THE INFLUENCE OF FIRE AND GRAZING ON TALLGRASS PRAIRIE STREAMS AND HERPETOFAUNA

by

DANELLE MARIE LARSON

B.A., University of Idaho, 2010

AN ABSTRACT OF A DISSERTATION

submitted in partial fulfillment of the requirements for the degree

DOCTOR OF PHILOSOPHY

Division of Biology
College of Arts and Sciences

KANSAS STATE UNIVERSITY
Manhattan, Kansas

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Abstract

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This dissertation examined how prescribed burning, bison grazing, and patch-burn grazing (by cattle) influence water quality, stream biota, and riparian amphibians and reptiles at Konza Prairie, Kansas, or Osage Prairie, Missouri. Using Global Positioning System, we monitored bison and cattle distribution throughout watersheds. The immediate effects of prescribed burning were examined at both Konza and Osage Prairies. The impacts of bison on water quality were determined by using a long-term dataset from Konza Prairie and compared watersheds with and without bison. Amphibian and reptile assemblages were monitored for two years at Osage, and assemblage data were analyzed using redundancy analysis, permuted analysis of variance, and occupancy modeling. A patch-burn grazing experiment occurred for 5 years at Osage (2 years pretreatment data and 3 years of treatments) and was analyzed using a before-after, control-impact design.

Prescribed burning had minimal effects on water chemistry. At Konza Prairie, bison did not alter water quality likely because they spent negligible time (<5%) in streams. Contrarily, cattle at Osage Prairie significantly increased stream concentrations of total suspended solids, nutrients, *Escherichia coli* bacteria, algal biomass, and primary production. Unlike bison, cattle spent significant time (~21%) in streams if allowed access to riparian zones. In watersheds with cattle excluded from streams by riparian fencing, water quality contaminant concentrations increased significantly, but not to the magnitude of unfenced streams. Amphibian abundance and richness were not different among patch types; instead, they were restricted to specific basins. However, reptiles displayed preference for certain patch-types, and had the highest abundance and richness in watersheds with fire and grazing.

These results have implications for natural resource management. Riparian fencing of cattle may be a useful practice in areas where water resource protection is the priority. However, overland flow may alter water quality in watersheds with grazers despite fencing. Land managers will need to define management objectives and accept trade-offs in water quality, amphibian and reptile habitat, and cattle production.

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List of Symbols

S: species richness

Ψ: occupancy probability

p: detection probability

γ: local recolonization

ε: local extinction

List of Abbreviations

EPT: Ephemeroptera, Plecoptera, and Trichoptera

CR: community respiration

GPP: gross primary production

NEP: net ecosystem production

BOM: benthic organic matter

CPOM: coarse particulate organic matter

FPOM: fine particulate organic matter

VFPOM: very fine particulate organic matter

TSS: total suspended solids

ISS: inorganic suspended solids

VSS: volatile suspended solids

GPS: Global positioning system

Comp: Principal Component

PBG: patch-burn grazing

RDA: redundancy analysis

PERMANOVA: permuted analysis of variance

KPBS: Konza Prairie Biological Station

BACIP: before-after, control-impact design with samples paired in time

Chapter 1 - Introduction

The case for more watershed science

Streams are fundamental for the survival of many species, including humans. They are critical habitat for many organisms, and an essential commodity for human health and prosperity. In particular, functioning headwater streams have the capacity to retain sediments and nutrients and also control downstream export (Peterson et al. 2001) and improve water quality. Running waters are unique aquatic habitats in that they are unidirectional and linear, greatly variable in space and time, and are open ecosystems that are closely linked to the surrounding landscape (Giller and Malmqvist 1998).

Terrestrial-aquatic linkages are strong for most stream networks. Streams are situated on the lowest landscape position, buffered by an adjacent riparian habitat, and encompassed by terrestrial landscape. As such, headwater streams will receive water, sediments, nutrients, and contaminants from the land if not intercepted by vegetation or soil (Giller and Malmqvist 1998). Land management decisions will ultimately dictate the state of flowing waters, and therefore lotic ecosystem management is best approached at the landscape scale (Fausch et al. 2002).

Ecological studies at the watershed-scale have greatly expanded our understanding of the intimate connection between land and streams (e.g., Likens et al. 1970, Webster and Patten 1979, Dodds et al. 1996, Beschta et al. 2000, Dodds and Oakes 2006). Similar studies also hint at the importance of riparian areas in regulating physiochemical properties of streams (e.g., Cooper et al. 1987, Lowrance et al. 1997, Naiman 2010). However, the fate of substances entering the stream is not always clear because riparian areas can dilute, concentrate, or modify those substances (Osborne and Kovacic 1993), so more studies are needed for predictive power of riparian function. However, few studies at the watershed scale exist because of the difficulty of dedicating entire basins and riparian areas towards a controlled, experimental design.

Despite the many large-scale studies regarding stream impacts from fire and livestock (e.g., review by Kauffman and Krueger 1984), the results are confounded or unclear because most studies addressing this topic lack explicit experimental designs and appropriate control sites (Sarr 2002, Rinne 1988). For example, some studies monitored streams with riparian exclosures as the reference/control site, despite the lack of research demonstrating the effectiveness of cattle exclusion or the capacity of the riparian area to buffer changes in water quality. Studies are needed that have an explicit experimental design at a watershed scale to test in-stream effects of fire, cattle grazing, and riparian exclusion of grazers.

Tallgrass prairie watershed science

The widespread alterations to the landscape and riparian areas across central North America have strongly influenced tallgrass prairie streams. Tallgrass prairie is a large and endangered grassland biome of North America (Fig 1.1). Tallgrass prairie streams are even more endangered because intact watersheds only exist where large tracts of prairie remain (Dodds et al. 2004). The majority of this grassland type was converted to row-crop agriculture (Samson and Knopf 1994). Further, grasslands worldwide have experienced riparian woody encroachment due to changes in fire-grazer interactions in the past century (Briggs et al. 2005).

Because native tallgrass prairie streams are rare, their ecological study is somewhat limited. Kings Creek on Konza Prairie in Kansas could be considered a model for native tallgrass prairie stream networks because it has been intensively studied (e.g., Whiles and Dodds 2002, Dodds et al. 2004, Franssen et al. 2006, Bertrand et al. 2009, Daniels and Grudzinski 2011).

However, tallgrass prairie extends across strong precipitation and geological gradients, which are likely to affect stream characteristics. We are in need of characterizing other tallgrass prairie streams outside of Konza Prairie to have a more comprehensive understanding of native grassland streams. Further, the data provided by quantifying tallgrass prairie stream characteristics could assist states with establishing water quality criteria to be in compliance with the Clean Water Act and help guide land management.

In tallgrass prairie, there is expressed local interest in comparing the effects of bison versus cattle grazing on water quality. In the Great Plains of North America, prairies evolved with bison (*Bison bison*), but by 1830 the species was near extinction because of hunting (Flores 1991, Shaw and Lee 1997). Today, domesticated cattle (*Bos taurus*) replace bison as the dominant grazers in tallgrass prairies. Bison might not cause water quality changes because they require less water than cattle, are able to tolerate summer temperatures, and avoid woody riparian areas (e.g., Plumb and Dodd 1993, Allred et al. 2011). Alternatively, bison behaviors such as grazing, foraging, traversing, wallowing, and pawing, could increase sediment and nutrient loads to streams. These propositions require testing by examining water quality and animal behavior in tallgrass prairie watersheds.

Herpetofauna need guardians

Herpetofauna (a taxonomic grouping of amphibians and reptiles) are fairly diverse in tallgrass prairies and regularly experience fire and grazing. Globally, these organisms are under threat of extinction from multiple stressors, particularly habitat loss and alterations. Further, we are data deficient in understanding many population declines (Stuart et al. 2004, Böhm et al. 2013). The herpetofauna strongly associated with aquatic habitats are usually the most vulnerable taxa (Stuart et al. 2004, Böhm et al. 2013). Herpetofauna in tallgrass prairie has suffered severe habitat loss from row-crop agriculture in the last century. The last native prairie refuges for these organisms routinely undergo prescribed fire and grazing, yet we lack information to understand how these practices impact animal assemblages and dispersal. Lastly, riparian zones and streams are crucial habitat for herpetofauna, so we need an understanding of how grazing pressures can alter vegetation structures and water quality that these organisms rely on.

Dissertation outline

The theme of this dissertation examines how the dominant land management practices in tallgrass prairie (i.e. prescribed burning and grazing by bison or cattle) impact water quality and aquatic organisms. Chapter 2 characterizes tallgrass prairie streams along a precipitation gradient using 3-year datasets from Konza Prairie and Osage Prairie (Larson et al. 2013a). Chapter 3 used a 5-year dataset from Konza Prairie to compare water quality in streams with and without bison, examine riparian usage by bison, and separately examined effects of prescribed fire on streams (Larson et al. 2013b). Chapter 4 consisted of an original 2-year dataset at Osage Prairie to capture the responses (i.e., abundance, species richness, and dispersal dynamics) of reptiles and amphibians to fire and grazing. Chapter 5 used a 5-year dataset to examine the effects of patch-burn grazing management on prairie streams, and quantify the importance of riparian fencing in mitigating potentially negative impacts. Chapter 6 contains concluding ideas, which synthesizes the major findings, explains how this research advances the field of aquatic ecology, and provides important information for prairie land management. This dissertation was developed with multiple collaborators and therefore is written in third-person. The citations for published works are provided on each Chapter title page and in the References section.

Figures

Figure 1.1 Map of historical range of tallgrass prairie within the USA. Konza Prairie Biological Station (Konza) and Osage Prairie Natural Area (Osage) are two remaining native tallgrass prairie swatches where this dissertation research was conducted.

Chapter 2 - Ecosystem characteristics of remnant, headwater tallgrass prairie streams

Larson DM, Dodds WK, Jackson K, Whiles MR, Winders KR. (2013) Ecosystem characteristics of remnant, headwater tallgrass prairie streams. *Journal of Environmental Quality* 42, 239-249.

Abstract

North America has lost more than 95% of its native tallgrass prairie due to land conversion, making prairie streams one of the most endangered ecosystems. Research on the basic ecosystem characteristics of remaining natural prairie streams will inform conservation and management. We examined the structure and function of headwater streams draining tallgrass prairie tracts at Osage Prairie in Missouri and the Konza Prairie Biological Station in Kansas, and compared those values to literature values for streams draining agricultural watersheds in the region. We quantified physicochemical and biological characteristics for 2 years. Streams at Osage and Konza were characterized by low nutrients and low suspended sediments (substantially lower than impacted sites in the region), slight heterotrophic status, and high temporal variability. Suspended sediments and nutrient concentrations were generally low in all prairie streams, but storms increased concentrations of both by 3 - 12 fold. Spring prescribed burns were followed by a slight increase in chlorophyll *a* and decreased nutrients, potentially due to greater light availability. Benthic macroinvertebrate communities at Osage showed seasonal patterns that were likely linked to variable hydrology. We found nine amphibian species using the Osage streams as habitat and/or breeding sites, but little usage at Konza likely due to dry conditions and low discharge. Our study indicates that two remnant tallgrass prairie streams along a longitudinal gradient are fairly similar in terms of physicochemical features and have good water quality relative to agricultural watersheds, but can differ considerably in macroinvertebrate and amphibian abundance.

Introduction

Tallgrass prairie and its streams are highly endangered ecosystems; most tallgrasses were plowed and converted to row crop agriculture over a century ago. Nearly all large tracts of remaining tallgrass prairie are currently maintained as pasture with cattle grazing and yearly burning. Where fire has been suppressed, woody vegetation is expanding into tallgrass prairie (Knight et al. 1994), potentially converting open canopy streams that characterize these grasslands to shaded, forested systems. Few open canopy tallgrass prairie streams with watersheds in their natural condition remain and little is known about characteristics of water quality, productivity, and community structure of these remaining systems. Tallgrass prairie streams are understudied, except at the Konza Prairie Biological Station (Konza) in Kansas (e.g., Gray et al. 1998, Dodds et al. 2004, Bernot et al. 2010). Konza lies at the far western range of tallgrass prairie; much less is known about streams in more mesic, eastern regions where a substantial portion of tallgrass prairie occurred historically (e.g., Iowa, Illinois, Missouri), and even less intact prairie remains.

Intermittent streams occur worldwide and are often characteristic of grasslands (Dodds et al. 2004). Hydrologic disturbances, including frequent drying and flooding, are important structuring components of many grassland streams (Lake 2000). Despite frequent and sometimes extreme hydrologic disturbance, these systems show high biological resilience; within days after resumption of flow or after scouring, they are re-colonized by microbes, then invertebrates, and finally vertebrates (Murdock et al. 2010, 2011).

Fire is a natural and critical process in tallgrass prairie, with historic fire intervals of 2-10 years (Abrams 1985). Fires influence stream characteristics in forest and shrub regions (Minshall et al. 1997, de Koff et al. 2006, Smith et al. 2010), however, we know less about how fire affects tallgrass prairie streams. Fire can remove ground cover leading to increased overland flow and soil erosion (Jordan et al. 2004), perhaps depositing sediments into the waterways. Total nitrogen (TN) and nitrate (NO_3^-) concentrations in Konza tallgrass prairie streams can increase both as a function of number of days and years following fire (Dodds et al. 1996). However, impacts of fire on sediment and nutrient inputs have not been characterized elsewhere.

Macroinvertebrate communities in tallgrass prairie streams are also relatively poorly studied, with most published information from streams on Konza. Tallgrass prairie stream hydrology is highly variable (Gray et al. 1998, Dodds et al. 2004), and because of frequent floods and droughts, many macroinvertebrates that inhabit them are resistant and/or resilient to natural disturbances (Fritz and Dodds 2004). Adaptations include short life cycles, seasonal reproduction, and behavioral avoidance (Gray 1981). Stream macroinvertebrate communities on Konza are moderately diverse and highly variable in space and time (e.g., Gray et al. 1998, Stagliano and Whiles 2002). Macroinvertebrate community composition in Konza streams is influenced by canopy cover (shading and leaf input), suggesting that management practices that alter riparian vegetation, such as fire and grazing (or lack thereof) will influence community structure (Whiting et al 2011) and that prairie streams are fundamentally different from forest streams. Further studies in other regions of the tallgrass prairie are needed to test generalities based on Konza and develop regional baselines and targets for assessment, management, and restoration.

Amphibians can also be abundant in tallgrass prairie streams, with up to 17 species associated with them for at least part of their life cycles (Collins 1993, Johnson 2000). Numerous species associated with tallgrass prairie streams are included in State Wildlife Action Plans as Species of Greatest Conservation Need in Kansas and Missouri. These include the Northern

Cricket Frog (*Acris crepitans*), Spring Peeper (*Pseudacris crucifer*), Green Frog (*Rana clamitans*), and Pickerel Frog (*Rana palustris*) (NBII, 2011). Amphibians are well known as sensitive environmental indicators, and thus a better understanding of native community structure associated with tallgrass prairie streams could be useful for assessing environmental quality.

Objectives

Our objectives were to quantify elements of the structure and function of headwater tallgrass prairie streams and to make general comparisons on physicochemical and biological attributes between and among six streams located at Osage Prairie (Missouri) and three streams at Konza (Kansas). In doing so, we also made larger, regional comparisons with literature-derived water quality data from agricultural streams (converted prairie streams). Given the significance and frequency of fire in the tallgrass prairie, we examined most of our study streams more intensively following spring prescribed burns at both sites.

Methods

Osage streams

The study streams at Osage Prairie Conservation Area are unnamed intermittent tributaries of the Landon Branch in southwestern Missouri, USA (37°44'25.61"N, 94°20'12.17"W; Figure 1). We sampled six streams within a 1.5 km radius of each other. Watershed areas ranged from 10 to 54 ha. Osage Prairie is a 628 hectare remnant prairie owned and managed by the Missouri Department of Conservation and The Nature Conservancy. Soil types of the Osage Prairie consist of Barco loam, Barden silt loam, and Coweta loam (well drained, gently sloping upland soils, Soil Survey Staff 2004). Past land use included haying and cattle grazing from the early 1900's to 1987. Current management consists of mid-summer triennial haying, a prescribed fire interval of 3-5 years, and mechanical removal of riparian trees >10cm diameter. The common management practices of haying, prescribed burning, and tree removal increases wildlife habitat (Kirsch 1974, Swengel 1996), while maintaining grasslands and increasing grass and forb diversity (Soleicki and Toney, 1986). In early April 2011, a prescribed burn was carried out in the lower third of each watershed. We sampled the streams at Osage Prairie from March 2009 through April 2011 once or twice monthly when flowing. We gathered precipitation data from Weather Underground (www.wunderground.com) at the Nevada, MO site (6 mi from Osage) for 3 weeks following fire.

Konza streams

Konza is located in the Flint Hills region of northeastern Kansas, USA and is owned and managed jointly by Kansas State University and The Nature Conservancy (39° 5'55.65"N, 96°36'19.91"W; Figure 1). The three studied watersheds (designated N4D, N2B and Shane) were within 3 km of each other. These watersheds ranged from 78 to 415 ha and have intermittent streams that drain native tallgrass prairie. Ivan soils (4051 Ivan Silt Loam) dominate the floodplains and are characterized as having deep, moderately well drained soil interspersed with rock fragments (Knapp et al. 2008, National Cooperative Soil Survey 2010). Watersheds N2B and N4D are in the Kings Creek basin have been bison grazed since 1987 at approximately 0.21 animal units per hectare. Shane Creek is the watershed north of Kings Creek and was ungrazed for decades before this study. N2B has a burn interval of 2 years, N4D is burned every 4 years, and Shane is burned approximately annually. Shane was burned on 12 April 2011 during our study and we monitored the stream for 3 weeks following the fire. We used rainfall data obtained from a rain gauge stationed at the headquarters of Konza to determine whether rainfall events occurred within the 3 weeks following prescribed prairie fire (raw data can be found at: http://www.konza.ksu.edu). As Konza streams are well studied, our results mostly emphasize the Osage Prairie streams, which are in a region from which few stream studies have been published, to our knowledge. Data for nutrients and sediments at Konza were obtained three times weekly when flowing.

Geomorphology and physicochemistry

We measured and averaged stream widths (to bankfull) and depths using multiple transects 100 m above the water sampling location. Canopy cover was averaged in the upstream 60 m of each reach using a densiometer and stream slope by a clinometer. Watershed areas and stream lengths were delineated using ArcGIS 10.0. Temperature and O_2 were recorded using YSI 6000 probes at 10 minute intervals. Discharge at Osage was measured by measuring dilution of a concentrated solution of KBr pumped at a known rate with an ion-specific Br^- probe (Thermo Orion). At Konza, discharge data were compiled for watersheds N4D and N2B only; measurements were taken at 5 minute intervals at a triangular throated flume, which provided mean daily discharge, maximum and minimum discharge and occurrence times, and total discharge volume for each 24 hour period (raw data can be found at: http://www.konza.ksu.edu).

Chemical properties

We collected water samples for nutrient analyses in acid-washed bottles from the thalweg about 5 cm below the surface and stored at -30ºC until analysis. Additional water collected from the single-stage samplers was used to characterize nutrient concentrations during storm flows. Storm flow is defined as an increase in discharge after a rain event of any amount. Samples were filtered through a glass-fiber filter (Whatman GFF, 0.7 µm retention) and analyzed for nitrate + nitrite ($NO_3^- + NO_2^-$, hereafter refereed to as nitrate), ammonium (NH_4^+), and soluble reactive phosphorus (SRP) concentrations (APHA 1995). Unfiltered stream water was analyzed for total nitrogen (TN) and total phosphorus (TP) concentrations by a persulfate oxidation method (Ameel et al. 1993). Three independent runs were performed using an OI-Analytical Flow Solution IV autoanalyzer to increase accuracy and values were averaged.

Chlorophyll a and ecosystem metabolism

We determined chlorophyll *a* concentrations for 3-5 in situ rocks per stream per sampling date at Osage streams only. Rocks were collected and returned to the laboratory frozen. In the laboratory, whole rocks were extracted with hot 95% ethanol ($79^{\circ}C$ for 5 minutes, followed by 12 h at $4^{\circ}C$, Sartory and Grobbelaar 1984) and extracts were analyzed with a fluorometric technique that avoids interference from phaeophytin (Welschmeyer 1995). Projected surface areas of the rocks were calculated by image analysis to express mass of chlorophyll per unit area.

We estimated whole-stream metabolism using the single station method (Bott 2006) at Osage. Metabolism estimates for Konza were obtained from prior published studies (Bernot et al. 2010, Riley 2011). Photosynthetically active radiation (PAR) was continuously measured using an Odyssey Photosynthetic Irradiance Recording System (Dataflow Systems PTY LTD) in an open area and temperature and O_2 saturation was recorded using YSI 6150 ROX optical O_2 probes at 10 min. intervals (YSI, Inc). The exchange rate of O_2 with the atmosphere was estimated based on O_2 saturation and single station reaeration rates determined from the decline in SF_6 concentration within the study stream reaches (60 m) during baseflow (Mulholland et al. 2001). We measured SF_6 concentration and peak area using a Shimadzu gas chromatograph GC-2014 with an electron capture detector. Reaeration rates of SF_6 were calculated as the difference between the natural log transformations of the mean SF_6 peak areas after correction for dilution indicated by the rhodamine WT dye concentration (Hauer and Lamberti 2006). Reaeration rates of SF_6 were converted to O_2 using a conversion factor of 1.345 (MacIntyre et al. 1995). If the direct measurement of aeration did not work due to missing samples or analytical errors, we modeled aeration (Riley 2011).

We modeled stream metabolism based on measured PAR, O_2, water temperature, barometric pressure, and air-water exchange rate of O_2 (aeration). We used a modeling approach to estimate community respiration (CR) and gross primary production (GPP) rates in each stream (Riley 2011). We used light to scale GPP rates, and made both CR and GPP rates dependent upon in-stream temperature. The “Solver” option in Excel found values for GPP and CR that minimized the sum of square of errors between the observed and modeled O_2 concentrations.

Suspended sediments

We collected water samples for baseflow total suspended solids (TSS) concentration analyses in acid-washed bottles from the thalweg when flowing. TSS water samples were filtered through pre-combusted (24-h at 475°C), pre-weighed glass-fiber filters (GFC Whatman, 1.2 µm retention) within 24 hours. Filters with retained material were dried at 60°C and ashed to 475°C (6 h) and re-weighed to find the amount of inorganic suspended solids (ISS) and volatile suspended solids (VSS) (APHA 1995). Analyses confirmed that wetting and re-drying was not necessary to obtain constant mass in these samples. Sampling for TSS was targeted for storm events using single-stage, US U-59B samplers which filled via siphoning for water collection during high flows (Ford 2007). These samples were retrieved within 2 days after high discharge and processed as above.

Benthic organic matter and macroinvertebrates

We collected macroinvertebrate and benthic organic matter samples from Osage Prairie once each season during the fall (September-November), winter (December-February), and spring (March-May) in 2009 to 2011 (n=9 sampling dates). Samples were collected from haphazardly choosen riffle/run habitats using a mini Surber sampler and from pools with a stovepipe corer (3 of each habitat every sampling date). We sampled within the same 300 m reach, but different habitats each sampling date. Macroinvertebrate and organic matter data from Surber samplers and cores were averaged and habitat-weighted based on proportions of riffle/run and pool habitats available in study reaches of each stream.

The mini Surber sampler had a sampling area of 0.023 m^2 and was equipped with a 250-μm mesh net. The sampler was placed evenly onto the substrata, allowing water to flow through the mesh net. Substrata within the frame were disturbed and larger particles scrubbed with a plastic brush within the sampling area. Contents from the mesh net were rinsed into a plastic bag and preserved in ~8% formalin.

For core samples, we pushed the stovepipe corer (314 cm^2 sampling area) into the substrata and all enclosed materials including water were removed to a depth of ~10 cm below the substrata surface and placed in a bucket. Material within the bucket was stirred by hand and elutriated through a 250 μm sieve. All materials retained on the 250 μm sieve were rinsed into a plastic bag and preserved. Inorganic substrata composition in Surber and core samples was estimated visually using a modified Wentworth scale (Wentworth 1922).

