald et al. 2005; Allred et al. 2011a).

We measured black bulb temperature to characterize the thermal landscape of tallgrass prairie. Black bulb temperature integrates air temperature and solar radiation to determine the environmental temperature as perceived by animals (Bakken 1976; Dzialowski 2005; Signer et al. 2011). We recorded black bulb temperature by measuring air temperature inside the center of a black steel sphere (15 cm diameter) placed at ground level. To capture temporal variation, black bulb temperature was recorded every five minutes during eight separate sampling periods. Sampling periods were weeklong and stratified across seasons (spring, summer, fall, winter) from 2010-2012. To capture spatial variation, we used four 50 m transects that varied in time since fire and presence of woody vegetation, both of which are drivers of bison and cattle behavior (Allred et al. 2011b). Within each transect, two by two meter plots were established at 0, 25, and 50 m; black bulb temperature was recorded at the corner of each plot resulting in 12 sampling points per transect. Transects were moved daily during each sampling period to improve thermal landscape characterization. We used linear regression to model black bulb temperature relative to air temperature (also collected at a five minute frequency) for habitats that varied in time since fire and woody vegetation. To correspond with animal data (see below), we omitted data collected in winter.

To examine the influence of temperature on herbivore behavior and site selection, we deployed global positioning system (GPS) collars on seven female bison from and seven cattle from April through September of 2009, 2010, and 2011. New animals were chosen each year. We recorded location information of animals at two different frequencies, alternating weekly from 12 minutes to one hour. Schedule of GPS fixes was equal for bison and cattle. We imported all GPS location data into a spatially enabled database (PostgreSQL/PostGIS). We mapped fire histories and water sources (ponds and streams) with handheld GPS units, aerial photographs, and United States Geological Survey 7.5 minute topographic maps. Herbaceous and woody vegetation was mapped for the site using a GeoEye-1 satellite image acquired September 20, 2009. The presence of woody vegetation within the area is not confounded with water sources (Allred et al. 2011b).

In addition to location information, GPS collars deployed on animals also record temperature every five minutes. Temperature sensors are located within the plastic encasement that houses electronics and batteries, and resides underneath the neck of the animal. Although this is not an accurate or appropriate measure of animal body temperature, it can be used to determine if bison and cattle respond differently to air temperature (question two). A one-to-one relationship (i.e. slope equals one) of collar and air temperature indicates that collar temperature is simply tracking air temperature and is not influenced by the animal or the animal's location. Deviation from a one-to-one relationship indicates that animals are altering collar temperature, most likely by changing physical location or shifting site selection preferences. We examined the relationship of collar temperature with air temperature for bison and cattle using linear regression. Relationships for bison and cattle were regarded as different if 95% confidence intervals of slope coefficients did not overlap.

To determine if species altered selection behavior with temperature (questions two and), we estimated resource selection functions using logistic regression models (Boyce et al. 2002). Rather than including all potential environmental factors as predictors (e.g., slope, etc.) we focused only on time since fire, distance to water, and distance to woody vegetation as these factors are primary drivers of bison and cattle site selection in tallgrass prairie (Allred et al. 2011b). To represent available habitat, we created three random locations for each observed location. We calculated time since fire, distance to water, and distance to woody vegetation for all locations; we also joined air temperature to all locations. Our principal resource selection function included interactions of air temperature with all primary drivers to first determine if temperature altered behavior. Because interactions with air temperature were significant, we estimated resource selection functions at different air temperature classes. Air temperature was subdivided into degree classes of four degree intervals (e.g., 4-7°C, 7-10°C, and so on). Resource selection functions were estimated using observed and random location data within each air temperature class. To be able to compare coefficients of environmental predictors we standardized variables by subtracting the mean and dividing by the standard deviation (Gelman & Hill 2007).

We compared long-term (2002-2011) bison and cattle productivity relative to mean annual temperature and mean annual precipitation (question three). Bison at the Tallgrass Prairie Preserve are weighed individually every November, while cattle are weighed en masse before leaving the preserve. Due to differences in management between bison and cattle from 2002-2007 and different resident and sampling times, we compare relative trends of herbivore productivity rather than absolute productivity. Because of livestock operation procedures (weighed en masse before shipping), we defined herbivore productivity as kg per individual animal. Relationships of productivity with mean annual temperature and mean annual precipitation were examined with linear regression. All analyses were performed in R (R Development Core Team 2012).

Results

Mean monthly air temperature and precipitation varied throughout 2009 to 2011, providing values below and above long-term averages for the site (1994-2011; Fig. 1). During the months of study (April through September), monthly mean air temperature for

2009 was typically below average; means for 2011, however, were above average. 2011 also had decreased precipitation, ranging from 50 to 25% less than long-term averages.

The tallgrass prairie thermal environment differed primarily between vegetation types. Black bulb temperature increased linearly with air temperature for both herbaceous and woody vegetation (Fig. 2A). Within woody vegetation, however, black bulb temperature increased less than herbaceous vegetation (no overlap of 95% confidence intervals) resulting in a cooler thermal environment at higher air temperatures. This was particularly noticeable during the warmest parts of the day (Fig. 2B). The amount of time since an area had been burned did not significantly influence black bulb temperature within herbaceous or woody vegetation ($p > 0.05$).