We processed organic components of benthic samples to estimate very fine particulate organic matter (VFPOM<250-μm), fine particulate organic matter (250-μm< FPOM <1mm), and coarse particulate organic matter (CPOM >1mm) following procedures of Whiting et al. (2011). We sampled VFPOM by collecting a known volume subsample of the material that passed through the 250 μm sieve in the field during elutriation of core samples. For Surber samples, VFPOM samples were obtained by collecting an additional core sample adjacent to Surber sample locations and collecting a subsample of material that passed through a 250 μm sieve during elutriation of the adjacent core sample. Coarse fractions of samples (material retained on a 1 mm sieve) were processed in their entirety. Fine fractions (material <1mm retained on a 250 μm sieve) were sometimes subsampled up to 1/8 using a Folsom plantkon splitter.

We removed all macroinvertebrates from samples and identified most to genus using Merritt et al. (2008). Some non-insect groups were identified to order and Chironomidae (Diptera) were classified as non-Tanypodinae or Tanypodinae. Body length (carapace length for crayfish) of each individual was measured to the nearest mm. Macroinvertebrates were assigned to functional feeding groups based on Merritt et al. (2008). Abundance (density) was estimated by correcting numbers for the area of the sampling device. Biomass was estimated using length-mass regressions following procedures of Benke et al. (1999). Seasonal values of taxa richness, Shannon diversity (H'), and an EPT index (number of Ephemeroptera, Plecoptera, and Trichoptera taxa) were calculated for each Osage stream based on samples collected over the entire study period during that season.

Amphibians

Amphibian sampling occurred every two weeks from February to June 2011 at Konza and Osage (7 sampling periods). We captured amphibians using a variety of methods to increase chances of capturing an array of species. Eight small, Promar© minnow traps were left floating in each stream 16-20 hr to capture tadpoles and swimming adults. Two coverboard arrays (1 array = 16 boards) were randomly placed within the riparian zone (within 7 m of the channel). The boards (61cm x 61 cm x 1.25 cm [Heyer et al. 1994]) were arranged in 2 rows, with all boards ~61 cm from each other. Once captured, we recorded species, sex, age class or Gosner Stage (Gosner, 1960), and snout-vent length. We conducted timed auditory surveys to estimate the number and species composition of calling anurans. We spent 5 minutes at Streams 2, 3, and 6 between 16:00 and 18:00, and recorded sounds according to an amphibian calling index for each species: (1) distinct, individual call; (2) distinct individual calls with overlap, and (3) full chorus (Dodd 2010).

Statistical analyses

We performed all statistical analyses using the software packages SAS 9.2 (SAS Institute, Inc 2011) and R 2.14.0 (R Foundation for Statistical Computing, 2011). Water quality data (except temperature and O_2) required log transformation to meet assumptions of normality and macroinvertebrate percentages were arcsine transformed prior to analyses. For benthic organic matter and invertebrates, we examined seasonal patterns on Osage and tested for differences among seasons with one way analysis of variance (ANOVA) and a post hoc Tukey’s honestly significant difference (HSD) test. We used ANOVA and Tukey’s HSD test to compare water quality among streams and across sites. We used linear regression to examine relationships among some variables. Because Konza's TSS data violated parametric assumptions, we used the non-parametric Kruskal-Wallis ANOVA for multiple comparisons to determine if TSS differed among Konza streams, and the non-parametric Kendal tau rank correlation to examine relationships between TSS and nutrients. We used Student's t-tests with Bonferroni correction to examine water quality before and after the fire at each stream. We report median concentrations for water quality data because data were highly heteroscedastic. Amphibian data are reported as raw counts.

Results

Geomorphology and physicochemistry

Osage streams are first-order, intermittent headwaters. Watershed areas and stream lengths of the Osage streams were small with areas ranging from 19 to 120 ha (Table 1). The average stream width was 1.52 ± 0.76 m (± 1 SD) and the average stream depth was 0.08 ± 0.03 m, although there are scattered pools with depths up to 0.75 m for amphibian larvae and fish habitat. The streams flowed year round in 2010. In 2011, the streams dried completely in mid-June and did not resume flow until December 2011. Despite close proximity of the Osage streams (<1.5 km apart), the temperatures and O_2 concentrations were significantly different among all streams ($p<0.001$; Table 2) and significantly varied with sampling season ($p<0.001$). Daily O_2 swings were often large; for example, Stream 1 was 1.1 mg L^{-1} O_2 at night and 10.0 mg L^{-1} O_2 in the day.

At Konza, watershed areas were larger but average discharge was lower compared to Osage (Table 1). Flow was documented in May 2009 to mid-June 2009 with a median baseflow discharge of 0.004 m^3 s^{-1}. Flow ceased from June to November (at Shane and N2B), and resumed in December 2009. Whereas streams Shane and N2B dried in the summer months, stream N4D had low flow with a median discharge value of 0.003 $m^3\ s^{-1}$. Data from historical records at Konza show these streams can be without flow for over a year or more or flow continuously (Dodds et al. 2004), but not during our study.

Chemical properties

At Osage, Streams 1 and 2 had greater total nutrient values ($p<0.001$), and medians for all Osage streams were 252 $\mu g\ L^{-1}$ TN and 37.1 $\mu g\ L^{-1}$ TP. There was no difference in either the TN concentrations ($p=0.472$) or TP concentrations ($p=0.363$) across sampling dates. The TN: TP molar ratio had a substantial range over the two year study (Table 2).

At Konza, TN was not different among watersheds ($p=0.104$) with a median of 392 $\mu g\ L^{-1}$ (Figure 2). Total phosphorus was greatest at N4D and Shane ($p=0.999$), and significantly higher than N2B ($p<0.001$). In December, both TP ($p=0.05$) and TN ($p=0.003$) were seven times higher and the TN: TP molar ratio was five times lower ($p<0.001$). Total suspended solids was positively correlated to TN ($\tau=0.133$; $p=0.036$) and TP ($\tau=0.301$; $p<0.001$), while the TN: TP was inversely correlated to TSS ($\tau = -0.201$; $p<0.001$). Storm flows significantly increased TN by 12 times ($p=0.015$), TP by three times ($p=0.003$) and thus decreased TN: TP by four times ($p=0.004$).

Between Osage and Konza, base flow TN and TP values differed among streams. The TN was greater at Konza ($p=0.003$), whereas TP was greater at Osage ($p=0.004$). The TN: TP molar ratio was three times greater at Konza than Osage ($p<0.001$) (Figure 2).

At Osage, inorganic nutrients were highly variable temporally, even at baseflow (Table 2). Ammonium (NH_4^+) concentrations did not vary by site ($p=0.828$) or following fire ($p=0.829$).

Ammonium increased with storm flow ($p=0.051$) (Table 2), yet was not associated with stage height with multiple changes in discharge ($p=0.417$) nor correlated with TSS ($R^2=0.04$). Similar to trends with TSS, the variance of NH_4^+ increased greatly with stage height. The soluble reactive phosphorus (SRP) concentrations did not vary by site at baseflow ($p=0.554$), but did increase approximately eight fold during stormflow events at each site ($p<0.001$) (Table 2). Nitrate (NO_3^-) concentrations varied spatially at the Osage streams, with Streams 1 and 3 having slightly higher values ($p=0.019$). There was no obvious seasonal trend at baseflow. Stormflows increased NO_3^- (Table 2), but was not affected by stage height ($p<0.001$).

We monitored the fire effects at both sites (inorganic nutrients at Osage, and total nutrients at Konza). At Osage, nitrate concentrations decreased fourfold following prescribed fire at Streams 2 and 4 ($p=0.015$) and SRP concentrations decreased by half ($p=0.014$). Ammonium (NH_4^+) concentrations were not affected by the fire ($p=0.829$). At Konza (Shane Creek), the fire reduced TN by 50% and TP by 200% ($p<0.001$), but increased TN: TP ($p<0.001$) by 17 times because the fire effect was greater on TP.

Chlorophyll a and ecosystem metabolism

Osage benthic chlorophyll *a* concentrations did not differ among the six streams ($p= 0.111$). Prescribed fire positively influenced concentrations ($p=0.051$) 2 weeks following the fire, but only at Streams 2 and 4 (where we also detected changes in nutrients). For all streams, the median chlorophyll *a* concentrations was 0.67 $\mu g\ cm^{-1}$ (Table 2), but demonstrated a fairly high degree of variance among sampling periods and a seasonal trend in concentration ($p<0.001$). Chlorophyll *a* was greatest in October ($p<0.001$) with a median of 2.7 $\mu g\ cm^{-1}$, followed by

February ($p=0.012$) with a median of 2.4 µg cm^{-1}. The low-light winter months of November, December, and January had the lowest median values that averaged 0.4 µg cm^{-1}.

Osage streams were overall net heterotrophic (GPP < CR). Stream 2 was net autotrophic (GPP > CR) in May 2010, with a net primary productivity (NPP) value of 0.11 g O_2 m^{-2} d^{-1}. GPP values across sites and time were less variable than CR (Table 2). Both GPP and CR followed a similar trend in relation to other parameters; both were marginally positively correlated to chlorophyll *a* content ($r^2=0.10$) but not to nutrients.

Suspended sediments

Base flow TSS values at Osage tended to be low values (<8 mg L-1) with little variability over sampling periods (Table 2). Increases in TSS from storm flow spanned orders of magnitude (Figure 2). Osage TSS storm flows were recorded in the months of May, June, August, October, and December, but the increases in TSS, ISS, or VSS from storm flows did not vary by storm event ($p=0.316$) or stage height ($p=0.308$). At greater stage heights, the variance of suspended sediment concentrations increased threefold. The summer and winter months had significantly greater TSS concentrations than other periods ($p=0.014$).

Median values of TSS were about tenfold greater at Osage that Konza (Figure 2, $p<0.001$), yet both regions had low values, with an overall median of 4.85 mg L^{-1}. Further, individual streams at Konza displayed different TSS ($\chi^2(2) = 204.05$, $p < 0.001$) and Osage Streams 1 and 2 had higher TSS ($p<0.001$). Despite these differences, most streams had suspended material with approximately 50% ISS and 50% VSS. The data from both sites were strongly variable among sampling periods and seasons. The TSS values during storm flows increased 3-12 fold compared to base flow TSS values at both sites ($p<0.001$). The prescribed fire did not significantly influence TSS concentrations (p=0.196) 3 weeks following the fire at either Osage or Konza, despite sparse vegetation, exposed soil, and mean total annual rainfall of 52.8 mm at Osage and 170 mm at Konza.

Benthic organic matter and macroinvertebrates

Total BOM values in Osage Prairie streams had no significant seasonal patterns. On average, across streams and seasons, total BOM composition in Osage streams was ~50% CPOM, ~10% FPOM, and ~40% VFPOM (Table 2). Standing stocks of VFPOM in the spring were ~1.7x higher than winter standing stocks. In contrast to total BOM and VFPOM, CPOM and FPOM were generally higher in fall and winter compared to spring, but these trends were not statistically significant.

Average total macroinvertebrate abundance in Osage Prairie streams ranged from 28,000 - 102,000 individuals m^{-2}, with higher values in winter and spring (Table 3). Despite a seasonal trend in abundance, total biomass showed no seasonal patterns. Total invertebrate abundance in Osage stream samples was correlated with total CPOM in samples ($r = 0.38$, $p=0.005$). Total invertebrate biomass was positively correlated with total CPOM ($r = 0.48$, $p < 0.001$) and BOM ($r = 0.33$, $p = 0.015$).

Taxonomic richness was similar across seasons, but the number of EPT taxa varied considerably with season, with highest values in winter and spring (Table 3). Diversity of macroinvertebrates was lowest during winter. Collector-gatherers were dominant in terms of abundance and biomass during all seasons, and collector-gatherer contribution to total abundance was significantly greater in fall than winter and spring (Figure 3). Collector-filterer contribution to abundance was also greatest in fall, whereas predators were highest in spring. Shredders and scrapers were poorly represented during all seasons. Collector-filterers, scrapers, and shredders had relatively low biomass throughout the year (Figure 3). Collector-filterers had high abundance but low biomass because this group was dominated by small bodied taxa such as Ostracoda and Cladocera.

Amphibians

At Osage, we captured 789 amphibians from February to early June 2011 representing 9 species (Table 5). Most individuals were American toad (*Bufo americanus;* n=231) and Southern leopard frog (*Rana sphenocephala;* n=484) tadpoles. Some *Rana sphenocephala* tadpoles hatched in fall, overwintered in the streams, and metamorphosed by June, evidenced by their presence and large size in early February, but we also documented spring breeding for this species. Similar numbers of amphibians were found in all the Osage streams, except Stream 6, which had ~6x higher tadpole counts.

Konza streams were primarily dry during the spring amphibian breeding season. We captured 14 adult amphibians representing 2 species from February to June 2011 at Konza (Table 5). The Western Chorus Frog (*Pseudacris triseriata*) called regularly in Shane Creek. No tadpoles were caught.

We found that the calling index was not a strong predictor of breeding success at either site (calling effort by many individuals didn't necessarily indicate tadpoles would be present), but did allow us to confirm the presence of some species. At Osage, the Cricket Frog (*Acris crepitans blanchardi*), Gray Treefrog (*Hyla veriscolor*), Spring Peeper (*Pseudacris crucifer*) and Plains Leopard Frog (*Rana blairi*) routinely called with an index value of 2 or 3 (multiple, distinct calls or full chorus); however, few or no tadpoles of these species were found (Table 5).

Calling varied with time of night and among sampling periods, probably as a function of weather conditions and season. By monitoring calling, were able to confirm the presence of the Western Chorus Frog (*Pseudacris triseriata*) at both Osage and Konza although we did not capture any Chorus Frogs.

Discussion

Overall, our results suggest that good water quality, high spatial and temporal variability, and moderate animal diversities characterize both sites. While there was considerable variation within sites in many variables we measured, we compared means and ranges with regional published reference data to put this data into context and to extend reference conditions developed previously using data from Konza alone. By "reference", we mean grasslands composed mostly of native plant species without row-crop agriculture, fertilization, or cattle grazing. Here, we discuss factors that might drive differences and similarities within and among sites as well as what our data mean with respect to baseline water quality and biotic integrity for tallgrass prairie streams.

Sediments and nutrients

Overall, the total suspended solid concentrations were almost ten times greater at Osage than at Konza. This difference is probably driven by geology (deeper soils at Osage) as the larger watersheds at Konza are subject to storms of similar intensity (although annual precipitation is less; Table 1) to those at Osage and have steeper elevation gradients as well, potentially leading to more intense flooding at Konza. Drier streams often carry more sediment (Dodds and Whiles 2004), thus we expected sediments to be higher at Konza if hydrology was the key factor controlling differences among the sites. We found inconsistent relationships between TSS concentration and stage height in our study streams. About 20% of stations in a continental study demonstrated insignificant exponential relationships between total suspended solids and discharge (Dodds and Whiles 2004), so our results are not unusual. Storms can account for disproportionate amounts of annual TSS and TP loads in streams (Banner et al. 2009), and our study was able to capture this trend across multiple storm events.

Relatively low nutrient concentrations in our study streams could be due to low inputs and/or high retention, and is reflected in extremely low chlorophyll content. The study streams may be P limited relative to N as indicated by deviations from the Redfield ratio (TN: TP molar ratio of 16:1). However, Konza has a median TN: TP molar ratio of 68:1, and experiments showed co-limitation of autotrophic periphyton in those streams (Tank and Dodds 2003, Johnson et al. 2009). By comparing benthic chlorophyll *a*, TN, and TP concentrations to the range of reference values from Dodds (2006) we could classify our streams as oligotrophic from most sampling periods; occasionally TN values would increase to mesotrophic status, and TP values spiked into eutrophication for reasons we could not account for. The high variation among sampling points and season demonstrate the importance of gathering multiple samples to determine stream condition, and verifies that nutrient criteria should be set on means rather than individual sampling events.

Baseflow nutrient and TSS concentrations are considerably lower than most other streams in the ecoregion which undergo intense agriculture (cropland or grazing). Baseflow TSS concentrations in our study streams were lower than 70% of all the continental U.S. streams studied by Dodds and Whiles (2004) and lower than 87% of Kansas and Missouri streams (Winders 2010), likely due to the agricultural and other watershed disturbances surrounding most streams in these states. Nutrient values in these tallgrass prairies were orders of magnitude lower than median values for converted, agricultural streams. Konza and Osage had five times lower median TN concentrations, and nine times lower TP concentrations (Dodds et al. 2009), almost certainly because of limited agricultural and urban inputs.

Metabolism and producer biomass

Osage Prairie streams had low GPP, relatively higher CR, and thus a negative NPP. Gross primary production could be low because of low nutrient concentrations (Mulholland et al. 2001), and perhaps light limitations. The GPP, CR, and NPP rates at Osage compared to those reported in Konza's streams (O'Brien et al. 2007) and to the range of "pristine stream" reference values from Dodds (2006), Mulholland et al. (2001), and Bernot et al. (2010). However, Konza often demonstrated fluctuations between strong heterotrophy and weak autotrophy (Riley and Dodds 2012), whereas Osage was consistently net heterotrophic. Interestingly, despite low GPP and low chlorophyll *a* values, these streams were often crowded with algal mats and filamentous algae. Canopy cover from small shrubs and tallgrasses could overhang and intercept light, limiting algae in reaches with canopy closure where we sampled. Alternatively, in areas with open reaches and high light intensity, photosynthetic efficiencies and chlorophyll pigment content can be lowered from either low synthesis or cellular damage (Beale and Appleman, 1971; Neidhardt et al. 1998).

Stream 2 at Osage physically resembled more of a wetland habitat and was functionally different than the other streams in several ways: higher TN and TP, positive NPP, higher sediment concentrations, higher CPOM and BOM, higher temperatures and greater diurnal swings of O_2 concentrations. We consider this a wetland stream because it was in a flat area, had heavy emergent macrophyte growth around the edges, and very low water velocity. This wetland stream was the only Osage stream to exhibit a net positive NPP, likely because it lacked any canopy cover and had greater nutrient concentrations. This wetland stream had the highest nutrients and sediments, but values were still low when compared to streams draining cropland (Dodds and Oakes 2004; Dodds et al. 2009). Wetland prairie streams were probably historically common in mesic regions of the USA, but many have been drained through extensive development of agricultural tile drainage because of their suitability for crop production (Samson and Knopf 1994). Although this is only a single stream, our data from this stream type broadens our concept of baseline ecosystem structure and function in streams encompassed by tall grass prairie.

Fire effects

Interestingly, the prescribed fires had effects on nutrients and algal biomass at some streams at Osage and Konza; fire decreased SRP and NO_3^- drastically while slightly increasing chlorophyll *a* content. The tallgrasses typically often overhang and shade these narrow stream channels, but following fire the vegetation is removed; a possible mechanism to explain the nutrient reduction following burning is algal growth and nutrient uptake in response to increased light availability. Prior data from Konza showed modest increases in nutrients following fire at the scale of days and years (Dodds et al. 1996), thus the effect of fire on nutrients is not clear. In forested ecosystems only moderate effects of fire on stream nutrient chemistry have been noted in the short-term (Richter et al. 1982), although longer term nutrient increases may be seen following fires (Minshall et al. 1989), consistent with results on Konza. Interestingly, these data show no change in stream TSS concentrations following fire; this supports a former study on

Konza that suggested burning did not significantly increase sediment loss or overland flow on the landscape (Duell 1990). Even though prairie burning removes most vegetation biomass and exposes soil for weeks, little upland soil (which includes both TSS and bound nutrients) is removed and transported to streams via overland flow.

Fauna

Macroinvertebrate communities in Osage streams were similar in functional structure to those reported from headwater streams on Konza in the western extent of the tallgrass prairie (e.g., Fritz and Dodds 2002, Stagliano and Whiles 2004, Whiting et al. 2010). One of the more notable patterns of functional structure in the Osage streams was the general lack of shredders, which conceptual models of stream continua suggest should be abundant in headwaters (Vannote et al. 1980). The general lack of shredders in Osage and other grassland streams is likely linked to the lack of forest canopy, which reduces allochthonous inputs and enhances primary production compared to forested headwaters. This lack of shredders suggests that grass is not adequate to support shredders or only small amounts of grass litter actually enter the stream channels. Ongoing forest expansion, which is linked to fire suppression and other human activities (Briggs et al. 2005), in many remaining tallgrass prairie riparian zones may alter the unique functional structure of these headwater streams.

Our results and prior investigations indicate pollution-intolerant taxa (e.g., EPT taxa) are not abundant in headwater tallgrass prairie streams compared to similar sized streams in forested regions. For example, Wallace et al. (1996) reported EPT of ~20 for 1st order streams in the Appalachian Mountains, which is substantially greater than our data for Osage streams. Tallgrass prairie headwater streams are generally intermittent or ephemeral, and the harshness is likely linked to lower EPT and overall taxonomic richness compared to headwaters in wetter regions (Fritz and Dodds 2005). However, some degree of hydrologic disturbance may enhance regional diversity, and many taxa we encountered in Osage streams are adapted to hydrologically variable habitats (Fritz and Dodds 2004, 2005).

Total macroinvertebrate abundance in the Osage streams was much greater, in some cases an order of magnitude higher, than estimates from Konza Prairie studies that used the same mesh and sieve sizes (Stagliano and Whiles 2002, Dodds et al. 2004, Whiting et al. 2011). Higher invertebrate abundances in Osage streams may be related to high organic matter standing stocks; BOM estimates from the Osage streams were 2-4 times greater than estimates from similar studies on Konza streams (Stagliano and Whiles 2002, Whiting et al. 2011); positive relationships between stream invertebrate abundances and benthic organic matter were evident in Osage streams, and have been documented elsewhere (Minshall 1984, Walther and Whiles 2011).

Macroinvertebrate seasonal patterns that we observed are consistent with other studies of temperate zone headwater streams (e.g., Robinson and Minshall 1986). Many temperate zone stream biological assessment efforts focus on late winter and early spring because macroinvertebrate abundance, biomass, and richness are greatest at this time (Gibson et al. 1996, Barbour et al. 1999). This pattern is a function of the typical univoltine life cycles of many stream insects, whereby individuals develop in the water from fall-spring and then emerge as adults in spring-summer. Our results suggest that biological assessments that focus on late winter and early spring sampling periods will capture greatest abundance and diversity for tallgrass prairie headwater streams.

The two sites varied considerably in amphibian abundance and diversity during the breeding seasons. Amphibians use these prairie streams, as indicated by the array of species (n=9) captured and spring and fall breeding at Osage Prairie. Activity at Konza and Osage's Stream 3 was likely discouraged by dry conditions at these sites during the breeding seasons. We found that using a variety of techniques, particularly stream trapping and aural surveys, increased the number of species detected. The numbers of frogs we captured and heard was highly variable in space and time, and this was likely related to variability in prevailing conditions during surveys (Dodd, 2010). Thus, if proper sampling techniques are used over multiple sampling events, amphibians could be an important monitoring tool for tallgrass prairie streams. Given the variability we found, use of amphibians for bioassessments of prairie streams is not recommended unless repeated, intensive sampling is feasible.

Small streams draining tallgrass prairie may be particularly important for maintaining amphibian populations. Many developing amphibians are vulnerable to predation by fish, and the small streams draining prairie are simply too small and intermittent to maintain substantial densities of predatory fish. Given the greater abundance of amphibians at Osage, loss of tallgrass prairie habitat in wetter regions will likely have a greater negative impact on amphibians than in drier areas that are simply not able to support high amphibian abundance and diversity.

Implications for conservation

Our results should be viewed with some caution because direct comparisons of streams from the two areas are complicated by a number of factors that make it difficult to ascribe mechanisms to the differences observed between the sites. Geology, precipitation, biogeography, and prairie management all varied across the sites. Osage has lower topography, deeper soils, smaller watersheds, substantially more annual precipitation (and subsequently higher discharge yield per unit area) and occurs in an area where we would expect animal diversity is to be higher because of a strong precipitation gradient between sites (PRISM 2011). Osage also has a history of haying rather than burning and grazing, making it representative of many current prairie conservation areas, but different from historical conditions likely dominated by burning and grazing. We did observe higher diversity and higher relative abundance with amphibian sampling at Osage compared to Konza, likely due to more hospitable habitat related to greater rainfall and stream discharge necessary for amphibian breeding. Our comparisons between Osage and Konza as well as among streams within each site, expand the range of values representative of catchments draining tallgrass prairie.

Conclusions

We examined unplowed, intermittent headwater streams in more mesic conditions (at Osage Prairie, MO) compared to Konza, the site with most available data on tallgrass prairie streams. Few characterizations of spatial and temporal variability of water quality and ecosystem processing rates have been published for mesic tallgrass prairie streams or wetland prairie streams. Descriptions of fundamental ecosystem characteristics in new regions are crucial for comparisons of water quality, stream metabolism, and communities to guide management activities. Despite the surprising variance in chemical and biological properties in these streams over small spatial scales, this study suggests that good water quality, moderate heterotrophic condition, and occurrence of some sensitive animal species are common traits of tallgrass prairie streams.

Acknowledgments

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Figures

Figure 2.1 The historical range of tallgrass prairie in the United States is shaded gray (replotted from NERP 2007). The stars indicate our study sites (Osage and Konza) where the entire watersheds are encompassed by native tallgrass prairie.

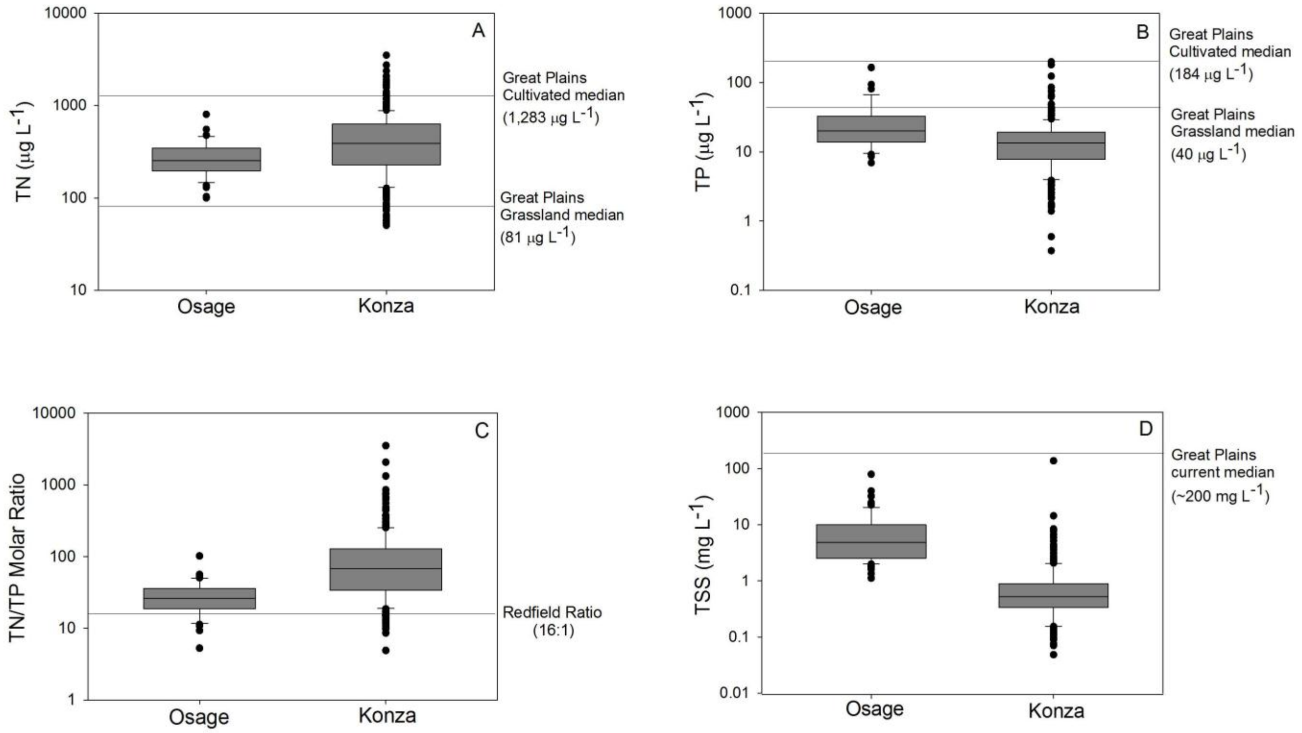

Figure 2.2 Boxplots (on log scale) comparing the values of total nitrogen (A), total phosphorus (B), total nitrogen: total phosphorus molar ratios (C), and total suspended solids (D) from Osage Prairie, MO and Konza Prairie, KS. The sites were statistically significant from each other in each parameter, yet both sites typically display low values. The Great Plains Grassland and Cultivated values are EPA Ecoregion, Level 1 criterion, and the Great Plains Current TSS values were obtained from Dodds and Whiles (2004). Both sites fall within EPA Ecoregion Level 1, the Great Plains.

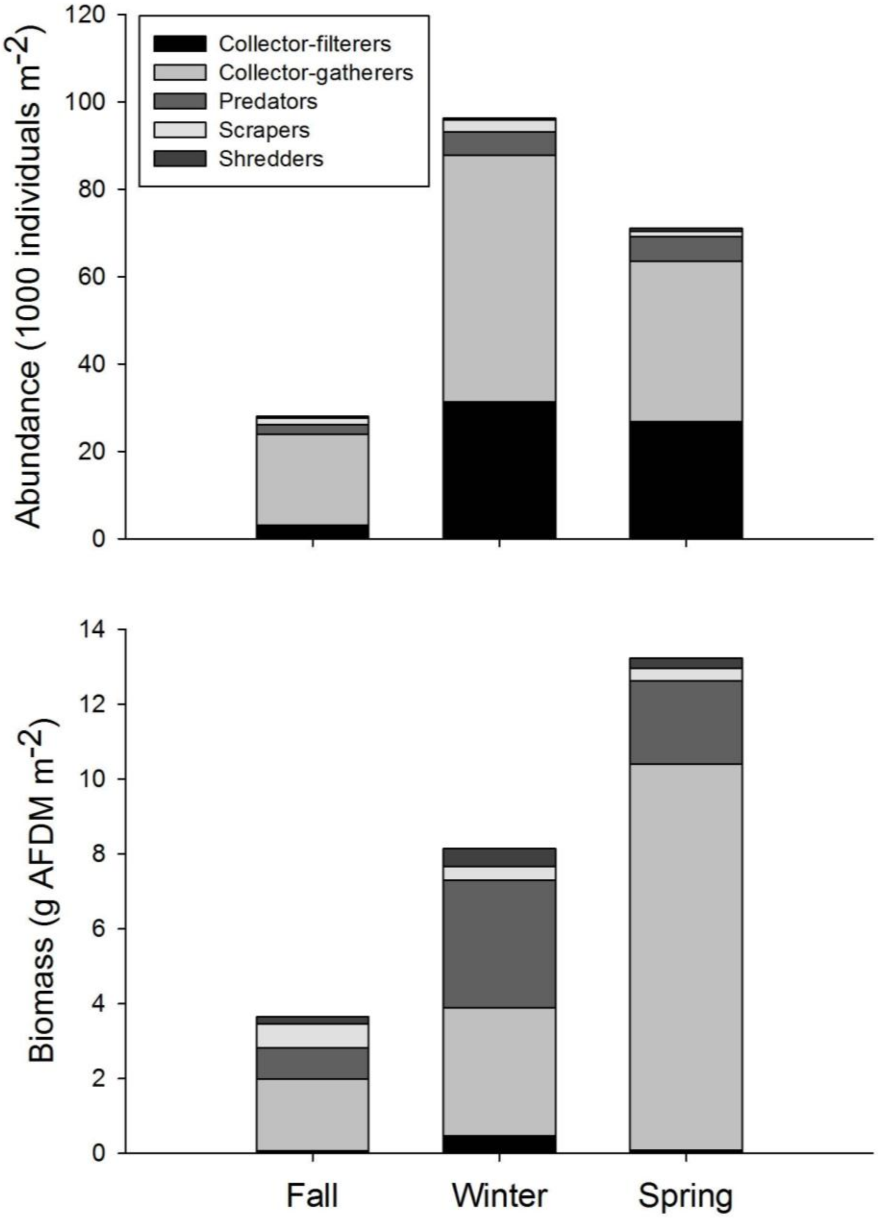

Figure 2.3 Habitat-weighted average abundance and biomass of macroinvertebrate functional feeding groups across three seasons at Osage Prairie, KS during 2009-2011 (nine sample dates). Seasons are categorized as: fall (September-November), winter (December-February), and spring (March-May). The summer (June-August) had no flow, so samples were not collected.

Tables

Table 2.1 Summary of the watershed and stream physical characteristics of tallgrass prairie streams at Osage Prairie, MO and Konza Prairie, KS, USA. Numbers in parentheses represent 1 standard error.

	Osage	**Konza**
Average watershed area (ha)	31 (±18)	204 (±183)
Average temperature range (^{oC})	-7.2 – 32	-2.7 – 26.6
Average annual total precipitation (mm)	1338	835
Strahler stream order	1	3
Stream length (m), range	465-1778	5886-8885
Stream slope (%)	<0.01	0.02
Average discharge (m^3 s^{-1})	0.07	0.009
Hydrologic system type	Not flashy, intermittent	Flashy, intermittent
Expected dry seasons	Summer	Any month
Dominant substrate type	Silt and vegetation	Cobbles
Canopy cover (%), range	0 - 68	N/A
Burn interval (years), range	3-5	1-4
Grazers, bison	N	Y

Table 2.2 Summary statistics for 6 headwater streams on Osage Prairie, MO, USA, from 2009-2011 (baseflow sample size=99; stormflow sample size=51). An asterisk (*) indicates stormflows significantly increased the median value ($p<0.05$), whereas blanks indicate no stormflow samples. Organic matter values are habitat-weighted.

	Baseflow		**Stormflow**	
	Range	**Median**	**Range**	**Median**
Nitrate (μg L^{-1})*	0.4 - 121	7.7	7.7 - 657	42.6
Ammonium (μg L^{-1})*	7.3 - 228	15.3	1.7 - 1083	22.4
Soluble reactive phosphorus (μg L^{-1})*	0.4 - 31	5.1	1.9 -554	40
Total suspended solids (mg L^{-1})*	1.1 - 7.8	4.8	7.8 - 2979	34.5
Inorganic suspended solids (mg L^{-1})*	0.2 - 33.5	2.6	2.8 - 85.2	24.9
Organic suspended solids (mg L^{-1})*	0.3 - 56	1.8	1.8 - 85.2	9.6
Coarse particulate organic matter (g AFDM m^{-2})	15 - 3192	663		
Fine particulate organic matter (g AFDM m^{-2})	2 - 1286	183		
Very fine particulate organic matter (g AFDM m^{-2})	14 - 3959	531		
Total benthic organic matter (g AFDM m^{-2})	96 - 4906	1373		

Total nitrogen (µg L^{-1})	100 - 803	252.8
Total phosphorus (µg L^{-1})	7 - 165	20.1
TN: TP (molar ratio)	5 - 102	26
Benthic chlorophyll *a* (µg L^{-1})	0.1 - 3.8	0.7
Gross primary production (g O_2 m^{-2} d^{-1})	0 - 1.6	0.4
Community respiration (g O_2 m^{-2} d^{-1})	-0.5 to -9	-1.7
Net ecosystem production (g O_2 m^{-2} d^{-1})	-7.4 to 0.1	-0.9
Temperature (^{oC})	0 - 21.5	14
Dissolved oxygen (mg L^{-1})	0.2 - 12.8	8.1

Table 2.3 Macroinvertebrate community characteristics in headwater streams at Osage Prairie, MO, USA during 2009-2011. Values are habitat-weighted averages for samples from 6 study streams. Numbers in parentheses represent 1 standard error. Across rows, values with different superscript letters are significantly different ($p<0.05$). EPT is the number of taxa within the orders Ephemeroptera, Plecoptera, and Trichoptera.

	Fall	**Winter**	**Spring**
Abundance (no. m^{-2})	28020 (1117)^{a}	102065 (3482)^{b}	71841 (2342)^{b}
Biomass (mg AFDM m^{-2})	3656 (234)	8306 (439)	13121 (1380)
Shannon Diversity	2.0 (0.02)^{ab}	1.8 (0.02)$^{\mathbf{b}}$	2.1 (0.01)^{a}
Richness	28.0 (0.1)	31.0 (0.3)	30.9 (0.2)
EPT	3.6 (0.3)^{a}	8.1 (0.2)^{b}	6.3 (0.1)^{b}

Table 2.4 Survey data from 6 tallgrass prairie streams on Osage Prairie, MO, USA in spring 2011 (7 sample periods) and 3 streams on Konza Prairie, KS, USA in spring 2011 (7 sample periods). Methods of capture included cover boards, minnow traps, and netting. Calls were recorded according to this index: (1) individual caller, (2) multiple individuals calling but calls distinct and (3) full chorus (Dodd, 2010). Blanks indicate no captures.

		Osage			**Konza**		
Common Name	**Scientific Name**	**Adults and Juveniles**	**Tadpoles & Larvae**	**Call Index**	**Adults and Juveniles**	**Tadpoles & Larvae**	**Call Index**
Cricket Frog	*Acris crepitans*	2		3	13		
American Toad	*Bufo americanus*	2	231	1, 2, 3			
Gray Treefrog	*Hyla versicolor*		1	3			
Spring Peeper	*Pseudacris crucifer*	1		2, 3			
Western Chorus Frog	*Pseudacris triseriata*			1			2,3
Bullfrog	*Rana catesbeiana*	1		1, 3			
Southern Leopard Frog	*Rana sphenocephala*	8	534	1, 2, 3			
Plain's Leopard Frog	*Rana blairi*	1		2	1		
Small-mouthed Salamander	*Ambystoma texanum*		8	N/A			
Total		15	774		14	0	

Chapter 3 - Blazing and grazing: influences of fire and bison on tallgrass prairie stream water quality

Larson DM, Grudzinski BP, Dodds WK, Daniels M, Skibbe A, Joern A. (2013) Blazing and grazing: influences of fire and bison on tallgrass prairie stream water quality. *Freshwater Science* 32(3), 779–791.

Abstract

Fire and grazers (such as *Bison bison*) were historically among the most important agents for maintaining and managing tallgrass prairie, but we know little about their influences on water-quality dynamics in streams. We analyzed 2 y of data on total suspended solids (TSS), total N (TN), and total P (TP) (3 samples per week per stream during flow) in 3 prairie streams with fire and bison grazing treatments at Konza Prairie Biological Station, Kansas (USA), to assess whether fire and bison increase the concentrations of these water-quality variables. We quantified the spatial and temporal locations of bison (~0.21 animal units/ha) with *Global Positioning System collars* and documented bison trails, paw patches, wallows, and naturally exposed sediment patches within riparian buffers. Three weeks post-fire, TN and TP decreased (*t*-test, $p < 0.001$), but TSS did not change. Bison spent <6% of their time within 10 m of the streams, increased the amount of exposed sediment in the riparian areas, and avoided wooded mainstem branches of stream (χ^2 test, $p < 0.001$). Temporal trends suggest that low discharge or increased bison density in the stream may increase TSS and TP during the summer months. Our results indicate a weak connection between TSS and nutrients with bison access to streams over our 2-y study and indicate that low TSS and nutrients characterize tallgrass prairie streams with fire and moderate bison densities relative to surrounding land uses.

Introduction

The tallgrass prairie ecosystem possesses historical and intimate connections with fire and bison (Bison bison), so both should be studied when considering drivers of prairie stream ecosystem properties. Grasslands worldwide have coevolved with herbivores. In the Great Plains region of the USA, prairies have most recently evolved with Bison bison, the North American Bison (Stebbins 1981). Bison herds of 10–60 million were recorded by early settlers in the Great Plains, but by 1830 the species was near extinction because of hunting (Flores 1991, Shaw and Lee 1997). Strong fire–grazing interactions in grasslands result in shifting mosaics of vegetation structure and quality through a series of recursive feedbacks (Fuhlendorf et al. 2009, Allred et al. 2011a), but how these feedbacks influence aquatic ecosystems is not well understood.

Prairies in regions with sufficient moisture to support trees are maintained as grasslands by a regular fire disturbance regime that enables grasses to thrive and eliminates or reduces woody plants (Stewart 1951). Surprisingly little research has been dedicated to fire effects on tallgrass prairie streams despite a recurrence interval of 1 to 10 y (Abrams 1985). Fire can decrease soil water-infiltration capacity and remove ground cover, which can lead to increased overland flow and soil erosion. In high-relief forested ecosystems, debris flows and high sedimentation have occurred following wildfire (Meyer et al. 2001, Moody and Martin 2001, Smith et al. 2010). Nevertheless, a study at Konza Prairie in Kansas (USA) suggested that burning did not significantly increase sediment loss or overland flow on the landscape (Duell 1990). Dodds et al. (1996) found that total N (TN) and NO3– concentrations in the water column increased as a function of number of days and years after fire in tallgrass prairie. However, they also found that N transport was related primarily to stream discharge. We are aware of only one study of stream sediment dynamics following fire in tallgrass prairie (Larson et al. 2013), and the nutrient trends in the literature are still unclear. After a prairie burn, large ungulates increase their time spent in burned areas (Daubenmire 1968, Vermeire et al. 2004). Thus, the presence of bison on burned ground could lead to interactive effects of fire and grazing on water quality.

Bison may affect water quality by their movement across the landscape and within creeks. Streams can be natural pathways for animal movement (Butler 1995). Animals tend to avoid traversing steep slopes and prefer to travel on gradually sloping terrain (Bruggeman et al. 2008), such as near flood plains and valley bottoms. Bison create well established stream crossing trails that can alter habitat by widening the channel and increasing the silt fraction of substrates, especially during storm flows (Butler 1995, Fritz et al. 1999). Trampling through streams could lead to sediment and nutrient suspension.

Other bison behaviors—grazing, foraging, wallowing, and pawing (a term that refers to intentional soil disturbance with hooves)—may affect water quality if the effects of these activities are functionally connected to streams by hillslope transport pathways. These bison behaviors increase bare ground and potential for sediment delivery to stream channels (Kondolf 1993, Greenwood and McKenzie 2001). Bison wallow regularly for many reasons, including shedding, rutting, group unity, itching, removing ectoparasites, and thermoregulation (McMillian et al. 2000). Wallowing can create patches of bare and compacted soil susceptible to erosion. Bison urinate in the wallows for either rutting or group cohesion, and this behavior could increase NH4+ and TN in the wallows and streams. Bison also paw large patches of soil adjacent to stream banks, perhaps to obtain minerals. All of these actions could increase sediment and nutrient input into streams.

Objectives

Despite our increasing knowledge of the importance of fire and grazing in terrestrial grassland ecology (Knapp 1998, van Langevelde et al. 2003, Archibald et al. 2005), little research has been done to investigate the influence, including sediment and nutrient export dynamics, of fire and bison on prairie streams. Thus, the primary objectives of our study were to assess whether relationships exist among tallgrass prairie stream concentrations of total suspended solids (TSS), total N (TN), and total P (TP) and prairie burning, bison grazing, and areal extent and type of bison effects near the stream from pawing, wallowing, and development of stream trail crossings. We quantified the proportion of time bison spent within watersheds and the riparian zone with data from Global Positioning System (GPS)-collared bison. We compared watersheds disturbed by bison and fire with reference watersheds and watersheds dominated by row–crop agriculture in this ecoregion.

Methods

Stream descriptions

We studied 3 headwater intermittent tallgrass prairie streams on Konza Prairie Biological Station (KPBS) in northeastern Kansas, USA (lat 39°5'55.65"N, long 96°36'19.91"W; Fig. 1). The KPBS is a large tract of unplowed, native tallgrass prairie (3497 ha) that is owned by the Nature Conservancy, managed by the Division of Biology at Kansas State University, and part of the Long Term Ecological Research (LTER) network. Ivan soils (4051 Ivan Silt Loam) dominate floodplains and are characterized as deep and moderately well drained with numerous rock fragments (Oviatt 1998). The stream substrate consists mostly of limestone and shale rock fragments, and limestone bedrock is exposed in short segments of the streams.

We acknowledge that our study lacks replication at the watershed scale and includes pseudoreplicated water samples. We were able to monitor only 2 bison-grazed watersheds and 1 control (no bison grazing) watershed because of the rarity of headwater streams grazed by bison (and without other conflicting upstream land uses, such as row-crop agriculture). Furthermore, all of the watersheds have been under different burn regimes for the last 15 y. All 3 study streams (Shane, N2B, and N4D) are characterized by native tallgrass prairie uplands and discontinuous riparian gallery forests with minimal human influence other than prescribed fire and bison management that mimics historical tallgrass prairie conditions (Knapp 1998). Shane Creek was ungrazed, whereas bison have grazed at Kings Creek (subwatersheds N4D and N2B) since May 1992 at ~0.21 animal units (AU)/ha. Bison graze freely among watersheds N2B and N4D and several other surrounding watersheds year round and are minimally managed (i.e., no supplemental water and only rarely winter fed). Prairie burning in these watersheds occurs in March or April at different fire intervals. The Shane Creek watershed is burned annually, whereas N2B and N4D have target burn intervals of 2 and 4 y, respectively. Watersheds N2B and N4D were last burned in April 2009 (before water collections), and the Shane Creek watershed was burned in 2010 (during water collections) (Table 1).

We manually delineated and measured watershed attributes, such as watershed area, longitudinal stream slope, stream sinuosity, floodplain area, and floodplain slope (Table 1) in ArcGIS (version 9.3; Environmental Systems Research Institute, Redlands, California). We digitized streams from a 2-m digital elevation model (DEM) based on the curvature of the stream morphology from the point of water sampling to the point where the streams terminated into hillslope. We calculated longitudinal stream slope as the difference between the high and low points of the streams divided by their length, and we calculated sinuosity as the length of the streams divided by the straight-line lengths. We digitized floodplain areas from the DEM as the flat area adjacent to the stream channel. We used the *slope* tool in ArcGIS to calculate the average floodplain slope. We used an interactive supervised classification method in ArcGIS to quantify woody riparian vegetation. We compiled discharge data (Q) for N2B only. We measured Q at 5-min intervals at a triangular throated flume. The stage height provided mean, maximum, and minimum daily Q (raw data can be found at: http://www.konza.ksu.edu).

Total suspended solids

Beginning May 2009 and ending September 2010, we collected TSS from each stream 2 to 3 times/wk when streams flowed. We took samples from the same location at the base of the watershed just above the weirs every sampling period. We sampled from the center of the channel in a location where water was ≥10 cm deep with care not to disturb benthic sediments at or upstream from the sampling location. If bison were in the water upstream of the sampling site at the time of sampling, we noted their presence. We also documented stormflow conditions, defined as an increase in Q (of any magnitude) following a precipitation event. We analyzed and calculated TSS, volatile suspended solids (VSS), and total inorganic solids (TIS) according to ESS Method 340.2 (USEPA 1997). We also dried and weighed filters a 2nd time to ensure that hydration did not confound results. Rewetting and redrying of multiple samples yielded <1% change in the measured mass so this procedure was discontinued after the first few months of sampling.

Nutrients

We collected water samples for nutrient analyses from the same locations as TSS in acid-washed bottles 3 times weekly from May 2009 to September 2010. We stored samples at –30°C until analysis. We analyzed unfiltered stream water for total N (TN) and total P (TP) concentrations by a persulfate oxidation method (Ameel et al. 1993) in triplicate with an OI-Analytical Flow Solution IV autoanalyzer (O.I. Corporation, College Station, Texas) and averaged values.