GPS collars deployed on bison and cattle collected approximately 500,000 locations over three years. Collar temperature (as observed within the collar housing) closely tracked air temperature but deviated from a one-to-one relationship and differed between the two species (Table 1). As these relationships are simply dependent upon collar and air temperature, the changing of physical location by animals likely altered collar temperature and caused deviations. The slope coefficient for cattle was smaller than bison (no overlap of 95% confidence intervals) and resulted in slightly cooler collar temperatures at warmer air temperatures. We recognize that the magnitude of difference between bison and cattle is not large, but that it still indicates a behavioral difference in response to temperature.

Resource selection functions indicated that environmental factors time since fire, distance to water, and distance to woody vegetation influenced the probability of use for both bison and cattle (Table 2). Time since fire and distance to woody vegetation had the greatest influence on site selection, consistent with other studies (Allred et al. 2011b). An interaction with air temperature was present with all model parameters, indicating that animal selection preferences varied according to air temperature. Resource selection functions were re-estimated at varying temperature classes to show patterns and probability of use with temperature (Figs. 3 and 4).

In general, the preference for recently burned areas did not change with increasing temperature for bison or cattle. Both species continued to prefer recently burned areas over areas with greater time since fire. The selection of areas closer to water, however, did increase and became stronger as air temperature rose. By approximately 26°C, both bison and cattle began to prefer areas closer to water; by 38°C that preference had increased almost ten fold. Preferences for woody vegetation also changed in regard to temperature. Site selection by bison and cattle was only limited by distance to woody vegetation in warmer temperatures. The preference of cattle to be closer to woody vegetation appeared at approximately 26°C and continued to strengthen as temperature increased. Woody vegetation did not influence bison behavior until the warmest temperatures, around 38°C. The probability of bison use increased with distance to woody vegetation for all but the warmest temperatures (Fig. 4C).

Bison and cattle productivity varied between 2002 and 2011 (Supplementary information). Due to differing management strategies prior to 2008 and differing sampling periods, only relative trends within species can be evaluated. Bison productivity did not correlate with mean annual temperature or mean annual precipitation. Cattle productivity, however, increased with mean annual precipitation ($p < 0.05$; Fig. 5) but did not correlate to mean annual temperature.

Discussion

Understanding the effect of climate change on ecosystem processes is important for the future conservation of ecosystem goods and services. While there are many experiments that manipulate CO_2, temperature, or precipitation in grasslands, these often examine grazing mechanisms, (e.g., forage quality or quantity), effects of grazing, or exclude grazing altogether, while others examine how changes in climate will affect grazer performance (Craine et al. 2012). Asking 'how will changes in climate affect grazing?' is a different question altogether, and is difficult to answer due to the many components involved. Understanding behavior is critical as it influences the spatiality of grazing intensity and subsequent effects. We discuss the implications of the altered behavior of the native bison (*Bison bison*) and introduced cattle (*Bos taurus*) with regard to temperature in a tallgrass prairie ecosystem.

The reaction of herbivores to increased temperature and heat stress will vary by species (or breed), geographic location, life stage, and nutritional requirements. In tallgrass prairie, both bison and cattle maximized their distance to water (i.e., selected sites away from water; cattle more so than bison) at lower air temperatures (4-24°C). At approximately 26°C, both species switched preferences and began to select sites closer to water as temperature increased. With exception of the hottest temperatures, cattle preferred areas closer to water more than bison. Predicted future daytime July temperatures for the Tallgrass Prairie Preserve varied between ~30°C and 36°C (Table 3), indicating that bison and cattle will continue to prefer areas closer to water as warming occurs. These preferences occurred in a grassland landscape where water is not limited, and will likely be even more pronounced in arid or semiarid grassland and rangelands where distance between water sources is greater.

Vegetation and ecosystem changes are likely to result as grazing animals choose areas closer to water sources. Grazing within riparian areas or areas near water reduces herbaceous cover, biomass, and productivity of vegetation (Kauffman et al. 1983; Clary 1995; Belsky et al. 1999; DelCurto et al. 2005). The concentration of grazing animals around water sources also increases nutrient concentration and becomes a source of nonpoint source pollution (Pell 1997; Belsky et al. 1999; Ballard & Krueger 2005). Predicted warming increases of 2.0 to 2.5°C in mean annual temperature (IPCC 2007) or 1.5 to 8.23°C in July daytime temperature (Table 3) for the area suggest that animals will continue to select sites closer to water, regardless of origin (native or introduced). Native bison may provide a small advantage in preventing riparian degradation and nonpoint source pollution due to grazing in increased temperatures, but it is important to note that introduced cattle may provide a similar advantage at cooler temperatures, as they tended to stay further from water sources.