Exposed sediment patches

We quantified the areas and slopes of all exposed sediment patches within 10 m of the stream channel to account for differences in potential sediment delivery to the bison-accessible streams N2B and N4D. Both watersheds were walked from the point of water sampling to the point upstream where the visible channel terminated to hillslope once in 2010. Exposed sediment patches within 10 m of the channel (i.e., riparian zone) were grouped into 3 source categories: 1) bison wallows, 2) bison pawed patches, and 3) natural bare banks (Fig. 2A–C). Wallows and paw patches are bison-caused exposed patches and have distinct identifying features. Wallows are circular depressions on low sloped terrain, and paw patches are typically on benches, have a distinct break in slope with the stream bank, have hoof markings, and are connected to bison trails. Naturally bare banks are defined as exposed patches above bankfull and cut banks that are in-stream exposures from water erosion. Bare banks are likely to be natural and not bison induced, but heavy trampling may increase the number and area of bare-bank patches. The criterion we used for measurement was ≥0.6 × 0.6-m area with <40% cover by stabilizing vegetation or large rock. We marked patch locations via GPS and measured area and slope for each exposed sediment patch with survey tape and a digital level. We counted the number of bison crossings at N2B and N4D and marked their location using GPS. The crossings were separated into mainstem (a 3rd-order stream section) and tributaries (<3rd-order stream sections).

Fire

We continued triweekly sampling of TSS and nutrients before and after a prescribed fire at Shane Creek on 3 March 2010. We used rainfall data obtained from a rain gauge stationed at the headquarters of KPBS to assess whether rain fall occurred within the 3 wk after prescribed burns (raw data available at: http://www.konza.ksu.edu).

Bison locations

Between 2008 and 2010, the Konza bison herd averaged 380 ± 31 before cull and decreased to 290 ± 19 individuals after cull in early November. We chose a 3% subset of matriarchal females for year-round tracking via Telonics® GPS collars (accuracy = ~4 m; Telonics, Mesa, Arizona) set to record data at 2 h intervals. We mapped and analyzed bison location data in ArcGIS to identify the overall density and frequency of bison within 10 m of the streams in both bison watersheds and to describe temporal dynamics of riparian use by the bison. We normalized data for area within each watershed.

Statistical analyses

Statistical analyses were run in SAS (version 9.1.3; SAS Institute Inc, Cary, North Carolina) and R (version 2.1.3; R Development Core Team, Vienna, Austria), with additional use of the R packages: *vegan* (Oksanen et al. 2011), *BiodiversityR* (Kindt and Coe 2005), *car* (Fox and Weisberg 2011), *coin* (Hothorn et al. 2006), and *labdsv* (Roberts 2010). All statistical outliers ($n = 6$; defined as ≥3 standard deviations from the mean) arose during storm flow or when bison were in the stream while we were sampling. We removed the outliers and repeated the analyses, but trends were consistent between analyses with and without outliers (data not shown), so we report results with outlier included to provide the most conservative estimates. We report median sediment and nutrient concentrations because rare events (such as storms and bison in the streams while sampling) had a disproportionate effect on the mean.

The TSS data violated assumptions of normality and equal variances, so we analyzed them with nonparametric tests. In an analysis of temporal autocorrelation, we found no statistical correlation after 4 wk, so we blocked data by month (roughly 4 wk). We used Friedman's Test (nonparametric analysis of variance with repeated measures with data blocked by month) followed by a post hoc Mann–Whitney U test with Bonferroni correction to test whether TSS, TIS, VSS, and VSS:TIS varied among the 3 watersheds (2 grazed, 1 ungrazed). We pooled data from all streams and used Kendall's τ rank correlation to assess whether TSS, VSS, TIS, and VSS:TIS were correlated with nutrients, discharge, rainfall, stormflow events, or bison presence in the stream during sampling. We used Mann–Whitney *U* tests to assess whether TSS increased in the 3 wk post-fire (after 3 wk, regrowth of grasses covers the bare soil) and whether the areas and slopes of the exposed sediments (natural and bison-induced) differed among watersheds.

Nutrient values required $\log(x)$-transformation to meet normality assumptions. We used 1-way analysis of variance (ANOVA) and a post hoc Least Squares Differences (LSD) to test for differences in nutrient concentrations among stream. We used Student's *t*-tests to evaluate whether fire altered nutrient concentrations.

We used a χ^2 goodness-of-fit test to compare the amount of time bison were present in the tributaries vs mainstem branches and riparian vs upland locations between the 2 grazed watersheds. We also used a χ^2 goodness-of-fit test to indicate which watershed characteristics (e.g., floodplain slope; Table 1) differed between watersheds.

We used principal component analysis (PCA) to illustrate the relationships among the response variables and to assess the similarities and differences among the 3 streams. We used TSS, VSS:TIS, TN, TP, and the TN:TP molar ratio as response variables. We also used a multiple linear regression with log(x)-transformation to determine if stormflow, bison presence in the stream during sampling, and fire explained significant amounts of variation in TSS, TN, and TP.

Results

Total suspended solids

TSS differed significantly among the streams ($\chi^2_{2\text{df}} = 204.05$, $p < 0.001$; Table 2, Fig. 3A), but not between grazed and ungrazed watersheds (mean rank by watershed = 340 for N4D, 172 for Shane [ungrazed], and 106 for N2B). Median TSS values were 10× greater at N4D than at the other 2 streams (Fig. 3A). These differences among the streams were consistent for VSS ($\chi^2_{2\text{df}} =145.67$, $p < 0.001$) and TIS ($\chi^2_{2\text{df}} = 240.87$, $p < 0.001$), and VSS:TIS ($\chi^2_{2\text{df}} = 200.45$, $p < 0.001$). TSS concentration increased 10× at N4D during July to November when the other streams were dry (Fig. 4A–C). We removed the TSS data for the dry months and reran Friedman's test to assess whether TSS differed among streams during the months with flow and still detected a ~10× difference at N4D ($\chi^2_{2\text{df}} = 226.38$, $p < 0.001$). However, TSS was generally 5× greater when bison were in the stream during sampling ($\tau = 0.137$, $p = 0.003$; Table 2). For the linear model, TSS ≈ Stormflow + BisonPresence + Fire, the variables Stormflow ($\beta = 3.65$,

t_{471} = 8.736, $p < 0.001$) and BisonPresence (β = 0.93, t_{471} = 3.125, p = 0.002) were significant predictors, but Fire was not. The total amount of variance explained by this model was 17.5%.

At N2B, daily mean Q was positively correlated with TSS (τ = 0.146, p = 0.02), VSS (τ = 0.150, p = 0.02), and TIS (τ = 0.1523, p = 0.01), but not VSS:TIS (τ = 0.105, p = 0.19). TSS was positively correlated with small rainfall events <24 mm/d (τ = 0.194, $p < 0.001$) and larger stormflow rain events >24 mm/d (τ = 0.167, $p < 0.001$). Q was correlated with month (τ = 0.254, p = 0.006) and increased from January until July. This increase corresponded to an increasing trend in TSS (Fig. 4A–C). N2B and Shane Creek had no flow from July to October 2009.

Nutrients

TP concentrations did not differ between N4D and Shane (p = 0.999), but TP in both was higher than in N2B ($p < 0.001$; Fig. 3B). TN concentrations did not differ among streams (p = 0.104; median = 392 µg/L; Table 2, Fig. 3C). Bison presence in the stream during sampling did not influence TN or TP (p = 0.574). Storm flows increased TN 12× (p = 0.015) and TP 3× (p = 0.003) and decreased TN:TP 4× (p = 0.004). TSS was positively correlated with TN (τ = 0.133, p = 0.036) and TP (τ = 0.301, $p < 0.001$; Fig. 5). TN:TP was inversely correlated with TSS (τ = –0.201, $p < 0.001$; Fig. 5). TP and TN:TP were greater in winter (November–January) than in other seasons (p = 0.004, p = 0.002). At N4D, TP was marginally greater in summer (July–October) than in other seasons (p = 0.067). None of the variables in the linear regression model, TN ≈ Stormflow + BisonPres + Fire, was a significant predictor of TN, and the model explained only 1.2% of the variance. The linear regression model, TP ≈ Stormflow + BisonPres + Fire explained 11% of the variance, and Stormflow significantly increased TP (β = 2.64, t_{471} = 61.004, $p < 0.001$), whereas Fire significantly decreased TP (β = –0.52, t_{471} = –2.419, p = 0.016).

Exposed sediment patches

In comparisons of exposed sediment characteristics between the bison-grazed watersheds (N4D and N2B), all values are reported as standardized by stream length. The total amount of exposed sediment was similar between watersheds (N2B: 0.183 m^2/m, N4D: 0.156 m^2/m; Table 1). The slopes of all types of exposed patches did not differ in either watershed (U = 3693, p = 0.675), had a median of 32°, and ranged from 4° to 85°. For both watersheds, ≥½ of the total exposed sediment area was contributed by bare banks (Table 1). We analyzed the total amount of exposed sediment from 200 m upstream of the water sampling locations to determine if high sediment exposure resulted in high TSS in N4D (N2B: 254 m^2, N4D: 117 m^2). Thus, the amounts of exposed sediment near the sampling source and throughout the watershed were not driving the 10× difference in TSS between these streams.

The areas of wallows and pawed patches (bison-induced exposed sediments) did not differ from the area of bare banks (p = 0.184) because many bare-bank areas were small and some pawed patch areas were large (up to 80 m^2). We counted 8 wallows and 32 paw patches within N4D’s 10-m streamside buffer, and 10 wallows and 12 paw patches within N2B’s 10-m streamside buffer. Watershed N2B had twice as much area of wallows (resulting from more wallows and larger wallow size) and half as much area from pawed patches (Table 1). At both streams, wallows were low-slope depressions (–2 ± 1.5% [SD]) and the distance averaged 6 m ± 5 m) from the stream bank.

Fire

TSS concentrations did not increase during the 3 wk after a prescribed prairie burn at Shane Creek in March 2010 (U = 623, p = 0.901). A total of 51 mm of rain fell from the start of the burn (which exposes soil) to 3 wk later (assuming grass reestablishment). Two 2 rain events >14 mm occurred on 1 d. The fire reduced TN by 50% and TP by 200% ($p < 0.001$), but the TN:TP molar ratio increased ($p < 0.001$) 17× because the effect of fire was greater on TP than on TN. The linear regression model, TP ≈ Stormflow + BisonPresence + Fire also showed that Fire significantly decreased TP ($\beta = -0.52$, $t_{471} = -2.419$, $p = 0.016$). Despite the immediate consequence of burning, the burn intervals of 1, 2, and 4 y did not substantially alter TSS concentrations. N4D had the highest TSS concentrations but the longest burn interval (4 y). Shane Creek had an annual burn interval, but low TSS and similar nutrient concentrations relative to the less frequently burned watersheds.

Bison locations

Bison were observed more frequently in the stream during sampling of N4D ($n = 7$) than of N2B ($n = 1$). Bison were observed in the stream during sampling immediately above the N4D sampling site during June, July, and August—a time which sediment concentrations and TP spiked and the other bison-accessible stream, N2B, was dry (Fig. 4A, B). This finding also corresponds with the GPS data, which showed that bison were observed 4× more often in N4D than N2B during these months (Table 3, Fig. 6). However, bison presence in the riparian buffer was 8× higher in December, January, and February than in other months (Fig. 6), a time when TSS concentrations were lowest and nutrients were highest.

Trends in the locations of GPS-collared bison were consistent across years sampled and between watersheds (Table 3). We standardized all GPS data by stream length. Bison were tracked more often in headwater tributary zones than the 3rd-order mainstem zones ($p < 0.001$). Bison spent a maximum of 6% of their time in the riparian zone and streams, and most of that time was spent in the riparian zones of tributaries ($p < 0.001$). In both years, bison spent nearly 2× as much time in N4D as in N2B ($p < 0.001$; Fig. 7, Table 3). In both streams, ~60% more wooded vegetation occurred at mainstem branches than at tributaries (Table 3). This difference may account for bison preference. The riparian zones in the bison watersheds make up 12 to 13% of the total watershed area, but bison spent only 6% of their time in the 10-m riparian zone, a result that suggests they may be selecting against riparian areas. The density of bison trail crossings was 48% greater in N2B than N4D. The density of trails at N2B was 0.024 crossings/m of stream length, compared to only 0.016 crossings/m at N4D. A bison stream crossing was documented approximately every 41 m of stream length at N2B and every 67 m at N4D.

Discussion

Our observed effects and discussion points should be considered tentative because our study design could not include true replication at the primary scale of interest and may have contained confounding factors (i.e., burn regime and other unmeasured watershed-scale differences, such as geology). Fire regime differed in each watershed and potentially confounds the effects of fire and bison on water-quality variables. Pseudoreplication occurred when water was sampled 3 times weekly at the same streams because the water samples were not independent of one another. However, our analysis of temporal autocorrelation and subsequent data treatment (i.e., blocking) minimized effects to the F-ratio. The strength and unique aspect of our study (e.g., long-term water-quality monitoring in bison-grazed watersheds in remnant tallgrass prairie) also is its statistical shortcoming. Therefore, future studies will be required to assess further the effects of bison on water quality and of other managed ungulates like elk and cattle on the tallgrass prairie.

The effects of bison presence and prescribed prairie burning on suspended sediment and nutrient concentrations appeared minor in the KPBS study catchments. The small amount of time (<6%) spent by bison the streams could explain why their effect on TSS and nutrients was minimal. Bison did increase TSS while standing in the stream and increased bare soil by wallowing and pawing in riparian areas, but their presence in the watersheds did not increase long-term sediment or nutrient concentrations when compared to an ungrazed watershed. The prescribed prairie burning did not have immediate effects on sediment nor did the yearly interval frequency of fire. The slight differences in nutrient concentrations among watersheds cannot be attributed clearly to bison, but burning did temporarily decrease nutrient levels.

We did not detect a direct effect of fire on TSS, but we did observe a significant decrease in nutrients. Prairie burning at Shane Creek and throughout the Great Plains typically occurs during early spring, a time when precipitation is greatest, and the potential for overland flow is high because of lack of vegetation. Above-ground biomass is completely burned during fires, but the roots still bind the soil because of stimulated root production (Johnson and Matchett 2001), making overland erosion unlikely on Konza Prairie (Oviatt 1998). During the 3 wk after fire when the soil was bare, relatively low amounts of precipitation (<16 mm/d) occurred on 7 d. The prescribed fire at Shane Creek reduced TN 50% and TP 200%, a trend consistent with reductions observed after 2 other tallgrass prairie burns (Larson et al. 2013). Nutrient reduction might have been caused by algal growth and nutrient uptake in response to increased light availability after burning. We were able to document fire effects only in an ungrazed watershed, so future investigators should examine whether introduction of grazers shortly after fire (a common practice in tallgrass prairie) alters TSS concentrations in streams.

Multiple lines of evidence suggest that bison prefer certain watersheds and that these preferences may change over time. Our GPS and observational data show that bison spent more time in watershed N4D than N2B in 2009 and 2010. However, watershed N2B had 2× the density of stream crossings and 2× the wallow area found in N4D. These stream crossings and riparian wallows could be scars from past bison use and may not reflect present bison activity, or they might show that bison tend to use N2B to get from one preferred area to another. Bison move to watersheds after a fire, and fire occurred in both watersheds N2B and N4D in spring 2009. Bison preference for a watershed also might be associated with discharge or the availability of permanent water. Bison favored N4D, the watershed that had a greater average Q and a supply of flowing water in summer.

Bison displayed affinity for nonwooded sections in upland tributaries. Bison seldom consume woody species (Knapp et al. 1999) and avoid wooded areas (Allred et al. 2011b). Our data showed that the bison spent a larger proportion of time in the smaller upland tributaries, which had less riparian woody cover (Table 3) than in the mainstems. Woody vegetation dominates the mainstem riparian zones of our study streams, and thick forest galleries surrounding the mainstem may hinder or deter access for bison. Avoidance of the wooded mainstems could be a result of lack of food, desire to be in windy areas to deter insects, or hindrance of animal movement.

How trends in animal density and seasonal patterns of grazing are connected to nutrient and sediment dynamics is not obvious. A seasonal 10× spike in TSS concentrations (Fig. 4A–C), an increase in TP, and a 4× increase in bison use at N4D compared to the dry N2B stream occurred during late summer and early autumn (Table 3). Thus, we can hypothesize that the bison had moved to N4D to have better access to water, resulting in the observed seasonal increase in TSS and TP concentrations in N4D. Bison require more water in summer than in other seasons because of increased metabolic activity and often shift from upland grazing to lowland grazing where plant productivity is greater (Knapp et al. 1999). In winter, bison eat snow to meet their water needs, a behavior that could limit the need to access streams. However, bison abundance in the riparian buffer and stream-water TP concentrations were highest in winter. Bison probably congregate in the lowlands in winter to shelter from cold and to obtain drinking water because snow is not prevalent at KPBS most years. Bison use of lowlands decreases in the summer and increases in the winter months (Fig. 6). If bison density affects water-quality variables, then sediment and nutrient concentrations could be seasonally influenced.

We monitored suspended sediment and nutrient export dynamics, but we were unable to detect potential local effects from fire and bison. Nutrient and sediment inputs may be limited to the site of impact and not the entire stream network. Headwaters often retain sediments and nutrients (Alexander et al. 2007), which could cause a failure to detect treatment differences based on our analyses of samples collected at a single station at the outlet of the watershed. Our analysis of total exposed sediment near the water-sampling location suggests exposed sediment could not explain the 10× increase of TSS at N4D. However, moderate bison use of the stream near the sampling location (Fig. 7) could have influenced TSS concentrations. A previous study showed locally constrained effects of bison at stream crossings, which had lower macroinvertebrate richness and greater amounts of fine sediments compared to sites immediately upstream from the crossings (Fritz et al. 1999). Bison do heavily trample the permanent springs on KPBS when most of the ephemeral reaches are dry and export is not possible (data not shown). Bison and fire could have significant local consequences for the biological communities and geomorphology that we did not measure.

Cattle are often viewed as potential surrogates for bison in Great Plains grasslands. These large ungulates are closely related and feed differently than other large herbivores native to the ecosystem (e.g., deer are browsers). Cattle and bison enhance prairie vegetation diversity similarly (Collins et al. 1998) and facilitate soil nutrient cycling (Knapp et al. 1999). However, few studies have examined the in-stream effects of either species in tallgrass prairie. Bison and cattle differ in their water consumption and locations of grazing lawns. Cattle prefer lowland grazing and require more water than bison (Christopherson et al. 1979, Allred et al. 2011b), so their effects on streams may differ. Baseline reference data for effects of bison on sediment and nutrient concentrations are needed to make comparisons to effects of cattle. Bison and cattle stocking densities must be taken into account when comparing animal effects. Bison densities at KPBS are considered low to moderate density (~0.21 AU/ha), whereas cattle densities in the Flint Hills region of Kansas are often 0.8 AU/ha or greater (Derner et al. 2006). Continuous cattle grazing can cause substantial increases in sediment and nutrient loss in Kansas (Olness et al. 1975), and we presume these sediment and nutrients enter waterways. More research is needed to compare the impacts of bison versus cattle in prairie streams because current knowledge hints at important species differences.

The greatest sediment and nutrient values recorded in our study fall below current ranges for most streams across this ecoregion. TSS reference values do not exist for this area, but our values from KPBS watersheds that experience bison and fire (median: ~2 mg/L TSS) are 2 orders of magnitude lower than values in streams draining watersheds affected by row-crop agriculture (median: ~200 mg/L TSS; Dodds and Whiles 2004). Smith et al. (2003) suggested reference nutrient ranges of 20 to 300 µg/L for TN and 7 to 75 µg/L for TP in the Great Plains/Shrublands ecoregion where our study took place. Our values (with bison and fire) fall within these ranges. Dodds et al. (2009) documented regional nutrient concentrations in streams influenced by humans 2× (TP) and 4× (TN) greater than values in our study. Our data indicate that bison and fire are not significant drivers of sediment and nutrient export in these tallgrass prairie streams. In all, the natural processes (i.e., fire and bison) occurring in tallgrass prairies does not hinder good stream-water quality.

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Figures

Figure 3.1 Map of Konza Prairie Biological Station, Kansas (USA), and the 3 studied watersheds (lat 39°5'55.65"N, long 96°36'19.91"W). N2B and N4D contain bison with unrestricted access between watersheds, whereas Shane Creek is ungrazed.

Figure 3.2 Photographs showing a large paw patch from bison (A), a bison wallow near a stream (B), and a natural exposed sediment patch (C). Photographs are from Konza Prairie Biological Station, Kansas.

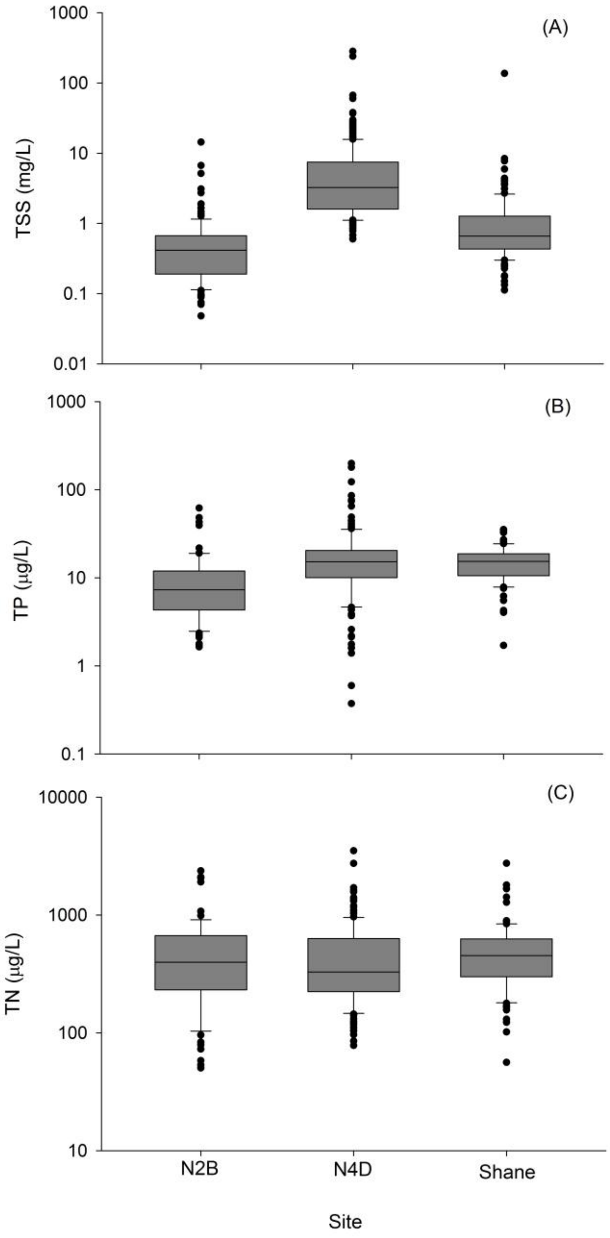

Figure 3.3 Boxplots (on log-scale) of total suspended solids (TSS) (A), total P (TP) (B), and total N (TN) (C) for 3 watersheds at Konza Prairie Biological Station, Kansas. Samples were taken 3 times weekly when streams were flowing from May 2009 through Sept 2010. Lines in boxes are medians, box ends are quartiles, whiskers show 95% confidence intervals, and dots show statistical outliers.

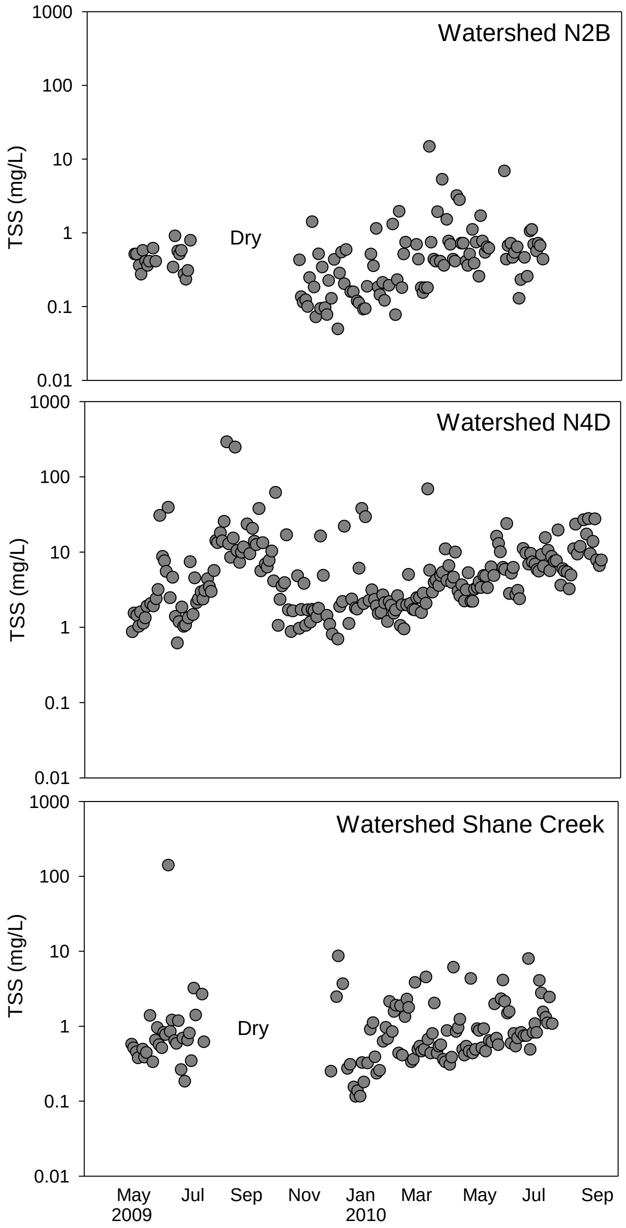

Figure 3.4 Temporal trends in total suspended solids (TSS) for stream N2B (A), N4D (B), and Shane's Creek (C) on Konza Prairie. The intermittent streams N2B and Shane were dry from July to November 2009, while TSS increased >10× at N4D (note the log scale). TSS did not increase during the 3 wk after a prescribed prairie burn at Shane Creek in March 2010.

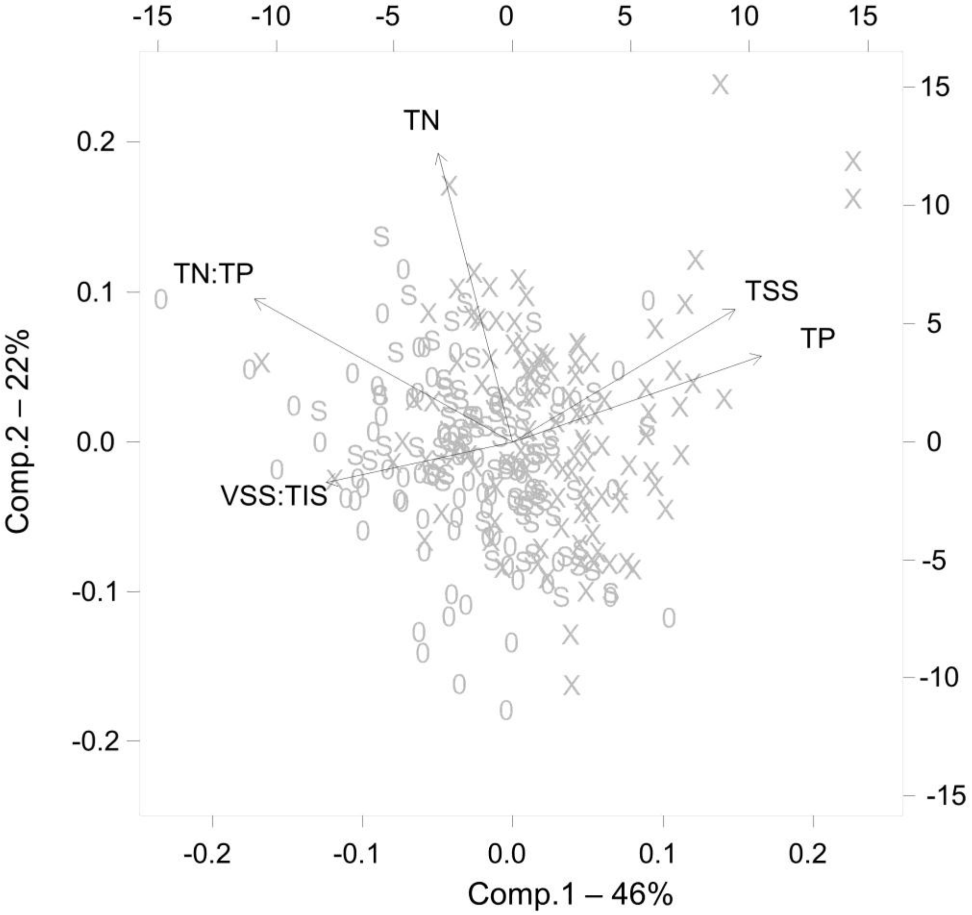

Figure 3.5 A principal component analysis biplot showing the relationship among 5 measured water-quality variables, all which are log(x)-transformed. Comp = component, TN = total N, TP = total P, TN:TP = TN:TP molar ratio, TSS = total suspended solids, and VSS:TIS = VSS:TIS ratio. The data are from 3 streams at Konza Prairie, Kansas. The points are coded by watershed: 0 = N2B, X = N4D, and S = Shane Creek.

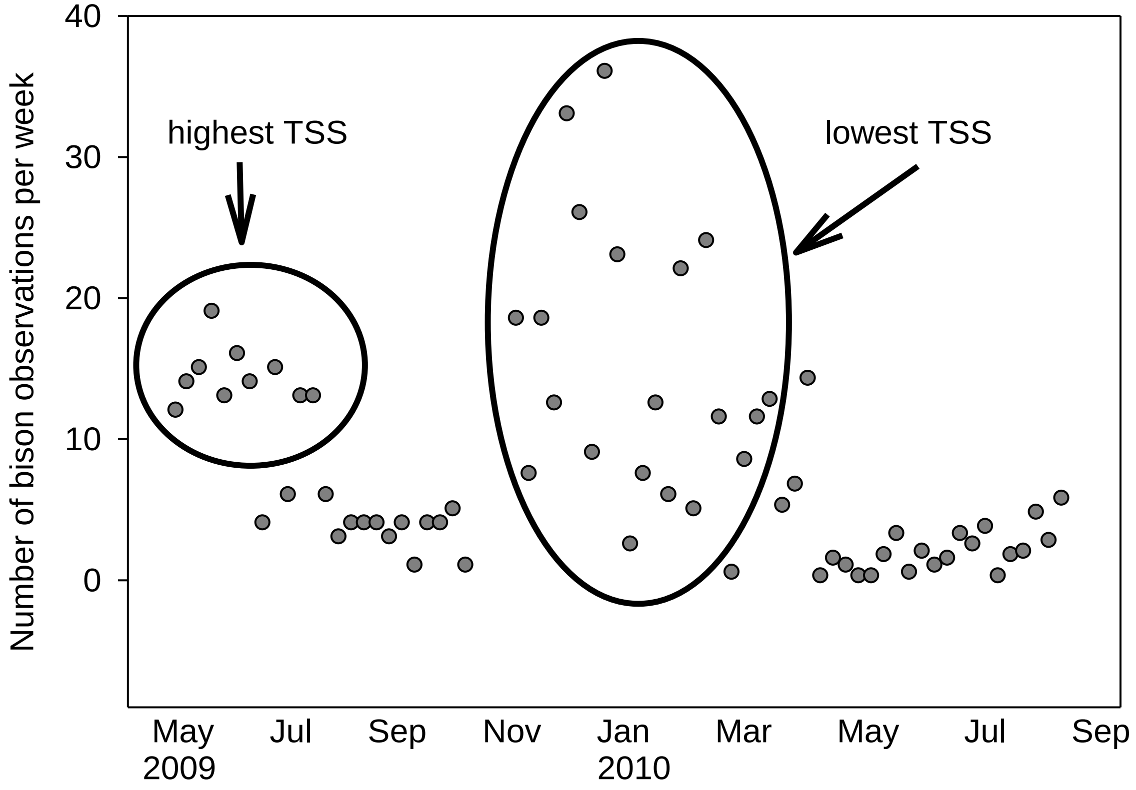

Figure 3.6 Temporal trends in bison use of the riparian buffer (within 10 m of stream N4D) at Konza Prairie Biological Station, Kansas, from May 2009 through August 2010. Ovals indicate periods during which total suspended solids (TSS) were highest or lowest.

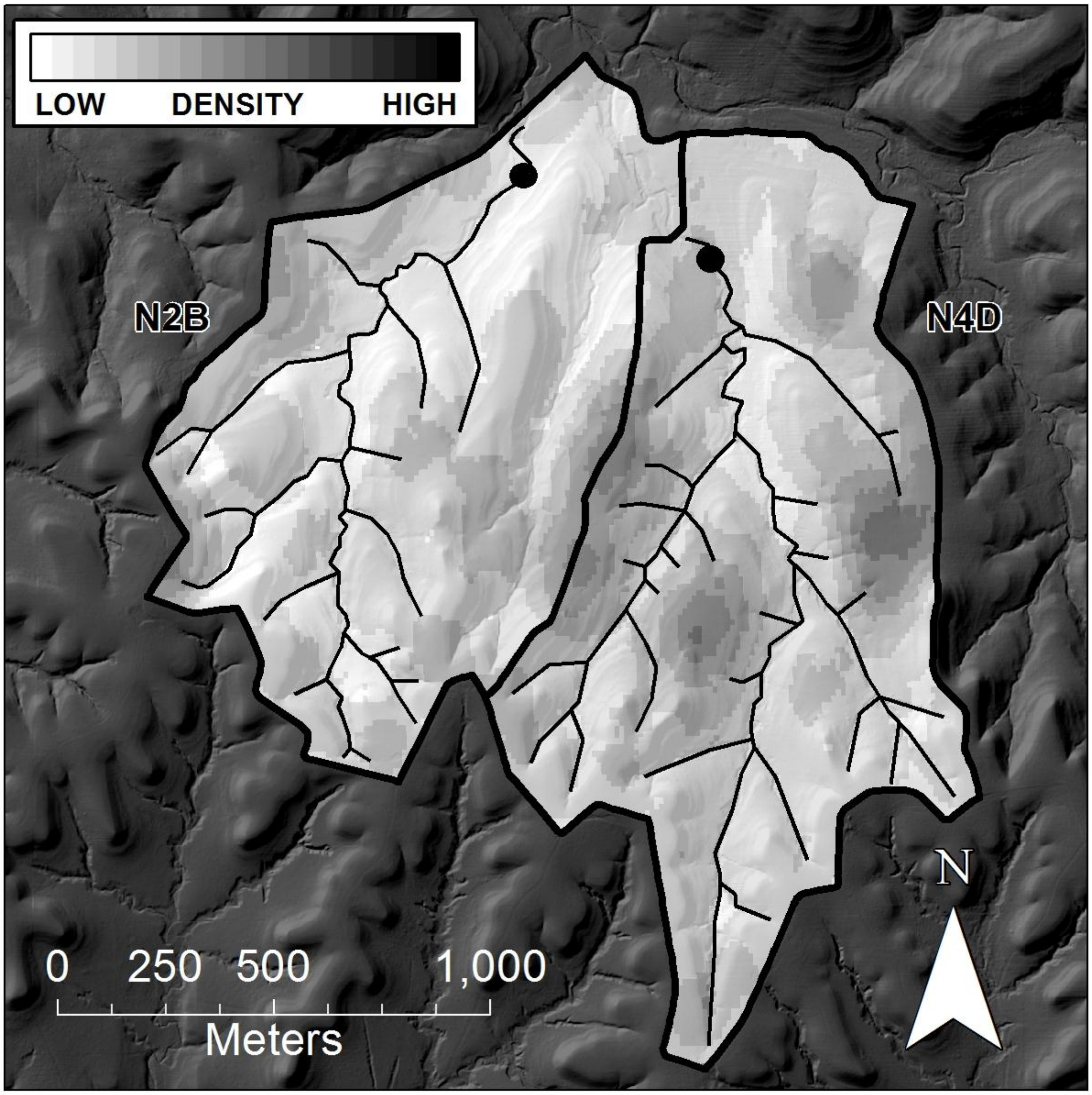

Figure 3.7 A map of the relative density of bison in watersheds N2B and N4D at Konza Prairie Biological Station, Kansas in April 2009. Bison spent 2× as much time in N4D and is N2B. Darker patches indicate a greater density of bison, and the black dots indicate location of water sampling.

Tables

Table 3.1 Summary of the watershed characteristics and management at Konza Prairie, Kansas. Values with different superscripts were significantly different among streams (χ^2 test, $\alpha/3 = 0.017$). The exposed sediments and % contribution of sediments were quantified in a 10-m buffer from the stream and standardized by stream length.

Characteristics	**Watershed**		
	N2B	N4D	Shane
Area (ha)	78	119	415
Bison grazing (year round; ~ 0.21 animal units/ha)	Yes	Yes	No
Burn interval (y)	2	4	1
Average floodplain slope (%)	7.5	8.0	8.6
Longitudinal slope (%)	0.02	0.02	0.02
Floodplain area (m^2/m stream)	65^a	46^b	101^c
Average daily discharge (m^3/s)	0.009		
Sinuosity ratio	1.6	1.4	1.4
Exposed sediments (m^2/m)	0.18	0.16	
Contribution of bison wallows to exposed sediment (% area)	12	7	
Contribution of bison pawing to exposed sediment (% area)	12	28	
Contribution of naturally bare banks to exposed sediment (% area)	76	65	

Table 3.2 Median suspended solids and nutrient concentrations at 3 streams on Konza Prairie, Kansas. We examined total suspended solids (TSS), total volatile solids (VSS), total inorganic solids (TIS), total N (TN), and total P (TP) to determine effects of bison presence and prescribed fire. Values with different superscript letters are significantly different among streams (Mann–Whitney *U* test, α/3 = 0.017). * indicates that nutrient values were significantly lower after than before a prescribed burn (*t*-test, α = 0.05).

Variable	**Stream**		
	N2B	N4D	Shane
Number of TSS samples	116	196	127
Median TSS - no bison in water during sampling (mg/L)	0.42^{a}	3.95^{b}	0.66^{a}
Median TSS - bison in water during sampling (mg/L)	0.09^{a}	8.46^{c}	
Median VSS (mg/L)	0.10^{a}	0.35^{b}	0.17^{a}
Median TIS (mg/L)	0.30^{a}	3.40^{b}	0.50^{a}
Median VSS:TIS	0.4^{a}	0.12^{b}	0.32^{a}
Number of nutrient samples	76	133	80
Median TN (µg/L)	398	328	451
Median TP (µg/L)	7^{a}	15^{b}	15^{b}
Median TN:TP molar ratio (µg/L)	48	22	31
Median TN - after fire (µg/L)			406*
Median TP - after fire (µg/L)			6*
Median TN:TP molar ratio - after fire (µg/L)			1*

Table 3.3 The number of bison global positioning system (GPS) coordinates (2-h measurement interval) in watersheds N4D and N2B on Konza Prairie, Kansas. All values are normalized by watershed area or stream length. The tributaries are 1st- and 2nd-order streams, and the mainstem is the 3rd-order stream section. The riparian zone was delineated as a 10-m buffer from the stream center line.

Variable	Year	N4D tributaries	N4D mainstem	N4D all	N2B tributaries	N2B mainstem	N2B all	% difference among tributaries	% difference among mainstems
Number of watershed observations	2009			5092			3410		
	2010			5699			3453		
	Mean			5396			3432		
Number of riparian observations	2009	224	157	381	118	107	226	62	38
	2010	267	82	349	118	124	242	77	–41
	Mean	246	119	365	118	116	234	70	3
% observations in riparian zone	2009	5.1	0.6	6	1.6	0.6	2	106	–4
	2010	6.1	0.3	6	1.6	0.7	2	118	–79
	Mean	5.6	0.4	6	1.6	0.6	2	112	–38
Number of observations in summer	2009	59	44	103	6	20	26	163	75

% woody vegetation in riparian buffer	2009	34	56	45	39	61	50	-14	–9

Chapter 4 - Grassland fire and cattle grazing regulate reptile and amphibian community patch dynamics

Larson DM. Fire and cattle grazing regulate reptile and amphibian patch dynamics. *Environmental Management*, in review.

Abstract

Fire and grazing are common management schemes of grasslands globally, and are potentially important drivers of reptilian and amphibian (herpetofauna) metapopulation dynamics. Few studies have assessed the impacts of fire, cattle grazing, and their legacies on herpetofauna assemblages in any grassland biome. A patch-burn grazing study (PBG) at Osage Prairie, Missouri, USA in 2011-2012 created landscape patches with treatments of grazing, fire, and legacy effects. As response variables to the application of treatments, I used robust-design occupancy modeling to estimate patch occupancy and detection rate within patches, and dispersal (i.e., recolonization and extinction) across patches. I conducted redundancy analysis (RDA) and a permuted multivariate analysis of variance (PERMANOVA) to determine if patch type and the associated environmental factors explained herpetofauna assemblage structure. Estimates for reptiles indicate occupancy was seasonally constant in control patches ($\psi \sim 0.5$), but declined to $\psi \sim 0.15$ in patches following the applications of fire and grazing. Local extinctions for reptiles were greatest in patches with fire or light grazing ($\varepsilon \sim 0.7$). For the riparian herpetofaunal community, patch type and grass height were important predictors of abundance; further, the turtles, lizards, snakes, and adult amphibians selected for different patch types. Site and in-stream characteristics, but not patch type, predicted the aquatic amphibian community. The varying responses from taxonomic groups demonstrates habitat partitioning across multiple patch types undergoing treatments of fire, cattle grazing, and legacy effects. Prairies will need an array of patch types if the goal is to accommodate multiple herpetofauna species and maximize diversity.

Introduction

Despite fire and grazing are the prevailing management tools for grasslands, little information is known how these practices influence amphibians and reptiles (herpetofauna). Worldwide, these organisms are under threat of extinction from multiple stressors, especially reduced habitat and habitat alterations, or are often data deficient (Stuart et al. 2004, Böhm et al. 2013). This study examines herpetofaunal responses (i.e., occupancy, abundance, and dispersal) to prescribed fire, cattle grazing, the interaction, and legacy effects from patch-burn grazing (PBG) in tallgrass prairie. Patch-burn grazing is a relatively new concept envisioned to create habitat heterogeneity for wildlife while maintaining cattle production; if shown to be effective, PBG could change the traditional grassland management paradigm.

Tallgrass prairie and other grassland types historically covered vast portions of the globe, but these ecosystems are now fragmented parcels. The remaining tallgrass prairie swatches are typically managed for intensive cattle grazing by private landowners, and less commonly ecosystem integrity and research. The predominant management tools are fire, grazing, and haying, which are essential for grassland maintenance and enhancing diversity (Stewart 1951). Most fires occur at an interval of 1-10 years (Abrams 1985) and cover large expanses of the landscape. The majority of cattle grazing regimes in tallgrass prairies are high stock densities (0.8 animal units/ha or greater) for a full stock season (May–Oct) (Derner et al. 2006). Given that native grasslands, and particularly tallgrass prairie, can be considered an endangered ecosystem with intensive land management, research is needed to understand how these practices influence herpetofauna.

Despite fire and grazing are common practices in grasslands, few studies have addressed the consequences to herpetofauna. The lack of research is surprising due to the moderately–high diversity of herpetofauna in prairies. For example, tallgrass prairie is habitat for at least 17 species of amphibians and 25 species of reptiles (Johnson 2000). None of these species are endemic to tallgrass prairie, and most species have large ranges which expand across eastern and central North America that encompass several biomes (Conant and Collins 1998). Studies thus far focused on a single species (e.g., collared lizards; Blevins & With 2011), a single management technique, usually fire (e.g., Cavitt 2000, Wilgers & Horne 2006), and/or other biomes (e.g., Argentinean grasslands; Cano & Leynaud 2009, montane forests of North America; Pilliod et al. 2003, and Australian arid-woodlands; James 2003).

The potential negative impacts of fire and grazing on herpetofauna are many. The breeding season and peak activity of herpetofauna is tightly connected to the fire and grazing season in tallgrass prairie, both typically beginning around April. Direct mortality of herpetofauna from fire is well documented (e.g., Russell et al. 1999). Vegetation structures (such as grass height and litter depth) in grasslands are reduced by both burning and grazing, which a decrease in litter can decrease soil moisture and negatively affects the skin respiration capacity of amphibians (Duellman & Trueb 1994). Further, vegetative cover provides refuge from predators and high temperatures (Seebacher & Alford 2002) and if removed, could make herpetofauna vulnerable. Cattle can increase nitrogenous waste and sediment yields to aquatic systems, both of which can have negative impacts to amphibian larval development, survival and post-metamorphic recruitment (Rouse et al. 1999, Schmutzer et al. 2008).

Despite the potential negative consequences of fire and grazing, these are natural processes grassland herpetofauna have presumably co–evolved with. Historically, there were strong fire–grazer interactions in a patch–work design across the landscape (Fuhlendorf et al. 2009). Patch–burn grazing (PBG), sometimes referred to as pyric-herbivory, is a new management framework intended to promote habitat and animal diversity while continuing cattle production. The PBG design mimics a natural, historical regime and is implemented whereby fire and grazers are induced over patches in space and time, creating heterogeneous landscapes. The landscape mosaic provided by PBG created an ideal opportunity to study multiple management techniques on the patch dynamics of herpetofauna.

Objectives

The goals of this study were to determine how the herpetofauna assemblage responded to fire, cattle grazing, the interaction, and legacy effects in tallgrass prairie undergoing PBG. As animal response variables to treatments, I estimated and compared the parameters of occupancy (ψ), detection (p), local recolonization (γ), local extinction (ε), and species richness (S) among patches from repeated field surveys. I also related amphibian and reptile community assemblages to patch types and the associated habitat variables. I hypothesized that herpetofauna occupancy, abundance, and richness would be lowest in patches with fire and cattle grazing because these habitats would be unsuitable or unfavorable. I expected patch extinction to increase in the treated patches following the application of fire and/or grazing, either because herpetofauna would behaviorally avoid those patches and/or experience greater mortality. Because I predicted extinction in treated patches to increase, I also expected recolonization of neighboring control patches to increase. I suspected detection probability of herpetofauna would be imperfect. Lastly, I questioned if herpetofauna would respond differently to patch types depending on taxonomy and life history traits, and therefore examined responses to the lowest hierarchical level possible for the analyses used (i.e., Order, Class, or Species).

Methods

Study site description and study design

This study encompassed 4 small watersheds (10–54 ha) at Osage Prairie Conservation Area near Nevada, MO, USA in spring 2011 and spring 2012 (Fig. 1). Each stream in the watershed was a first-order, intermittent stream typically flowing from fall to early summer. Watershed and stream characteristics were similar within and across study sites (Larson et al. 2013a), so I expected differences in animal assemblages to reflect applied treatments. All the watersheds were completely encompassed by native tallgrass prairie, where past management included prescribed burning approximately every 5 years, triennial haying in small patches, and the occasional removal of riparian trees >10 cm in diameter.