Many riparian areas offer both water and shade from solar radiation to grazing animals. Animals, particularly cattle, have been documented to gather in these areas to hydrate and maintain thermoregulation (Bailey 2005). In tallgrass prairies, woody vegetation can provide a significantly cooler thermal environment than herbaceous grassland, decreasing by 2°C in the morning and evening hours, and up to 16°C in the heat of the day. Unlike preferences for water, there is a clear distinction in preference for woody vegetation between bison and cattle. Cattle stay away from woody vegetation at lower temperatures (4-24°C), but switch preferences at higher temperatures and select areas closer to woody vegetation. In contrast, bison have greater avoidance of woody vegetation and do not select areas closer to woody vegetation until the hottest temperatures (36-39°C). Even in these hot conditions, bison prefer woody vegetation less than cattle. It is less likely that bison will graze or rest in wooded areas and therefore minimize impact. Cattle, however, are attracted to such areas, and predicted warming for the southern Great Plains (Table 3) will result in greater selection of woody vegetation. This attraction will be augmented if areas with woody vegetation contain water, increasing the potential for degraded water quality and bank stability (Trimble & Mendel 1995; Belsky & Blumenthal 1997). The use of native bison in place of introduced livestock may be able to mitigate or lesson some of these adverse behavioral effects caused by increased temperature.

Animal productivity varied among years, but was not dependent upon mean annual temperature, and only cattle productivity correlated with mean annual precipitation. While animal behavior can contribute to productivity, it follows other important ecosystem characteristics, namely plant productivity and quality. Animal body mass is driven primarily by the energy and protein content of forage, and the ability to store such within the body (Owen-Smith 2002). These forage characteristics will often vary in space and time, creating heterogeneity of forage resources (Fynn 2012). Deviations in productivity or weight gain due to temperature and precipitation changes may be mitigated by broad landscapes and ‘free ranging’ livestock management, both present at the Tallgrass Prairie Preserve. Changes or trends in productivity may have been tempered by the fact animals had greater availability of resources to select from and were allowed to adapt foraging patterns and preferences to resource variability. Furthermore, mean annual climate characteristics may not be the most suitable metric for examining animal productivity. Craine et al. (2009) found that bison performance was dependent upon the timing of precipitation throughout the year. Early growing season precipitation led to decreased weight gain, while late growing season precipitation increased weight gain. Further study is needed to determine the patterns of climate with bison and cattle productivity, including examination of appropriate climatic variables (annual or monthly means, etc.) and the variability of climatic events.

The management of cattle within this study is representative of that throughout the southern Great Plains. In particular, European cattle breeds (e.g., Black angus, Hereford, etc.) are common for livestock operations. These breeds originated from *Bos taurus* and have less thermoregulatory capability than the other primary species *Bos indicus* (Hansen 2004), which includes Zebu and Brahman breeds. Breeds within both species are likely to alter their behavior differently to changes in temperature. Breeds that are accustomed to greater temperatures or more arid regions (e.g., Brahmans) will likely perform more similar to bison with increasing temperature than those that are not. Examining differing cattle breeds and incorporating appropriate breeds into conservation and commercial practices will help with conservation goals and mitigate results due to climate change (Rook et al. 2004).

The presence of bison throughout the Great Plains is primarily due to a) the intent to restore native ecological processes and disturbances to North American grasslands and

b) their use as an agricultural commodity, i.e. meat production. Bison are labeled a keystone species of the Great Plains due to their ability to increase heterogeneity, increase biodiversity, and alter nutrient cycling processes through grazing and general disturbance patterns (Knapp et al. 1999). Academic research groups, federal agencies, nongovernmental organizations, and prairie enthusiasts often promote or restore bison for this very purpose (Manning 1995; Reynolds et al. 2003; Sanderson et al. 2008; National Park Service 2009). While such work is valuable and does help achieve conservation goals, it is important to recognize that bison (perhaps specifically bison grazing) are just one component of the restoration of ecological processes. In particular, they are just one ungulate species. Many other factors, including landscape diversity, additional disturbance regimes (i.e., fire), and diversity of flora and fauna contribute significantly to overall conservation value (Allred et al. 2011b). These grassland characteristics should be considered equal to and alongside the discussion of native versus introduced herbivores.

An increasing demand for bison meat has resulted in greater use of bison for agricultural purposes (Joseph et al. 2010). There are twenty times more bison individuals in commercial livestock herds than in conservation herds (Gates et al. 2010). While these animals contribute to species conservation, the potential for ecosystem conservation or restoration is low. Many of these animals (though not all) are intensively managed in simplified livestock operations (e.g., feedlots, small pastures, homogenous landscapes, etc.) that do not incorporate other factors critical to ecosystem conservation. When such management is present, discussions of the behavior and effects of native versus introduced herbivores for conservation purposes (as in this paper) become a low priority

(Allred et al. 2011b). Management unrelated to species must be taken in order to improve conservation value.

Given the large amounts of privately owned land, the vast number of cattle present, and the economic industry of cattle ranching, the success of large native herbivores in United States grasslands is inherently linked to commercial livestock operations. Cultural, social, and economical barriers exist that limit desire, incentive, and opportunity for landowners to replace introduced cattle with native herbivores (Freese et al. 2007). Though we present the similarities and differences, as well as potential advantages and disadvantages for using native bison or introduced cattle in a changing climate, the odds of livestock owners changing from one species to another, or a change in overall land management strategy, is unlikely due to the present barriers. Examining the dynamics and mechanisms of these barriers is required to better understand the motivations necessary for ecosystem conservation. More importantly, improved communication, cooperation, and outreach are essential in order to inform landowners, agricultural organizations, and conservation agencies of conservation priorities and strategies.

Because of their dominant impact on grasslands, understanding how herbivores alter behavior in response to climatic events is necessary to realize the full effects of climate change. In the tallgrass prairies of the Great Plains, native bison and introduced cattle respond similarly in many ways to increasing temperature. Small differences exist, however, that may potentially affect conservation efforts within this endangered ecosystem, particularly in regard to riparian areas and water sources. The use of bison may mitigate adverse effects of overgrazing or loitering in or near riparian areas as air temperatures increase. Additionally, the restoration of native bison along with other native grassland properties (e.g., fire, broad landscapes, biodiversity) will improve overall conservation value. Though bison are commonly used for conservation purposes (as well as small commercial livestock operations) and cattle for large commercial livestock operations, it is important to point out that these are interchangeable, i.e. bison for commercial purposes and cattle for conservation purposes. Recognizing that the commercial cattle industry is a dominant feature of the Great Plains, and developing or employing conservation practices compatible with livestock operations are the first steps to broad scale conservation in the face of climate change.

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Tables

Table 1

Linear regression coefficients from relationships of GPS collar and air temperature (*Tair*) for native bison (*Bison bison*) and introduced cattle (*Bos taurus*) at the Tallgrass Prairie Preserve, USA. Collar temperature of both species tracked air temperature, but cattle collar temperatures deviated more than bison. Asterisks (*) indicate significance at $p < 0.05$. 95% confidence intervals for air temperature did not overlap between species.

Species	*Tair*	*Intercept*
Bison	0.96*	2.85*
Cattle	0.90*	4.37*

Table 2

Estimated resource selection coefficients for native bison (*Bison bison*) and introduced cattle (*Bos taurus*) at the Tallgrass Prairie Preserve, USA. Model parameters include time since fire (TSF), distance to water (Water), distance to woody vegetation (Woody), air temperature (Tair) and interactions with air temperature. Standardized variables are shown for coefficient comparison.

Specie	*TSF*	*Water*	*Wood*	*Tai*	*TSF×Tai*	*Water×Tai*	*Woody×Tai*	*Intercep*
Bison	-	-	0.046	0.0	-0.005*	-0.022*	-0.011*	0.249*
Cattle	-	-	-	0.0	-0.003*	-0.034*	-0.016*	0.248*

* $p < 0.005$

Table 3

Predicted mean July daytime (0600-2100 hours) temperature (°C) by mid century (2050) and end of century (2080) for low, medium, and high emissions scenarios at the Tallgrass Prairie Preserve, USA. Temperature increases vary by general circulation model. Temperature increase data retrieved from the ClimateWizard (Girvetz et al. 2009) and added to base mean July daytime temperature (28.11°C).

	Mid century (2050s)			End century (2080s)		
Model	Low	Medium	High	Low	Medium	High
CGCM3.1(T47)[a]	29.66	30.58	31.14	30.49	31.04	33.03
CSIRO-Mk3.0[b]	29.96	30.06	30.34	29.84	31.71	32.07
GISS-ER[c]	29.99	30.05	30.99	30.60	31.21	32.49
ECHAM5/MPI-	30.24	30.79	30.58	30.82	32.42	32.19
CCSM3[e]	30.59	31.48	31.43	30.18	32.10	34.05
UKMO-HadCM3[f]	32.48	33.15	32.88	33.14	34.65	36.34

[a] Canadian Centre for Climate Modeling and Analysis

[b] CSIRO Atmospheric Research

[c] NASA / Goddard Institute for Space Studies

[d] Max Planck Institute for Meteorology

[e] National Center for Atmospheric Research

[f] Hadley Centre for Climate Prediction and Research

Figures

Figure 1

Monthly climate dynamics at the Tallgrass Prairie Preserve, USA. Bars represent long-term averages (±SE; 1994-2011) while points represent specific years. A) Mean monthly air temperature and B) monthly precipitation.

Figure 2

Thermal representation of a tallgrass prairie ecosystem. Black bulb temperature as a function of A) air temperature (*Tair*) separated by vegetation type, herbaceous ($\hat{y} = 1.91 Tair - 22.33$; $r^2 = 0.72$, $p < 0.05$) and woody ($\hat{y} = 1.13 Tair - 3.45$; $r^2 = 0.84$, $p < 0.05$) and B) hour of day. Values are averaged over summer sampling periods. Black bulb temperature is relatively more stable in woody than herbaceous vegetation. Woody vegetation is also significantly cooler at warmer air temperatures and during the heat of the day.