Beginning April 2011, Osage Prairie watersheds underwent a designed PBG experiment. Each studied watershed was burned mid-April with one-third of the watershed burned (Fig 1). Two watersheds were inhabited by cattle (cow/calf pairs) at densities of 1 cow unit per 6 acres from mid-April to early August. In 2012, treatments were applied to different patches. The studied watersheds and patches are close enough (< 2km) to allow herpetofaunal movement across patches and watershed boundaries. The average distance between sampling points within patches was approximately 600 m, so the animals were likely able to disperse across patch types if they were to respond to treatments (Smith & Green 2005). For this study, there were six patch types: (1) Control (with no fire or grazing in the last five years); (2) Fire (patch burned that year, roughly in mid-April); (3) Lt Grazing (light cattle grazing beginning ~May 1); (4) F+G (fire in mid-April, followed by heavy cattle grazing ~May 1); (5) Fire-Legacy (patch-burned the previous year; no fire or grazers the sampled year); and (6) F+G-Legacy (F+G the previous year; none the sampled year).

Animal surveys

I surveyed for animals in March-May 2011 and 2012. Sampling occurred in each patch, 2-3 times per month but within 5 days of each other to meet population closure assumptions for occupancy modeling. All surveys were within a 10 m riparian zone and standardized in each patch. I captured herpetofauna using one coverboard array, a visual encounter survey along 3 permanent transects, two minnow traps, and four PVC pipes. Once captured, I collected information regarding species, age class and a photograph. All captured animals were released at the exact point of capture after the survey was completed in that patch (max. 0.5 h holding time) to avoid double counting. Detailed survey methods are available (Appendix A).

Habitat variables

I collected riparian vegetation data during each month, which includes ground cover (bare or grass), percent cover, litter depth, and grass height. Vegetation structure data were collected along two 10 m transects perpendicular to the stream, with a 1 x 5 m plot every 5 m along the transect (Daubenmire 1959). Data were averaged for each transect and associated with riparian fauna found in that plot. The maximum response values for percent cover, litter depth, and grass height was used for each patch type each year. I conducted an analysis of variance (ANOVA), followed by Tukey’s Honestly Significant Difference post hoc test to determine if vegetation structure differed among the six patch types.

I collected the following information for the aquatic community (amphibians captured in or along the stream): (1) average depth, (2) substrate type (silt or rock), (3) percent riparian canopy cover, and (4) percent in–stream vegetation. Aquatic habitat information was collected precisely where the amphibian was captured, and averaged for a 1 x 3 m plot in the stream. I collected and processed water samples (APHA 1995; Appendix A) to obtain total suspended solids (TSS) and ammonium (NH_4^+) concentrations to relate to amphibian tadpole abundance.

Species richness

I calculated species richness for reptiles and amphibians. Richness was the total number of species during the primary seasons 2 and 3 following treatments (n=6 sample dates). Using ANOVA and Tukey's HSD post hoc test, I compared richness of the six patch types, across watersheds, and sample years.

Multivariate statistics

The objective of this analysis was to relate herpetofauna community structure, land management treatments, and measured environmental variables using redundancy analysis (RDA). A RDA is an extension of multiple regression to include multiple response variables (i.e., the ecological community), where the community (Y) is constrained by linear combinations of the explanatory variables (X) (Appendix A). I conducted two separate RDA's for the different habitat types: the riparian community and the aquatic community. The herpetofauna species data were Chord transformed because this produced the highest amount of variation explained (Legendre & Gallagher 2001). A permuted (perm=9999) multivariate analysis of variance (PERMANOVA) was used to assess the significance of the overall RDA models, RDA axes, and

RDA terms using the *vegan* package (Oksanen et al. 2011) in R 2.14.1 (2011, R Development Core Team, Vienna, Austria).

Occupancy modeling

The goal of occupancy modeling in this study was to estimate occupancy (ψ) and detection (p) within a patch, and the rates of extinction (ε) and recolonization (γ) across patches (Appendix B). Occupancy is a state variable that can be used to assess the suitability of habitats; in this case, I compare herpetofaunal use of multiple patch types. The dispersal estimates (ε and γ) and changes in occupancy can infer animal response to management treatments. Occupancy modeling is necessary if detection is imperfect because false absences will result in an underestimation of the true occupancy level.

The robust-design occupancy model (or multi-season occupancy model) provides the four parameter estimates (ψ, p, ε, γ) based on detection/non-detection data. Parameter estimates for ψ and p are obtained for each of the primary seasons, and ε and γ are transition probabilities between primary seasons (see conceptual diagram in Appendix B). The four parameters are defined as follows: Occupancy (ψ) is the probability that a randomly sampled site is occupied by a species (i.e., a species is detected and accurately identified in a sampled site). Detection (p) is the probability an animal is captured, given it is present, at a site. Extinction (ε) is the probability that a site occupied in season t is unoccupied in season $t+1$. Recolonization (γ) is the probability that an unoccupied site in season t is occupied in season $t +1$.

The conceptual basis for robust design occupancy models can be complex; especially with my sampling design where treatments are applied through time and a treatment corresponds to a new primary season. For simplicity, I only include four patch types for occupancy analysis:

(1) Control, (2) Fire, (3) Lt Grazing, and (4) F+G. In this study, a primary season (S) is delineated by the application of treatments and corresponds to the months of March–May. So, S1 is prior to any fire or grazing (Control season; March), S2 is following the application of fire (Fire season; April), and S3 is following the application of fire and grazers (F+G season; May). To meet occupancy model assumptions of population closure during a primary season (Mackenzie et al. 2002), I sampled 3 times in each primary season within 5 days, in every patch. Across primary seasons (i.e., as treatments are applied), the model assumes an open population allowing for recolonization and extinction across patches. I predicted herpetofauna to respond to treatments via movement across patches, so therefore I estimated γ and ε between each primary season.

I used the robust–design occupancy model using the program MARK v.6.2 and an information–theoretic approach (Burnham & Anderson 2002) to evaluate which of the a priori model(s) best explain the relationship between the variables (i.e., time (between primary seasons), treatment, and/or interaction) and occupancy. Although covariates can be included in the AIC_c models, the potential combinations for *a priori* models with covariates were immense, so driving environmental factors were identified by multivariate procedures instead. Inestimable parameters are not reported. See Appendices A and B for more details on occupancy modeling.

Results

Captures

Across two years, I captured a total of 150 reptiles representing 14 species. The common reptiles were the Ground Skink (*Scincella lateralis*), Ornate Box Turtle (*Terrapene ornata*), and

Garter Snake (*Thamnophis sirtalis*). I captured 1,045 amphibians of 10 species. Southern Leopard Frog and American Toad tadpoles dominated these counts (Appendix C).

Vegetation and water quality responses to treatments

All the measured vegetation structures differed among patch type: *% cover* ($F_{(5,26)}$=16.72, p<0.001), *litter depth* ($F_{(5,26)}$=87.19, p<0.001), and *grass height* ($F_{(5,26)}$=7.68, p=0.010). In general, the Control and Lt Grazing patches had the greatest *grass height*, *litter depth*, and *% cover*; and the patches of Fire and F+G had significantly less vegetation. The Fire-Legacy and F+G-Legacy patches had greater *grass heights* and *% cover* than the Fire and F+G patches, which shows a vegetation recovery trajectory from the previous years' fire and grazing (Appendix D). These results justify the demarcation of the 6 patch types.

Total suspended solids (TSS) were similar at all watersheds prior to treatments ($F_{(3,30)}$=2.92, p=0.879) with a median of 4.85 mg/L (range: 1.1-78.7 mg/L). The prescribed fire did not influence TSS at any stream ($F_{(3, 14)}$=1.39, p=0.196). However, following the introduction of cattle to the two grazed watersheds, the median TSS increased four-fold (median: 15.54 mg/L; $F_{(2,132)}$=3.12, p=0.050).

Ammonium (NH_4^+) concentrations did not vary by watershed for 2 years prior to treatments ($F_{(3,63)}$=1.06, p=0.385) or following prescribed fire ($F_{(3,11)}$=0.59, p=0.829). Median NH_4^+ concentrations for ungrazed watersheds was 16.3 µg/L (range: 7-123 µg/L), but rose to 41.9 µg/L (range: 7-627 µg/L) after cattle were put on pasture in grazed watersheds in 2011 ($F_{(1,102)}$=2.60, p=0.010).

Fire mortality

Four patches were burned on March 20, 2011. I surveyed within 1 day of the fires and observed 6 dead and burnt turtles. Two were identified as Ornate Box Turtles (*Terrapene ornata*), one as a Western Painted Turtle (*Chrysmys picta bellii*), and three were not identifiable to species because of the burn severity. I was not able to fully assess fire mortality for snakes and lizards due to small body sizes, large burn patches, and surveying hours after the fires, which allowed time for scavenging.

Species richness

Across all patches and years, I captured 16 reptile species (Appendix C). Reptile species richness per *patch type* had a mean of 3 species and a maximum of 8 species. Richness for reptiles was influenced by *patch type* ($F_{(5,14)}$=3.31, p=0.035), with the Control and Lt Grazing patches containing slightly less species than the others (Appendix E). Reptile richness was not influenced by *watershed* ($F_{(3,18)}$=0.46, p=0.518) or *year* sampled ($F_{(1,18)}$=3.15, p=0.092).

In total, I captured 10 amphibian species (Appendix C). Amphibian richness not was affected by *patch type* ($F_{(5,14)}$=0.435, p=0.817), *watershed* ($F_{(3,18)}$=0.44, p=0.180), or *year* ($F_{(1,18)}$=3.65, p=0.072). In a patch, the mean richness of amphibians was 2 species with a maximum richness of 5 species (Appendix E).

Riparian redundancy analysis

A permutation test for the riparian RDA revealed the full model was highly significant ($F_{(12,26)}$=6.46, p=0.005). The first two axes of the full RDA model were significant (RDA1 ($F_{(1,35)}$=66.98, p=0.004 and RDA2 ($F_{(1,35)}$=36.57, p=0.005), and cumulatively these axes explained 74% of the variance in community structure. The PERMANOVA identified *patch type* ($F_{(5,22)}$=4.59, p<0.001) and *grass height* ($F_{(1,26)}$=3.11, p=0.048) as significant predictors of the riparian community (Appendix F).

Graphically, the RDA showed substantial structure in patch types, environmental variables, and riparian community associations (Fig. 2). The patch type Fire-Legacy clustered well in ordination space, with a strong association with snakes and high *% cover* (70-100%). Turtles were tightly associated with large *grass heights* (30-75 cm) and linked with the Lt Grazing treatment. Lizard abundance varied by *year*, with year 2012 having greater catches. Lizards were also closely connected with the Fire, F+G, and F+G-Legacy treatments, which had *bare* ground cover and shallow *litter depth* (0-17 mm). Adult amphibians were positively loaded on RDA1 concomitant with tall *grass heights* and high percentages of *grass cover*. Complete *grass cover* (100%) and deep *litter depths* (21- 55 mm) were characteristic of the Controls, but no reptile taxonomic groups selected for this treatment.

Aquatic redundancy analysis

The full aquatic RDA model was significant ($F_{(18,55)}$=1.46, p=0.051), as were the first two axes (RDA1, $F_{(1,67)}$=19.86, p=0.005; RDA2, $F_{(1,67)}$=7.44, p=0.005). Cumulatively, the two RDA axes explained 44% of the variation in community structure. The RDA triplot showed little structure regarding sites, environmental factors, and the aquatic community (Fig. 3). Adult amphibians showed a high affinity for *watershed*. All watersheds had adults detected; however, one watershed (with grazers) was occupied by 60% of the adults, likely because the watershed also contained two breeding ponds. The PERMANOVA found the variables *year*, *watershed*, *in-stream cover*, and *substrate* to be significant (Appendix F).

Robust-design occupancy modeling

Akaike's Information Criterion (AIC_c) identified a single, most parsimonious model regarding reptile occupancy, detection, and dispersal (Appendix G) with a high Akaike weight (w_i=0.89). The top AIC_c model determined occupancy and extinction were interactive effects of patch type and time, whereas detection and recolonization increased across seasons. The 95% confidence intervals for occupancy and detection were narrow, but large for dispersal estimates.

Occupancy (ψ) of reptiles corresponded to a patch type and time interaction (Appendix G). Reptile ψ was roughly 45% in all patch types prior to application of treatments. The ψ in the Control patches hovered between ~40-50% across primary seasons, but without trend (Fig. 4a). Conversely, ψ in the Fire and Lt Grazing patches decreased rapidly through time as treatments were applied, by ~50% (Figs. 4b and 4c). In the F+G patches, Seasons 1 and 2 had inestimable parameters; however, during Season 3, ψ was at the lowest estimate of only 13% (Fig 4d).

Extinction probability (ε) was an interaction of patch type and time (Appendix G). Unfortunately, the Control and F+G patches contained inestimable parameters. For the Lt Grazing patch, the extinction probability transition 2 occurs before the introduction of grazers, but still shows a likely effect from the prescribed fires (Fig. 5a). The Fire patches had a ~20% increase in ε during seasonal transition 2, following the prescribed fire (Fig. 5c).

Detection (p) estimates ranged from 40-50%, and increased marginally through time in all patch types (Fig. 5d). Similarly, recolonization (γ) was a function of time (and not patch) and increased only ~10% (Fig. 5b). The slight increase in p and γ suggests either my reptile capture ability improved with time, or these parameters are functions of reptile abundance as animals are more likely active and detected in Season 3.

Because amphibian abundance did not differ among patch types, I didn't expect to find dispersal differences across patches and did not proceed with occupancy modeling for the aquatic amphibian community.

Discussion

This is a first experiment that revealed the response of grassland herpetofauna community to various treatments of patch-burn grazing and recovery. Although this study occurred in tallgrass prairie, a rare and endangered ecosystem today, these 40+ herpetofauna species have large geographical ranges across North America and regularly experience prescribed fire and livestock enterprise, making results of this study widely applicable. To my knowledge, this is one of few experimental studies to examine animal occupancy and dispersal immediately following land management treatments. This analytical approach has potential for similar applications for other wildlife or to measure dispersal in response to other management techniques.

Distribution and dispersal due to land management

Amphibians did not have a statistically significant, direct response to treatments. Experiments with the American Toad (*Bufo americanus*) show this species possesses homing capabilities and will navigate to the same breeding pool annually, even when other breeding sites are available (Oldham 1966). Adult amphibians were closely associated with a particular watershed irrespective of treatment (Fig. 3), which demonstrates site fidelity. Further, tadpole location across treatments is dependent upon where adults choose to place the eggs. The evidence of site fidelity and the restriction of tadpoles to a basin could explain why the analyses did not find trends in amphibian community structure with land use.

This experimental approach and the notion of site fidelity assumed amphibians had a “choice” for breeding locations and placement of their eggs. However, amphibians are restricted to sites with adequate water (which is limited in ephemeral tallgrass prairie ponds and streams). Further, row crop agriculture and intensive cattle grazing are the dominant land uses across this region and amphibians had few options of breeding in basins without agricultural influence. Lastly, amphibian eggs were often laid prior to the initiation of fire and grazing, and in these cases the only way for tadpole response is to swim up or downstream ~ 0.5 km, which could be an energy demanding task during development.

Although I did not find direct amphibian avoidance of treatments, this does not preclude the possibility of negative consequences not measured here. Although prairie burning does not alter basic water chemistry (Larson et al. 2013a, b), the presence of cattle in riparian zones did. The cattle increased sediments and ammonium concentrations, which can be detrimental to tadpole development (Rouse et al. 1999, Schmutzer et al. 2008). Further, cattle trampling can widen stream channels (Belsky et al. 1999) where amphibians breed, which would reduce water depth and deplete water faster in these ephemeral systems.

Recolonization (γ) for reptiles was a low rate of <10%. Stable occupancy estimates in the Control patches showed that animal activity was not increasing through the primary seasons, so is not the likely reason for increased γ. Interpretation of γ should be cautioned because it is a limited estimate of dispersal according to the narrow definition (an unoccupied patch in time t becomes occupied in time $t+1$). Therefore, colonization in an occupied patch would not be detected. A future challenge for community ecologists is obtaining more accurate estimates of dispersal, and particularly colonization.

The occupancy (ψ) and extinction (ε) estimates through time suggest reptiles were directly responding to treatments: either by behavioral avoidance and/or a greater mortality in treated patches. Decreased ψ and increased ε may have occurred in treated patches because vegetation cover is removed (Appendix D), making some reptiles, like large snakes, more vulnerable to predation (Wilgers & Horne, 2007). Fire can cause mortality if animals are not able to escape or find refuge within the burned area (Russell et al. 1999), and I did document burned reptile carcasses which can affect ψ and ε estimates. Alternatively, the reptiles are avoiding competition and predation from each other and have separation of Grinnellian niches.

Niche differentiation and patch dynamics

Multiple lines of evidence indicate habitat partitioning by reptiles across prairie patch types. Reptile richness was greater in the Fire, F+G, and Legacy patches, and the RDA triplot (Fig. 2) showed clear separation of taxonomic groups to specific patch types. Turtles, snakes, and lizards are insectivores (to various degrees) and occupy similar trophic levels, which can invoke competition. Also, some snakes are predators of other reptiles, which may drive the separation of taxonomic groups to other patches to avoid predation. However, the disturbances and opportunity to disperse across patch types may lessen the need to summon the competitive exclusion principle (Hardin 1960). Similarly, the lizards may be a “fugitive species” (Hutchinson 1959), which are good dispersers and take advantage of newly burned habitats to avoid predators or superior competitors. The changing landscape of multiple patch types may be a primary mechanism for increasing alpha-diversity by allowing niche differentiation and reducing negative species interactions.

The higher reptile richness and abundance in Fire and F+G patches appeared to be driven by small–bodied lizards and snakes. These smaller reptiles are generally insectivores or eat other reptiles (Johnson 2000). Following fire and grazing the insect density and diversity increases (Callaham et al. 2003, Joern 2005), as well as reptile richness (Appendix E), thus potentially attracting reptiles foraging for food. Large reptiles were not observed in the Fire and F+G patches, likely because they are more vulnerable to predation (Wilgers & Horne 2007) and either avoid these low vegetated patches or have higher predation rates.

The habitat partitioning of reptiles suggests no taxonomic groups have selected specifically for Control patches in this study. The classic *Levins metapopulation model* (Levins 1969) expects that for metapopulations, some suitable patches will likely be unoccupied. Further, although control patch types appear unnecessary in the landscape, the consequences of reducing the number of patches and types can decrease rates of population growth (Mittelbach 2012). Despite the herpetofauna are not selecting the Controls during the study time frame of March-May, these patches may still be important features for population regulation and community assemblage at other times of year.

Management implications

Successful grassland conservation requires understanding the effects of disturbance and landscape heterogeneity on animal response. Fire and grazing are natural and essential ecosystem processes in all grasslands, and therefore will be continued. However, the majority of remaining tallgrass prairie is currently managed by annual prescribed burning and high-density grazing in large landscape patches (Derner et al. 2006); neither annual burns nor heavy grazing mimic the historical patterns or co-evolution with grassland herpetofauna.

Several studies suggest PBG is feasible and has benefits to plants and wildlife across many grassland types. Studies indicate that PBG does not hinder cattle weights (Limb et al. 2011), and can reduce cattle pests (Scasta et al. 2012) and invasive plant species (Cummings et al. 2007), making PBG a viable and attractive option for livestock farmers. Studies of PBG thus far show positive effects on bird (Fuhlendorf et al. 2006), small mammal (Fuhlendorf et al. 2010), and insect (Engle et al. 2008) biomass and/or diversity. In this study, herpetofauna selected for different conditions of burning and grazing, which provides additional support for the PBG design in terms of increasing animal diversity at the watershed and landscape scales. Consequently, the conservation of grassland herpetofauna requires an array of patch types.

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Figures

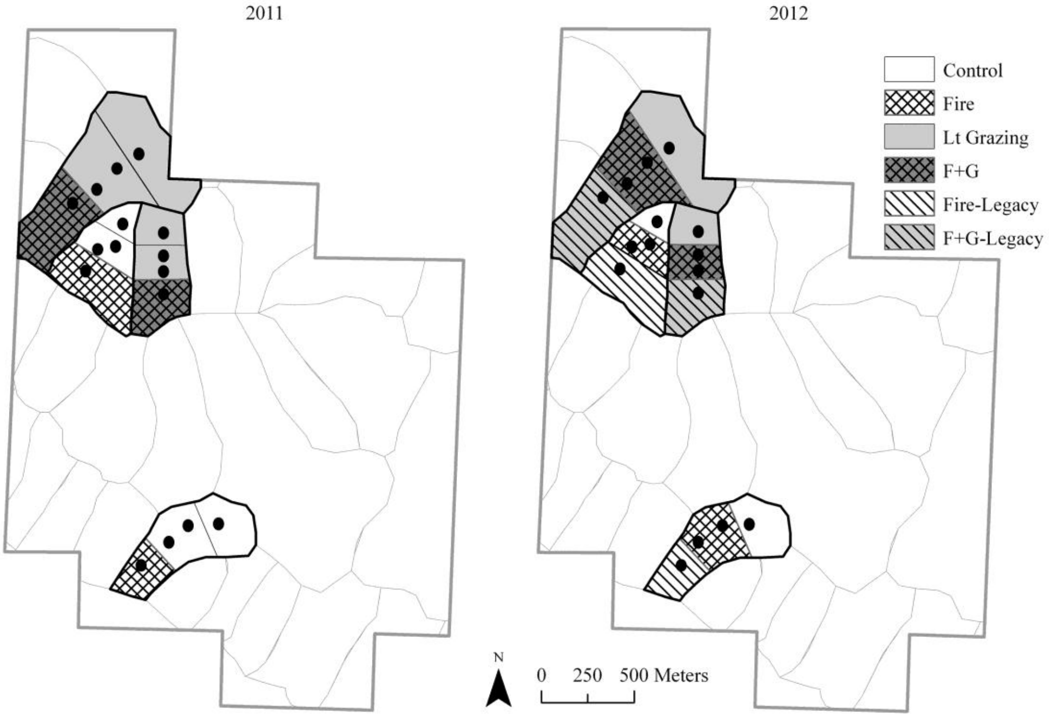

Figure 4.1 Landscape patches at Osage Prairie, MO, USA. Four watersheds were divided into three patches each (studied watersheds outlined in bold). Every patch was labeled one of six patch types: Control (no fire or grazing in last 5 yr), Fire, Lt Grazing (light cattle grazing), Fire-Legacy (burned previous year), F+G-Legacy (burned and grazed previous year), and F+G (burned and grazed during sampling). Permanent sampling locations are indicated by the black dots and are within the stream's 10 m riparian zone. Patch type changed in every patch from 2011 to 2012.