Figure 3

Resource selection coefficients at varying air temperature classes for native bison (*Bison bison*) and introduced cattle (*Bos taurus*) at the Tallgrass Prairie Preserve, USA for environmental factors time since fire (TSF), distance to water (Water), and distance to woody vegetation (Woody). Standardized variables are shown for coefficient comparison. Text on right indicates the direction or preference of selection, e.g. animals prefer areas that are more recently burned or that are closer to water. The crossing of the horizontal line at 0.00 indicates a change in preference. One resource selection function was estimated per animal species per temperature class. Note scale differences for each graph.

Figure 4

Probability of use relative to selected air temperatures (differing lines; 4, 12, 20, 28, and 36°C) for A) time since fire, B) distance to water, and C) distance to woody vegetation as predicted by resource selection functions for native bison (*Bison bison*) and introduced cattle (*Bos taurus*) at the Tallgrass Prairie Preserve, USA. Air temperature has little effect on the influence of time since fire for both species, but heavily impacts the probability of use as related to distance to water and woody vegetation.

Figure 5

Mean herbivore productivity (kg per individual animal) of native bison (*Bison bison*) and introduced cattle (*Bos taurus*) at the Tallgrass Prairie Preserve, USA relative to mean annual temperature (MAT) and mean annual precipitation (MAP) for 2002 through 2011. Due to differences in management between bison and cattle from 2002-2007 and different resident and sampling times, we defined productivity as kg per individual and compared relative trends of herbivore productivity rather than absolute. Cattle productivity increased with MAP (dashed lined; $\hat{y} = 0.07MAP - 324.46$; $r^2 = 0.42$, $p < 0.05$). No other trends of productivity were significant ($p > 0.05$).

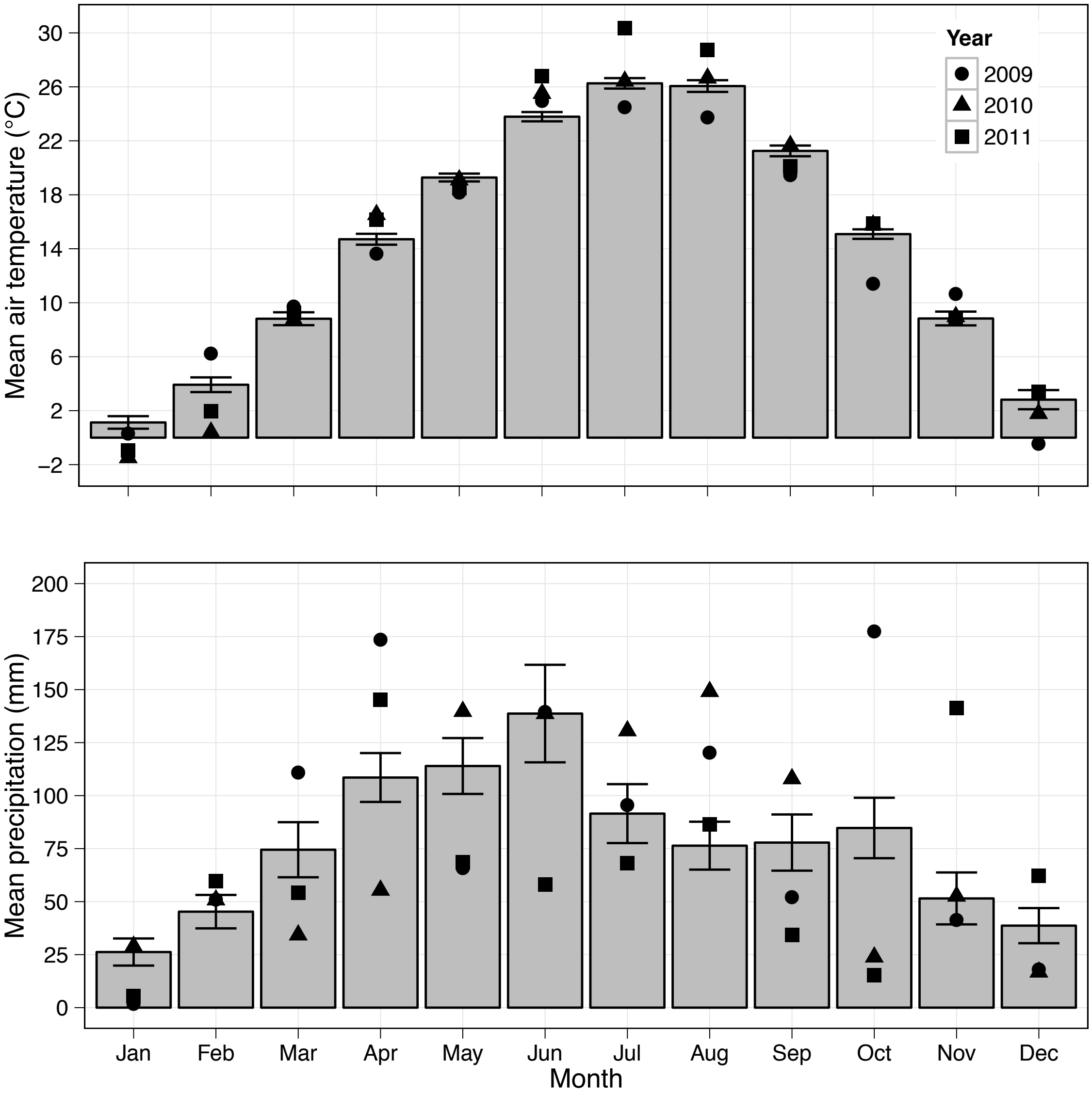
Mean air temperature (°C)
30
26
22
18
14
10
6
2
−2
Year
● 2009
▲ 2010
■ 2011
Mean precipitation (mm)
200
175
150
125
100
75
50
25
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

Figure 1

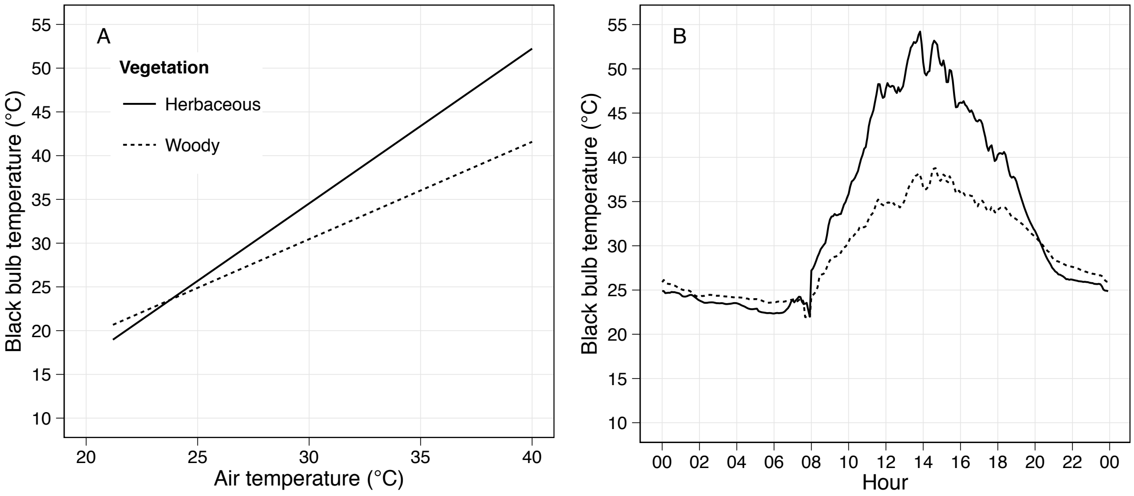
A
Vegetation
Herbaceous
Woody
Black bulb temperature (°C)
55
50
45
40
35
30
25
20
15
10
20
25
30
35
40
Air temperature (°C)
B
Black bulb temperature (°C)
00
02
04
06
08
10
12
14
16
18
20
22
00
Hour

Figure 2

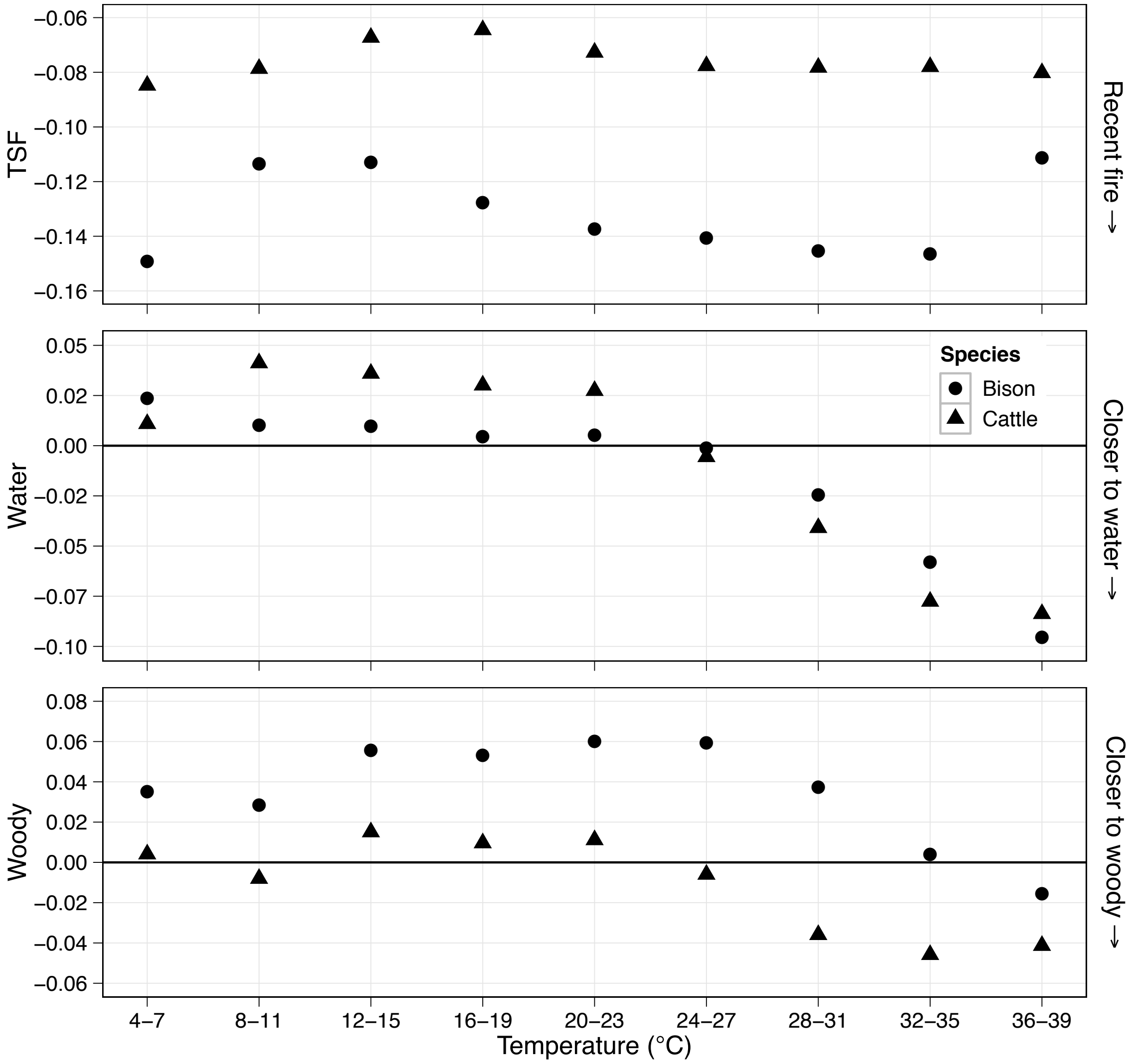
TSF
−0.06
−0.08
−0.10
−0.12
−0.14
−0.16
Recent fire →
Water
0.05
0.02
0.00
−0.02
−0.05
−0.07
−0.10
Closer to water →
Species
● Bison
▲ Cattle
Woody
0.08
0.06
0.04
0.02
0.00
−0.02
−0.04
−0.06
Closer to woody →
4−7
8−11
12−15
16−19
20−23
24−27
28−31
32−35
36−39
Temperature (°C)