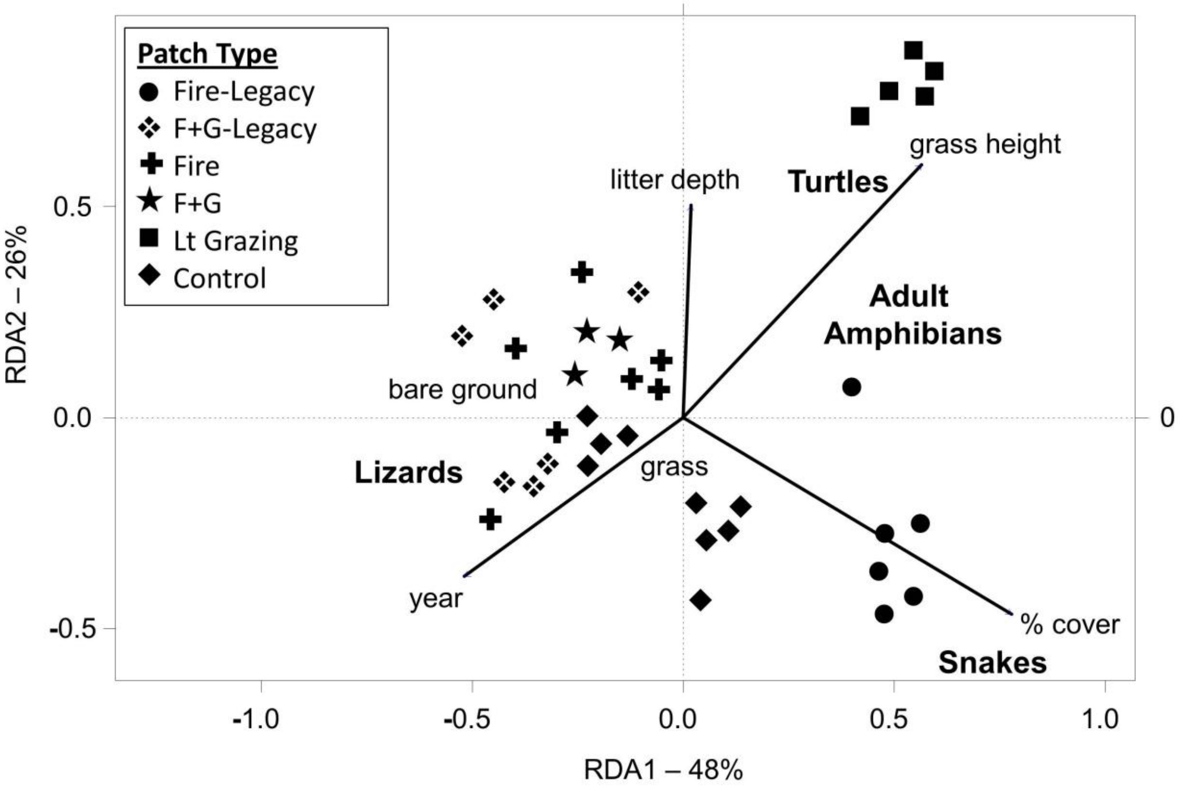

Figure 4.2 A redundancy analysis (RDA) triplot for a riparian community (turtles, snakes, lizards, and adult amphibians) from Osage Prairie, MO in 2011 and 2012. The animals were captured across 6 patch types indicated by symbols; the environmental factors are in lower caps; and the taxonomic groups are bolded. The full RDA model was highly significant (p=0.005), as were axes RDA1 (p=0.004) and RDA2 (p=0.005). A permuted multivariate analysis of variance (PERMANOVA) identified significant terms: treatment/patch type (p<0.001) and grass height (p=0.048).

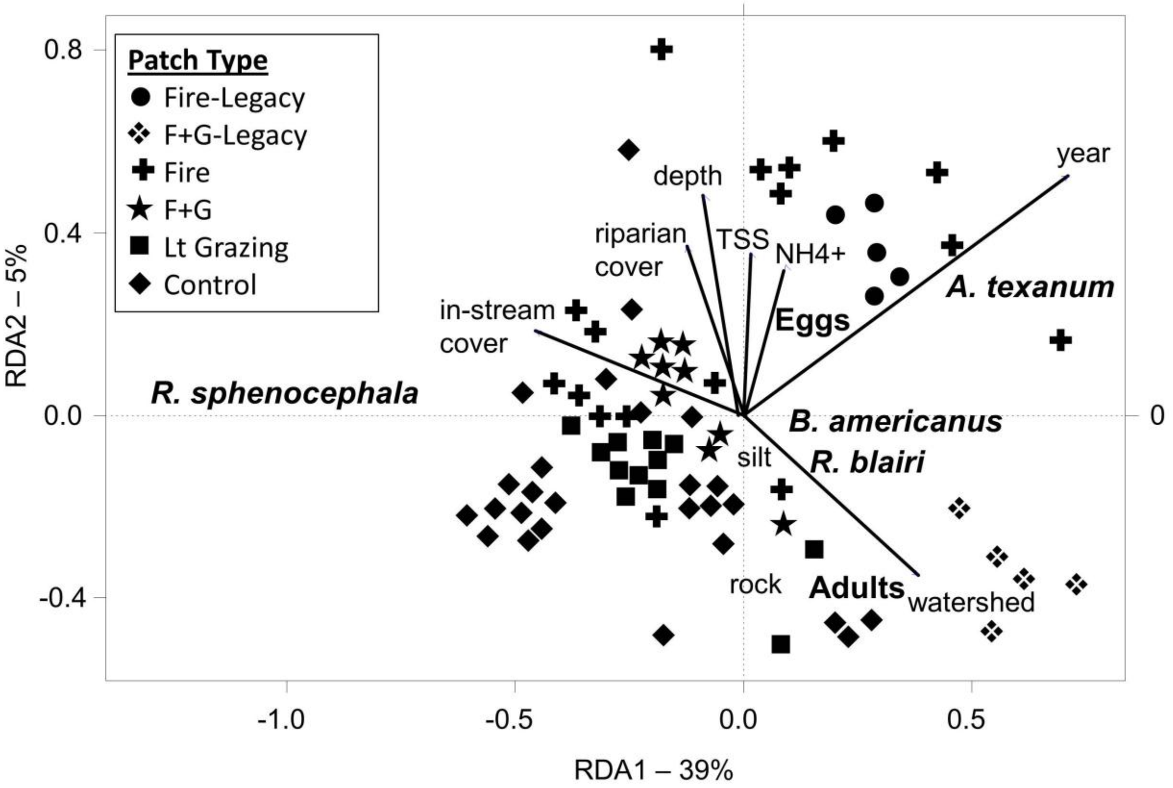

Figure 4.3 A redundancy analysis (RDA) triplot for the aquatic community from Osage Prairie, MO in 2011 and 2012. The taxonomic groups are colored black and include: *Rana (Lithobates) sphenocephalus* tadpoles, *Rana (Lithobates) blairi* tadpoles, *Ambystoma texanum* salamander larvae, *Bufo americanus* tadpoles, egg masses, and adult amphibians (includes multiple species). The aquatic amphibians were captured across 6 patch types indicated by symbols; the environmental factors are in lower caps; and the taxonomic groups are bolded. The full RDA model was significant (p=0.005), as were the axes (RDA1, p=0.005; RDA2, p=0.005). A permuted multivariate analysis of variance (PERMANOVA) identified significant terms: year (p<0.001), site (p=0.002), in-stream cover (p=0.007), and substrate type (p=0.029).

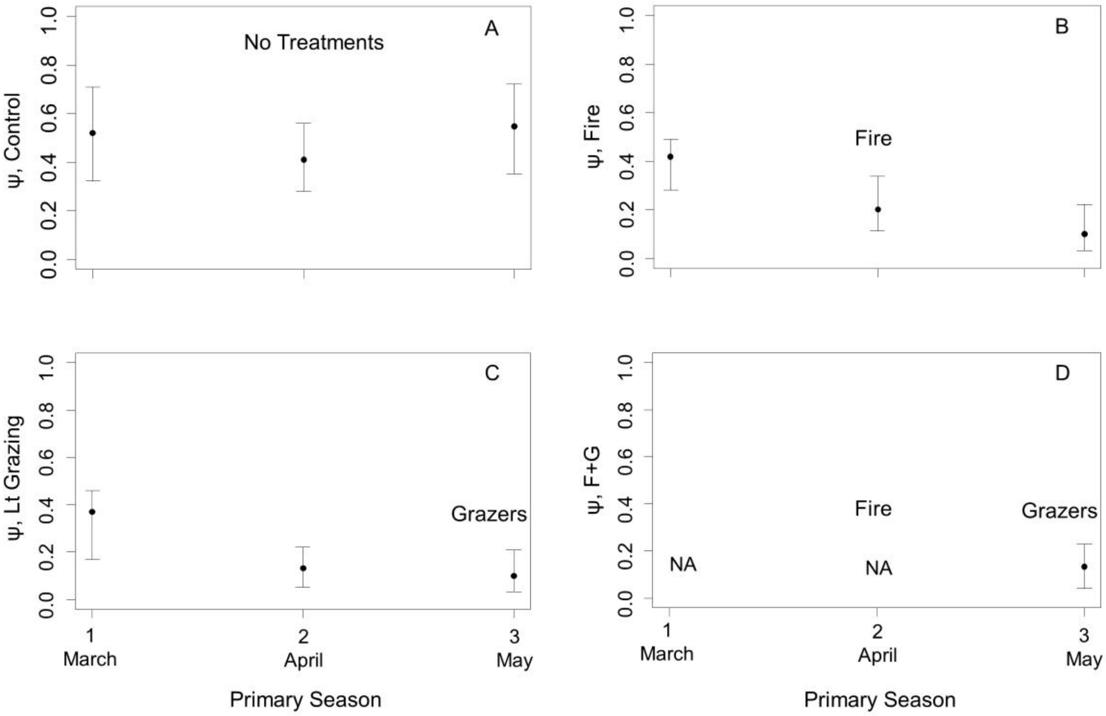

Figure 4.4 The estimate and 95% confidence intervals for reptile occupancy (ψ) in spring 2011 and 2012 at Osage Prairie, MO across seasons, where Primary Season 1 corresponds to ~March, 2 to ~April, and Primary Season 3 to ~May. The highest ranked AIC_c model included patch type and time effects (g*t). NA indicates inestimable parameters.

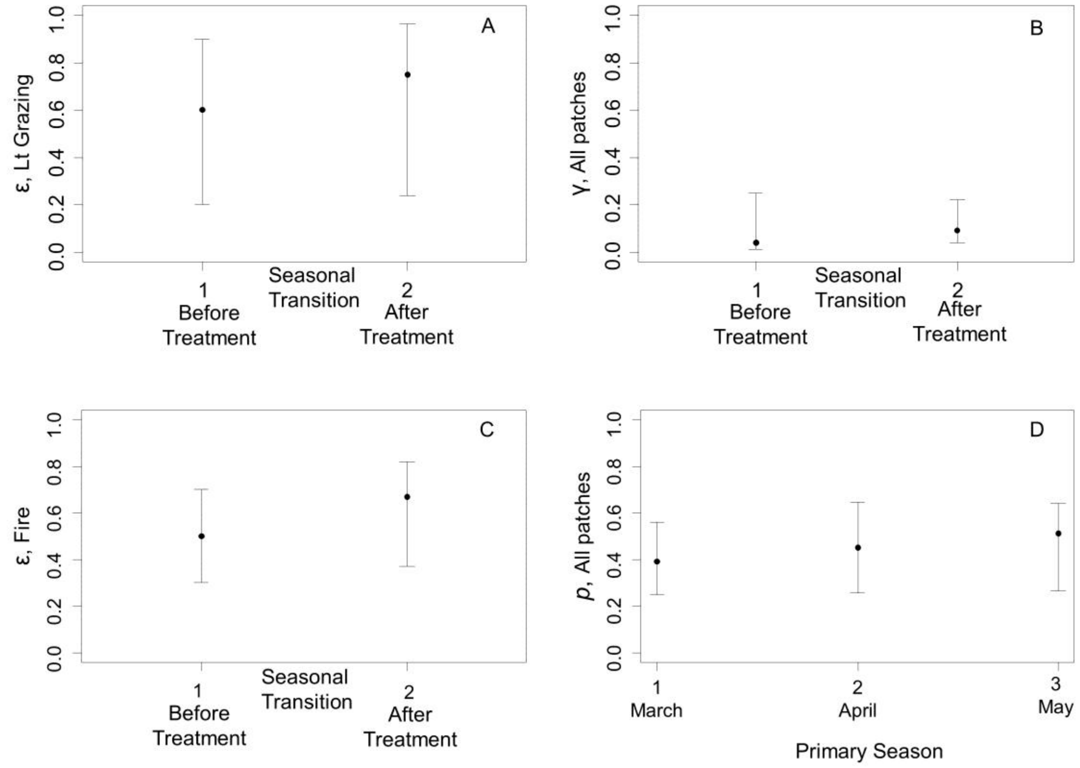

Figure 4.5 The estimate and 95% confidence intervals for reptile extinction (ε), recolonization (γ), and detection probability (p) in spring 2011 and 2012 at Osage Prairie, MO across seasons, where Primary Season 1 corresponds to ~March, 2 to ~April, and Primary Season 3 to ~May. The highest ranked AIC$_c$ model for ε included patch type and time effects (but 2 patch types were inestimable); and the highest ranked AIC$_c$ model for γ and p included time effects only.

Chapter 5 - Ecological state shifts in grassland streams following fire and cattle grazing: a multi-watershed experiment

Abstract

Fire and grazing are common in grasslands worldwide and are necessary for maintenance of grass cover and cattle production. The effects of grazing and fire on streams are not well characterized at watershed-scales (i.e., the scale most relevant for management and capturing ecosystem disturbance). Further, the fundamental role of riparian areas in grassland streams and the effectiveness of riparian fencing on protecting water quality are not well established. We examined alterations to stream water quality and biology from patch-burn grazing in a five-year, replicated watershed-scale experiment that used a Before-After, Control-Impact (BACI) design. Treatments included a patch-burn control watershed, and patch-burn grazing in two riparian fenced and two unfenced watersheds. We further assessed the effectiveness of riparian fencing for mitigating potential water quality impacts by monitoring water quality and cattle movement using Global Positioning System. After initiation of patch-burn grazing, we detected significant increases in total suspended solids, nutrients, *Escherichia coli*, chlorophyll *a* (algal biomass), and gross primary productivity in all watersheds with patch-burn grazing, but the greatest increases were in watersheds with unfenced riparian zones. The largest changes in water quality values were recorded when cows were on pasture, and the concentrations tended to decline when cattle were removed, suggesting system resiliency. Cattle aggregated along streams in unfenced pastures more than 20% of the grazing season. Therefore, patch-burn grazing is a measurable disturbance that altered the ecological state of streams, but riparian fencing lessened cattle perturbation.

Introduction

Headwater streams and their riparian areas are critical resources for many organisms, including people. Headwaters (i.e., streams near the source) have a disproportionate influence on material export and downstream water quality (Alexander et al. 2007, Dodds and Oakes 2008). A riparian zone is an ecotone near stream sides where the vegetation can regulate hydrologic, biogeochemical and ecological processes. As examples, riparian zones can trap particles before entering streams and stabilize channels (Thorne 1990) and effectively remove nitrate from subsurface waters (Hill 1996). Native vegetation in these zones is correlated with low nutrient concentrations in streams (Dodds and Oakes 2006, Banner et al. 2009). Therefore, riparian protection and special management approaches are often promoted to improve water quality and buffer the effects of land management on aquatic resources (Osborne and Kovacic 1993, Muscutt et al. 1993).

Headwater streams and riparian areas in grasslands may be influenced by land management practices, particularly fire and grazing. In grasslands worldwide, fire and grazing are dominant ecosystem processes which alter above and below ground productivity, diversity, nutrient cycling, and carbon flow (e.g., Belsky 1992, Milchunas and Lauenroth 1993, Biondini et al. 1998, Frank and Groffman 1998, Neary et al. 1998, Olff and Ritchie 1998, Knapp et al. 1999, Knapp et al. 2004). Regular fire (~2-20 years; Abrams 1985, McPherson et al. 1995) is necessary for maintaining mesic grasslands against woody overgrowth (Stewart 1951), and many prairies are used for livestock production. Globally, cattle biomass has increased in the last century and is eight-fold greater than the total biomass of all native terrestrial mammals (Smil 2011). Many types of grassland have adapted to a fire-grazer interaction, whereby native grazers follow the fires to graze on the newly burned grasses (Fuhlendorf et al. 2008, Allred et al. 2011), which creates landscape heterogeneity and periods of intense grazing and rest. Despite the prevalence of and documented effects from fire and grazing in terrestrial grasslands, we have little understanding how these practices influence water quality and biology of grassland streams.

Patch-burn grazing (PBG), also referred to as pyric-herbivory, is a management technique designed to mimic the historical regime with fire-grazer interactions in grasslands. The aim of PBG is to promote habitat heterogeneity and biodiversity while continuing cattle production by controlling heterogeneity of fire and grazing over patches in space and time (Fuhlendorf and Engle 2004). The PBG management approach is being progressively adopted on public and private lands due to its conservation benefits of promoting terrestrial plant and animal diversity (e.g., Fuhlendorf et al. 2006, 2010, Engle et al. 2008). Further, PBG is being implemented in tallgrass prairie of North America, which is an endangered ecosystem due to conversion to row-crop agriculture and woody encroachment (Briggs et al. 2005). However, controversy remains because we lack information on how fire and grazing will affect aquatic ecosystems and downstream water quality. Similar approaches may be used in other grasslands around the world where greater diversity and heterogeneity are desired.

Studies have emphasized impacts of fire or livestock on streams; however, most do not address the potential of riparian fencing to mitigate changes or examine temporal disturbance dynamics from discontinuous grazing. Fires effect stream characteristics in forests and shrublands (Minshall et al. 1997, de Koff et al. 2006, Smith et al. 2010), but information is lacking for tallgrass prairie streams (except see Dodds et al. 1996, Larson et al. 2013a,b). In general, there is a negative correlation with livestock and water quality (e.g., western USA deserts, Belsky et al. 1999; USA forests of the Pacific Northwest, Kauffman and Krueger 1984;

humid, southern USA forest, Agouridis et al. 2005; UK pastures, Hooda et al. 2000). There is no consensus in the literature regarding the effectiveness of riparian fencing for mitigating water quality impacts, and studies to date show a variety of responses. We are unaware of studies that examine water quality changes from fire-grazer interactions or the efficacy of riparian fencing in the endangered tallgrass prairie ecosystem. Experiments addressing livestock impacts and riparian fencing are rare because it is difficult to have replication and treatment at the watershed scale. To date, most reports are observational studies that lacked an explicit experimental design with pretreatment data, lacked appropriate reference/control sites, or were conducted on a scale not compliant with the research question. Therefore, there is need for definite experimental designs to test fire and grazing on stream ecosystems (Larsen et al. 1998, Belsky et al. 1999, Sarr 2002, Rinne 1988).

There are several requirements to further our understanding of fire and grazing influences on stream ecology. First, entire and separate watersheds need to be the experimental unit because in-stream processing and downstream transport do not allow independence of experimental sites along the same stream. Second, annual variation requires that studies be done across multiple years to distinguish natural disturbances (e.g., flooding and drying) from the treatment disturbance. Third, replicated watersheds are needed to demonstrate the results are reproducible. Lastly, control watersheds without cattle are required to compare to grazing treatments for two reasons: the effectiveness of riparian fencing in mitigating cattle effects on water quality and the functional capacity of prairie riparian areas is still unknown. Here we describe a replicated, whole-watershed, multi-year experiment to rigorously test the effects of fire and grazing disturbance on ecosystem state shifts.

Our objective was to determine the influences of heterogenous fire and cattle grazing on tallgrass prairie streams within and without riparian fencing. We investigated responses of water quality (e.g., nutrients, sediments, and *Escherichia coli* bacteria concentrations), biological structure, and function (e.g., algal biomass and whole-stream metabolism) before and after the implementation of PBG. We hypothesized PBG would increase concentrations of nutrients, sediments, and coliform bacteria, some of which would cascade to affect the microbial community. We further predicted that the strongest effects would be observed when cattle were on pasture, and these effects would diminish when cattle were removed. Therefore, we expected tallgrass prairie streams would shift to an alternative state following patch-burn grazing but could exhibit resiliency after the cattle were removed.

Methods

Description of study sites

We studied six small watersheds on Osage Prairie Conservation Area in southwestern Missouri, USA (37°44'25.61"N, 94°20'12.17"W; Figure 1). Osage Prairie is a 628 hectare remnant prairie owned and managed by the Missouri Department of Conservation and The Nature Conservancy. Past land use included haying and cattle grazing from the early 1900’s to 1987. Current watershed management consists of mid-summer triennial haying, a prescribed fire interval of 3-5 years, and mechanical removal of riparian trees >10cm diameter to increase wildlife habitat and plant diversity (Kirsch 1974, Soleicki and Toney, 1986, Swengel 1996). The watershed areas ranged from 19-120 ha and were completely encompassed by native tallgrass prairie. The streams were all first-order with an average discharge of 70 L/s, and typically dried from June until the fall season. Detailed descriptions of water chemistry, geomorphology, hydrology, biological assemblages, and ecosystem function prior to this PBG experiment are reported in Larson et al. (2013a).

Experimental design

We used a before–after, control–impact design with samples paired in time (BACI; Downes 2002) to test for PBG effects on streams. The BACI design is intended to assess environmental perturbations, including both pulse and press disturbances (Gotelli and Ellison 2004). The BACI analysis focuses on the change at the impact sites relative to the control sites, after an experimental treatment is applied. The paired differences extend the traditional BACI by using multiple measurements at each site through time to separate treatment differences across sites from natural variation (e.g., seasonal effects). In this study, we have spatial replication of some treatment plots and temporal replication with measurements both before and after the application of PBG. Replication across space (i.e., watersheds) increases certainty that results are applicable to multiple sites with the same perturbation. The temporal replication ensures the temporal trajectory can be measured, increases precision of estimates, and allows testing of time and treatment interactions (Kuehl 2000, Gotelli and Ellison 2004). The problems and corrections for spatial and temporal autocorrelation are addressed in the *Statistical Analyses* section below.

The pretreatment phase of the study was from September 2009-March 2011, in which all watersheds had no fire in the last 5 years, or grazing in the last 25 years. The treatment period followed from April 2011-July 2013 when we implemented PBG. This experiment had three grazing treatments with all watersheds patch-burned: no grazers (“control”; n=1 watershed), open access grazing where cattle had free access to the riparian area and streams (“unfenced riparian”; n=2 watersheds), and grazing with riparian fencing (10 m, two stranded poly electric tape) on each side of the geomorphically active stream channel ("fenced riparian"; n=2 watersheds). We acknowledge buffer width is a complex aspect of riparian protection, but we chose a fixed, 10 m riparian width according to regional standards, government agency recommendations, the fact that our watersheds were relatively small, and data suggested 10 m riparian zones was sufficient to capture most nonpoint-source runoff in grasslands (e.g., Dillaha et al. 1989, Daniels and Gilliam 1996, Lim et al. 1998, Lee et al. 2004). In mid-April 2011, 2012, and 2013 a prescribed patch-burn was carried out in a third of all watersheds (Fig. 1). The four watersheds with PBG had yearling calves stocked at a density of ~0.42 animal units/ha (where one animal unit=227-363 kg). Cattle were on pasture from 1 May to 31 July in each of the three treatment years, and were consistently provided with water tanks located in the upper area of each watershed and as far from the stream as possible. Detailed baseline watershed characteristics in the pretreatment period are described in Larson et al. (2013a).

Water quality field sampling

We sampled each stream monthly when flowing at the base of each watershed (Fig. 1). In total, we repeatedly measured water quality across 36 sampling periods (18 samples in the pre-treatment phase and 18 samples in the treatment phase). We collected water samples for total suspended solids, nutrients, and *E. coli* bacteria in acid-washed bottles from the thalweg about 5 cm below the water surface at the same location at the base of each watershed. We collected 3-5 rocks per stream for chlorophyll *a* determination. The water samples and rocks were transported on ice to the laboratory, and nutrient samples and chlorophyll *a* samples were stored frozen at -30ºC until analysis. The water for *E. coli* enumeration was refrigerated for a maximum of 12 h before processing.

For whole-stream metabolism estimates, we collected data on channel width and depth, temperature, dissolved oxygen (O_2), barometric pressure, discharge, and photosynthetically active radiation (PAR). We measured and averaged stream widths (to bankfull) and depths using multiple transects 100 m above the water sampling location. Temperature, O_2, and barometric pressure were recorded using YSI 6150 ROX optical O_2 probes at 10 min. intervals (YSI, Inc, Yellowsprings, Ohio, USA). Discharge was obtained by measuring dilution of a concentrated solution of KBr pumped at a known rate with an ion-specific Bromide probe (Thermo Fisher Scientific Inc., Waltham, Massachusetts, USA). Photosynthetically active radiation was measured at 10 min intervals using an Odyssey Photosynthetic Irradiance Recording System (Dataflow Systems PTY LTD, Christchurch, New Zealand) in an open canopy area.

Water quality laboratory analyses

The total suspended solids (TSS) water samples were filtered through pre-combusted (24 h at 475°C), pre-weighed glass-fiber filters (GFC Whatman, 1.2 µm retention) within 48 h of collection. Filters with retained material were dried at 105°C and re-weighed to find the amount of TSS (APHA 1995).