Figure 3

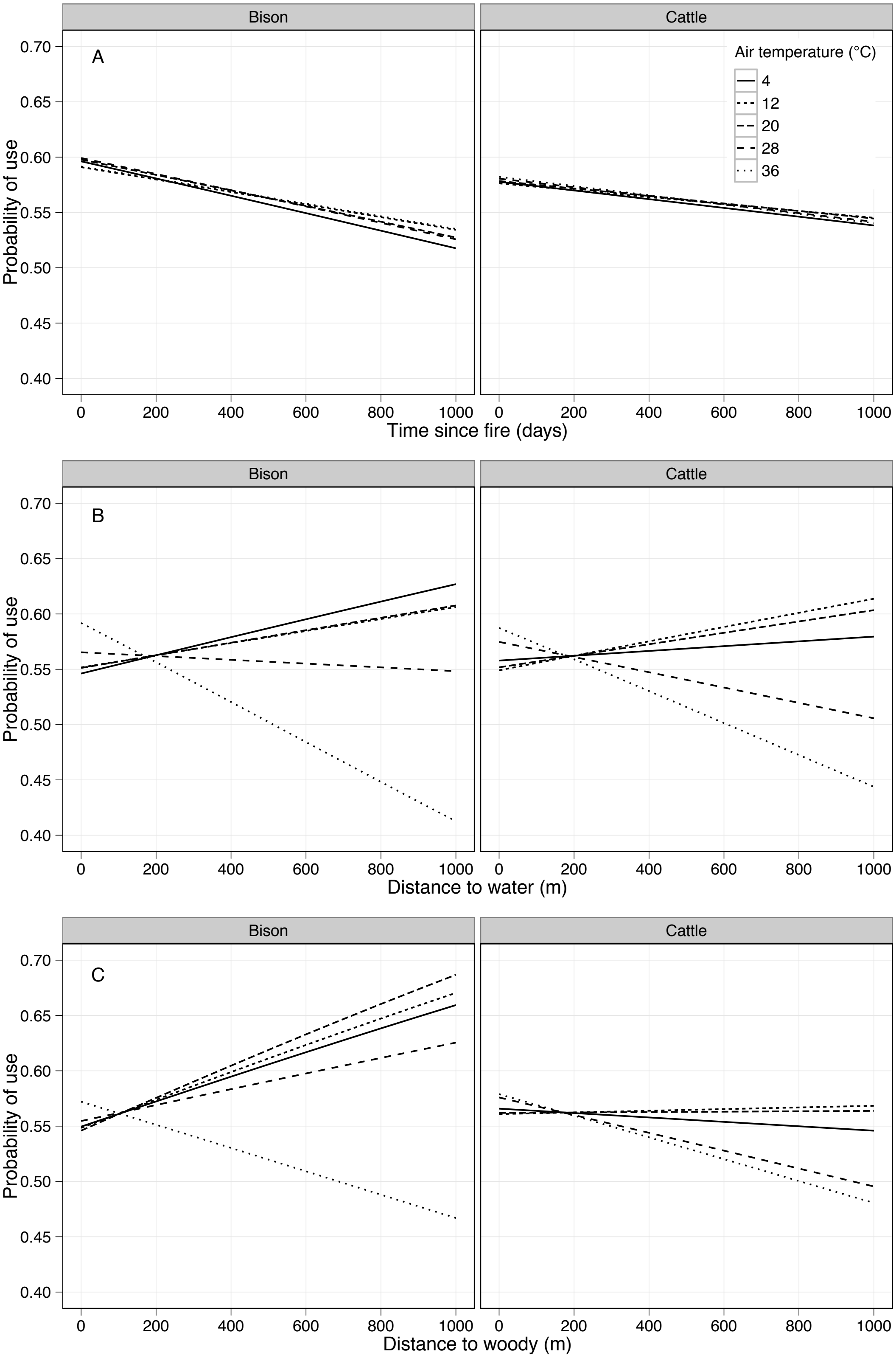
Bison
Cattle
A
B
C
Air temperature (°C)
4
12
20
28
36
Probability of use
0.70
0.65
0.60
0.55
0.50
0.45
0.40
0
200
400
600
800
1000
Time since fire (days)
Distance to water (m)
Distance to woody (m)

Figure 4

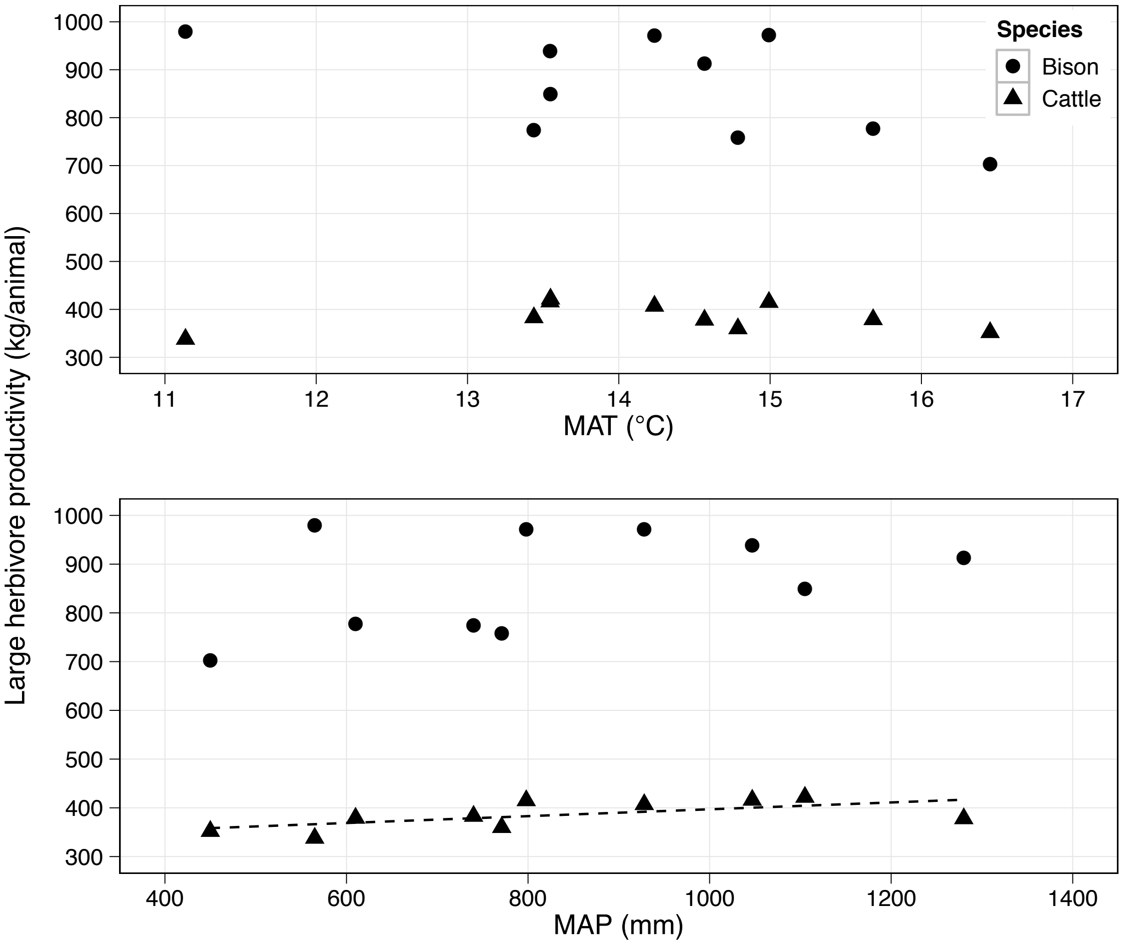
Large herbivore productivity (kg/animal)
1000
900
800
700
600
500
400
300
11
12
13
14
15
16
17
MAT (°C)
Species
● Bison
▲ Cattle
1000
900
800
700
600
500
400
300
400
600
800
1000
1200
1400
MAP (mm)

Figure 5

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