Inorganic nutrient samples were filtered through a glass-fiber filter (Whatman GFF, 0.7 µm retention) and analyzed for nitrate + nitrite (NO_3^-), ammonium (NH_4^+), and soluble reactive phosphorus (SRP) concentrations (APHA 1995). Unfiltered stream water was analyzed for total nitrogen (TN) and total phosphorus (TP) concentrations by a persulfate oxidation method (Ameel et al. 1993). The nutrient runs were performed using an OI-Analytical Flow Solution IV autoanalyzer.

We analyzed samples for *E. coli* bacteria using the EPA Method 1603 (Environmental Protection Agency 2005). We filtered 100 mL of stream water through a membrane filter (to retain the bacteria) and plated on modified membrane-thermotolerant agar. The plates were incubated at 35°C for 2 h to acclimate the bacteria, and then incubated at 44.5°C for 22 h for culture. After incubation, we manually counted the colony forming units (CFU); if the CFU exceeded 125 per plate, we reduced the water volume by half and repeated the procedure.

For chlorophyll *a* determination, whole rocks were extracted with hot 95% ethanol (79°C for 5 minutes, followed by 12 h at 4°C; Sartory and Grobbelaar 1984) and extracts were analyzed fluorometrically (Welschmeyer 1995). Projected surface areas of the rocks were calculated by image analysis to express mass of chlorophyll *a* per unit area.

We estimated whole-stream metabolism using the single station method (Bott 2006) .We used a modeling approach to estimate community respiration (CR), gross primary production (GPP), and rearation rates in each stream (Riley 2012, Dodds et al. 2013). Specifically, we used light to scale GPP rates and made all the rates dependent on water temperature (Riley 2012).

Modelling the responses from PBG

We performed all statistical analyses using the software package R 3.0.2 (R Foundation for Statistical Computing, 2013). Pretreatment data suggested five of the six study streams were statistically similar in water quality and biology, but one stream was more characteristic of a wetland and exhibited different water chemistry (Larson et al. 2013a). Therefore, we only used data from five watersheds to represent the effects of PBG on streams. Because the five watersheds were statistically similar in water quality during the pretreatment phase, we averaged the values across each sampling period for replicated treatments. We included data from 18 pretreatment and 18 treatment sampling dates (sampled monthly when flowing) in all the analyses for the following response variables: total suspended solids, total nitrogen, ammonium, nitrate, total phosphorus, soluble reactive phosphorus, and chlorophyll *a*. Sample sizes were smaller for *Escherichia coli* bacterial counts (14 sampling periods) because we added this variable later in the study, as well as whole-stream metabolism (ten sampling periods) because we could not sample during winter when streams froze. We only reported baseflow conditions because stormflow data were insufficient for analyses and starkly different from baseflow. We did not remove the few outliers (>2SD from the mean) from the analyses because they appeared to be natural extremes and the log-transformation successfully normalized the data.

We ran two principal components analyses (PCA) to graphically illustrate the relationship between the treatments and measured water quality variables. One PCA biplot (Fig. 2) contains data from the control site only with the before and after periods to examine any possible fire effects or temporal trends in water quality (not attributed to PBG). The other biplot (Fig. 3) contains a component score associated with a sampling date in the after/treatment period only, and we differentiated periods when cattle were on and off pasture. The variance inflation factor found no redundancy in the log-transformed response variables, so all were included.

In this BACI design, the response variable analyzed is the difference value between the control and impact (C-I) for each sampling period, and is used in a Welch's t-test to compare the before and after period (factor: time). The associated p-value from the t-test is an interaction term (BA*CI), and a significant p-value indicates a probable change in the after period at the impact sites, but not the control site. Because water quality data are naturally variable and the power to detect differences was low, we considered a statistically significant difference among treatments at a significance value of alpha=0.10. However, we also refer readers to the analysis of variance table (Table 2) and all figures for interpretation of results.

We acknowledge BACI analyses and repeated measures designs require additivity and no temporal autocorrelation of data points (Stewart-Oaten et al. 1986, Smith et al. 1993), and we took several steps to address these concerns. In a BACI analysis, additivity suggests the responses at the control sites are parallel to responses at the impact sites during the pretreatment phase, which is essential to ensure similar temporal trajectories. To test additivity, we plotted values over time to examine graphical, temporal trends in the data not associated with treatment (Smith et al. 1993, Stewart-Oaten and Bence 2001) and conducted repeated measures ANOVA to test differences and interactions among sites (Larson et al. 2013a). To test temporal independence of the time series data (because autocorrelation can cause Type I errors), we computed the Ljung-Box test statistic. Further, by using the difference value (Control-Impact) as the response variable, we further minimized problems associated with serial autocorrelation from pseudo-replicated data (Stewart-Oaten et al. 1986). We agree with Murtaugh (2001) that interpretation of BACI results should also be graphical and not rely solely on *p*-values from statistical tests.

Our control site was subjected to burning, but not grazing. Because fire is an essential process for maintaining grasslands (Steward 1951), the presence of periodic fire was considered a reference condition (see Larson et al. 2013a,b, Table 3). Further, fire almost always accompanies cattle grazing in mesic grasslands, so a grazing-only treatment is unlikely. Our control is used as a covariate to eliminate natural environmental variations, such as season and fire (Stewart-Oaten and Bence 2001). The lack of replication does not allow us to statistically test for burning effects at the control; however, we searched for fire effects graphically (Fig. 2

and 4). Because the control site was burned, the results from the BACI analysis represent the interaction of fire and cattle from the PBG design.

Cattle behavior in riparian areas

We monitored the position of one stocker calf per watershed each year using LOTEK GPS_3300 wireless collars (Newmarket, Canada) set to record data at 1 h intervals. Using ArcGIS (version 10.0; Environmental Systems Research Institute, Redlands, California), we digitized streams using the 2012 orthoimagery of Vernon County, Missouri. We mapped and analyzed cattle location data using ArcGIS to identify the overall frequency of cattle within the 10 m riparian area and burn patches in both fenced and unfenced watersheds.

We collected riparian vegetation data in June 2010-2013 to determine if vegetation structures differed between fenced and unfenced riparian areas due to livestock grazing. Vegetation structures included percentage of cover, litter depth, and grass height and were measured in each fire patch within fenced and unfenced PBG watersheds. Specifically, vegetation data were collected in the fire patch along two 10 m transects perpendicular to the stream, with a 1 x 5 m plot every 5 m along the transect (Daubenmire 1959). The data were averaged for each year of measurement and treated as an independent sample in logistic regression (because the dependent variable, “riparian fencing/no fencing,” was categorical and the predictors were continuous).

Results

Water quality following Patch-Burn Grazing

The first two principal component axes explained 70% of the variation in this dataset (Fig. 3). The eigenvectors show a gradient of concentrations for several water quality variables across sample dates in the after period. The greatest concentrations of all the variables were in unfenced riparian and fenced riparian watersheds when cattle were on pasture. Nutrient, sediment and *E. coli* concentrations were consistently low through time in the control watershed.

Total suspended solids (TSS)

A significant increase occurred for TSS during PBG in the unfenced riparian watersheds, but not in the fenced riparian watersheds (Table 2). Across the pretreatment period, TSS had a mean of 11 mg/L, yet was highly variable across sample dates. The largest TSS values occurred when cattle were on unfenced pastures; the mean TSS in unfenced riparian streams increased to 18 mg/L (max: 59 mg/L) when cows were on pasture in unfenced watersheds.

Nutrients

During the pretreatment phase at all streams, total nitrogen (TN) was consistently low (<300 µg/L; Fig. 4). After initiation of PBG, concentrations increased 1-4 folds in both fenced and unfenced streams. The values of TN were often greatest when cattle were on pasture in the unfenced pastures, and within two treatment years TN exceeded 2,000 ug/L. The TN concentrations tended to decline when cattle were removed, but the mean values when cows were off pasture were slightly higher than the pretreatment period, suggesting some resiliency but not full recovery from PBG.

Ammonium values did not statistically differ across sites in the before/after periods or when cows were on/off pasture (Table 2). However, the mean and variance doubled during PBG (Table 1).

Nitrate (NO_3^-) values significantly increased in unfenced riparian and fenced riparian watersheds after implementing PBG (Tables 1 and 2). In the pretreatment phase and in the control watershed, NO_3^- had a low mean of 11 µg/L. During PBG, mean NO_3^- increased to 536 µg/L, and in some instances increased to more than 3 mg/L, particularly when cows were on pasture. Data was insufficient to test the effects of cows on pasture. Nitrate did increase slightly in the control watershed in the after period, but the magnitude of change was greater for the other treatments (Table 2).

Total phosphorus values increased more than an order of magnitude in the after period at the unfenced riparian and fenced riparian watersheds. When cattle were on pasture, we detected a more dramatic increase in TP within unfenced riparian watersheds compared to fenced riparian streams (Table 2).

Soluble reactive phosphorus (SRP) did not change for any treatment following PBG. We did not detect changes to SRP when cattle were on pastures, either (Table 2). Overall, SRP concentrations were very low with a mean of 6 µg/L.

Escherichia coli bacterial counts

Escherichia coli bacterial counts were significantly greater in the after period at PBG watersheds, regardless of fencing (Table 2; Fig. 5). We obtained similar, significant results when cows were on pastures. In the before period, *E. coli* had a mean of <1 colony forming units (CFU; maximum of 15 CFU). During PBG, *E. coli* remained negligible at the control site but increased in unfenced riparian (median: 51 CFU) and fenced riparian watersheds (median: 17

CFU). When cows were on pasture, values increased as high as 2,213 CFU. When cows were removed from pasture, *E. coli* values declined to control/baseline values within 1-2 months (Fig. 5).

Chlorophyll a

Benthic chlorophyll *a* (algal biomass) statistically increased in unfenced riparian watersheds in the after period, but not in fenced riparian watersheds (Table 2). When cows were on pasture, chlorophyll *a* increased slightly in both the fenced and unfenced watersheds. In the before period, all streams had a mean of 6 µg/cm^2 chlorophyll *a*; in the after period, the control remained constant but the fenced riparian and unfenced riparian watersheds increased to a mean of 9 µg/cm^2, with values up to 22 µg/cm^2 chlorophyll *a*. Chlorophyll *a* was highly correlated to ammonium (NH_4^+) on the PCA biplot (Fig. 3).

Whole-stream metabolism

We detected a slight but statistically significant increase in gross primary production (GPP) at both fenced and unfenced watersheds (Tables 1 and 2). The increase in GPP corresponded with an increase in chlorophyll *a* biomass following PBG. The data showed diel O_2 swings that correlated with light and sometimes exceeded O_2 saturation, showing GPP occurred in these fairly open-canopy streams. All streams had diel O_2 swings that ranged from 3-4 mg O_2 each day, and the PBG treatments did not appear to affect the severity of oxygen changes. However, we did not find changes in community respiration (CR) or net ecosystem production (NEP). We had a small sample size (n=5) and the metabolism model estimates were highly variable with time. These streams were consistently net heterotrophic (i.e., CR > GPP), with a NEP mean of -1.50 g O_2 m^{-2} d^{-1}.

Cattle behavior in riparian areas

Cattle spent 23-77% of time in the patch-burn, depending on unit and year (Fig. 6). The riparian areas for the PBG watersheds ranged from 5-14% of the total watershed. In fenced streams, cattle were almost fully excluded from the 10 m riparian area; however, they had a few potential times of access (Fig. 6) when the fencing was temporarily knocked down, or the geo-location suggested cattle were inside the fencing, when they were not (only 3 m accuracy of collars). However, access to riparian areas in fenced watersheds constituted <1% of the cattle's time; in contrast, cattle spent ~ 21% of time in the unfenced riparian areas (pers. comm., J. Fulgoni). Cattle also concentrated at the watering tanks provided at the top of each watershed (Fig. 6).

The vegetation structures were visually distinct and statistically different between fenced and unfenced riparian watersheds. In the unfenced, PBG watersheds, the riparian areas were grazed by cattle (Fig. 6), contained no ground litter, had low percentage of grass cover, and short grass heights compared to the fenced riparian areas. The logistic regression model resulted in "complete separation" or "perfect model fit" for the predictor variables, litter and percentage of grass cover. Specifically, ungrazed areas had 4-5 mm litter and 100% grass cover, whereas grazed areas had 0-1 mm litter and 60-80% grass cover. A perfect model fit renders the parameter estimates, standard errors, and *p*-values meaningless (thus not reported), but highlights the distinct and extremely predictable pattern in vegetation structures between grazed and ungrazed riparian areas.

Discussion

Cattle can influence streams in a variety of ecosystems, and the tallgrass prairie is no exception. These influences (e.g., increased nutrients, bacterial loads, and algal production) are generally considered undesirable, negative impacts to water quality. However, ungulate grazing is a natural process in grasslands and a vital economic commodity, and will likely continue in many remaining grasslands worldwide. This study shows riparian fencing can mitigate water quality changes associated with grazed watersheds but not eliminate them; riparian fencing could be an option where riparian protection is a priority. This is the first study we are aware of to use the BACI approach at a replicated, watershed-scale to examine the effects of fire and grazing on streams.

Fire effects

Prescribed fire did not have lasting, measurable effects on water quality or stream biota in these tallgrass prairie streams. Fire is known to dramatically influence streams in forests and shrublands (Minshall et al., 1997; de Koff et al., 2006; Smith et al., 2010), but less is understood about grassland fires. The watershed-scale fires at Osage Prairie removed ground cover for about 3 weeks during the spring rainy season, so it is surprising that overland flow processes were not significant (Duell 1990) and did not create a long-term stream response. Contrary to this pattern, nitrate and total nitrogen deceased slightly as years since fire increased in Kansas tallgrass prairie streams (Dodds et al. 1996). The Osage streams and others in tallgrass prairie exhibited a short-term, pulsed response within 3 weeks after the fires (Larson et al. 2013a,b); specifically, we observed a ~200% decrease in nitrate and soluble reactive phosphorus, and an increase in algal biomass. We suspect this trend is due to the fires removing vegetation that shades the stream, and then light increases allows for algal growth and nutrient uptake from the water column. The fire effects in tallgrass prairie are still not concrete, but studies suggest fire impacts on nutrient and sediment transport are minimal.

Comparison of PBG streams to other land uses

How does the magnitude of impact from PBG relate to reference conditions and the ecological state of other regional streams? This study assumed reference conditions are watersheds without fire or grazing in the last five years, which was the historical median fire interval for tallgrass prairie (Abrams 1985). The control streams at Osage Prairie throughout the study had similar water quality conditions compared to reference tallgrass prairie streams (Table 3; U.S. EPA 1998, Smith et al. 2003, Dodds and Oakes 2004). Further, water quality at Osage's Control sites matched streams at Konza Prairie in Kansas that had bison grazing within its watersheds (Table 3).

During the PBG treatment phase, we detected strong deviations from the control stream and recommended reference conditions for tallgrass prairie streams (Table 3). At streams with PBG (regardless of riparian fencing), the average TN and TSS concentrations doubled and the TP concentrations quadrupled compared to reference conditions and the control site. These data show that cattle grazing is a measurable disturbance that can cause streams to exceed suggested reference conditions for this ecoregion.

The only water quality parameter with established reference criteria by the state of Missouri is *Escherichia coli*, which is considered recreationally safe at <125 colony forming units (Environmental Protection Agency 1986). When cattle were off pasture, values were always below this criterion; however, when cattle were on pasture in both fenced and unfenced watersheds, most water samples exceeded the standard. We documented a value as high as 2,216 CFU in an unfenced riparian watershed during PBG.

The whole-stream metabolism rates (Table 1) were similar to suggested reference values (Dodds 2006, Mulholland et al. 2001, Bernot et al. 2010) and to other tallgrass prairie streams (O'Brien et al. 2007). Ecosystem metabolism in these tallgrass prairie streams can be highly variable with season (Larson et al. 2013a), and therefore could have made it difficult to detect changes in ecosystem function following treatments, especially with our small sample size for metabolism estimates. However, we detected an increase of gross primary production (as well as chlorophyll *a* content), which suggests an alteration to ecosystem structure and function. The increase of benthic primary production could alter the food web and macroinvertebrate community composition of these streams (Jackson 2013).

The PBG values are noticeably lower than other regional streams under row-crop agriculture (Table 3). For example, the average TSS from Osage's PBG streams was 17 mg/L (maximum of 59 mg/L); in regional streams with row-crop agriculture, the average is an order of magnitude greater (Dodds and Whiles 2004). Similarly, the average TN at Osage PBG streams was half of the mean for row-crop agriculture streams. However, the average TP values with PBG approached those of row-crop agricultural streams, which could alter productivity and function of streams (Dodds and Whiles 2010).

Livestock management techniques may reduce perturbation

Several livestock management techniques may reduce impacts to riparian areas and are promoted as Best Management Practices (BMP; e.g., Mosley et al. 1997, Agouridis et al. 2005). These techniques include stocking with mature age classes, replacing cattle with bison, providing amenities (e.g. water away from streams and shade tents), patch-burn grazing, and/or riparian fencing. This study used stocker calves, which often hid in the riparian brush of unfenced watersheds (D. Larson, pers. Obs.), but we suspect stocking with mature age classes or different breeds could reduce riparian contact. An alternative approach would be to replace cattle with native bison because bison rarely occupy riparian zones and have minimal effects on water quality (Larson et al. 2013b), but we acknowledge the difficulties with managing bison herds in small pastures. Cattle tend to congregate near streams under riparian canopy to reduce body temperature and drink water, so providing shade tents, water troughs, and protein supplements can reduce the need to access streams (Rouda et al. 1995, Byers et al. 2005, Franklin et al. 2009). Despite management efforts, cattle may be attracted to riparian zones due to higher forage volume and palatability of riparian vegetation (Paulsen 1969), as well as the amenities of shade, predator protection, and water in one convenient location (Ames 1977, Bryant 1982).

Patch-burn grazing management may be a technique that reduces the riparian area cattle occupy in a given year by altering the attractiveness of riparian vegetation. The unburned patches received less attention from cattle (Fig. 5), which allowed riparian vegetation to reestablish (Larson, Ch. 4) and thus could potentially alleviate water quality impacts. Although this study showed alteration of water chemistry and biology, PBG may be a management compromise for water quality compared to conventional tallgrass prairie management. The current management regime in tallgrass prairie in the Flint Hills of Kansas currently consists of annual fire in large patches and high stock cattle densities (>0.8 animal units/ha) for a full stock season (Derner et al. 2006). In contrast, PBG reduces fire frequency and concentrates cattle impacts to smaller patches. A few studies in other ecosystems suggest rest-rotation management (i.e., periods of rest from grazers) can reduce riparian impacts and rehabilitate riparian areas (Hayes 1978, Davis

1982). We suspect that watershed and patch sizes, patch configuration, and placement of watering tanks could influence cattle behavior in streams, but more data are needed to test this hypothesis. Future study is needed to adequately compare water quality in watersheds with traditional management (i.e., annual burn and grazing) and patch-burn grazing (Sovell et al. 2000, Briske et al. 2008).

Riparian protection

Riparian protection is a central ecological concept with respect to biogeochemical controls and water quality management, but surprisingly few studies demonstrate the effectiveness of riparian fencing on excluding cattle and alleviating water quality impacts. Further, little is known about the functional capacity of riparian zones in native grassland to buffer against upland grazing (except see Sovell et al. 2000). In this study, the two-tinsel electrified fencing did mitigate water quality impacts (Fig. 3 and 4), but not entirely. Because the fencing was fairly robust at exclusion (Fig. 5) and yet we detected water quality changes, we suspect overland flow processes may be important drivers of tallgrass prairie stream ecology. For example, overland flow may be a mechanism for how the *E. coli* and nutrients entered the streams with fenced riparian areas. Because the riparian vegetation was intimately related to grazing, it is not clear whether the improved water quality in fenced watersheds was due to a buffering capacity from intact riparian vegetation and/or simply because cattle were not able to directly deposit fecal matter and walk through streams. Understanding fencing efficacy and overland flow is crucial because prior studies have used riparian-fenced watersheds as experimental units for the control treatment (e.g., Miller et al. 2010), which could downplay the magnitude of aquatic changes from cattle grazing. Although riparian fencing has several disadvantages such as costs and labor (Platts and Wagstaff 1984), it may be feasible and beneficial at sites where riparian protection is a management priority.

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Figures

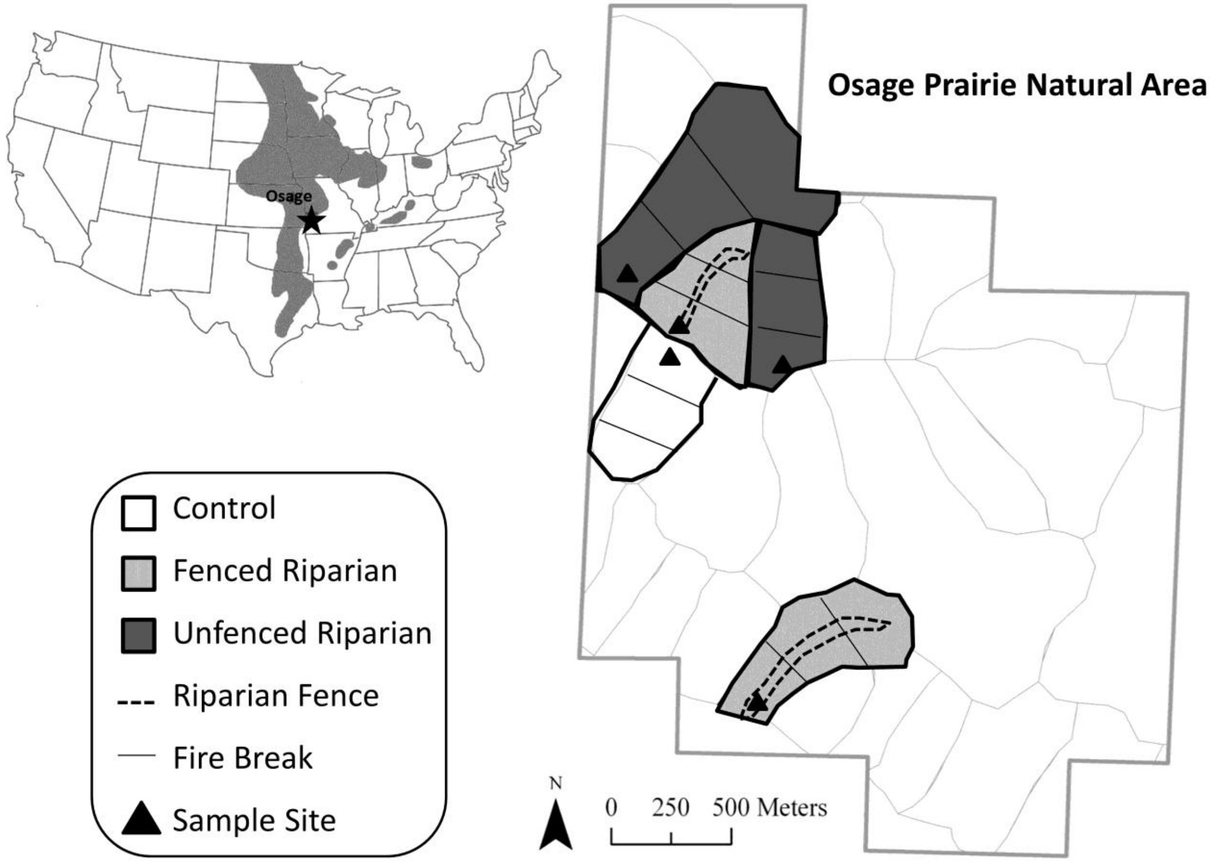

Figure 5.1. A map of Osage Prairie in Missouri, USA during a patch-burn grazing experiment in 2009-2013. The gray shading on the USA map represents the historical tallgrass prairie range. Three treatments were employed at Osage: (1) control (no grazing); (2) fenced riparian watersheds (with cattle but riparian fencing); and (3) unfenced riparian watersheds (cattle with stream access). Fire occurred in 1/3 of each watershed in years 2011-2013 as indicated by fire breaks. The triangle designates the water sampling location at the base of each watershed.

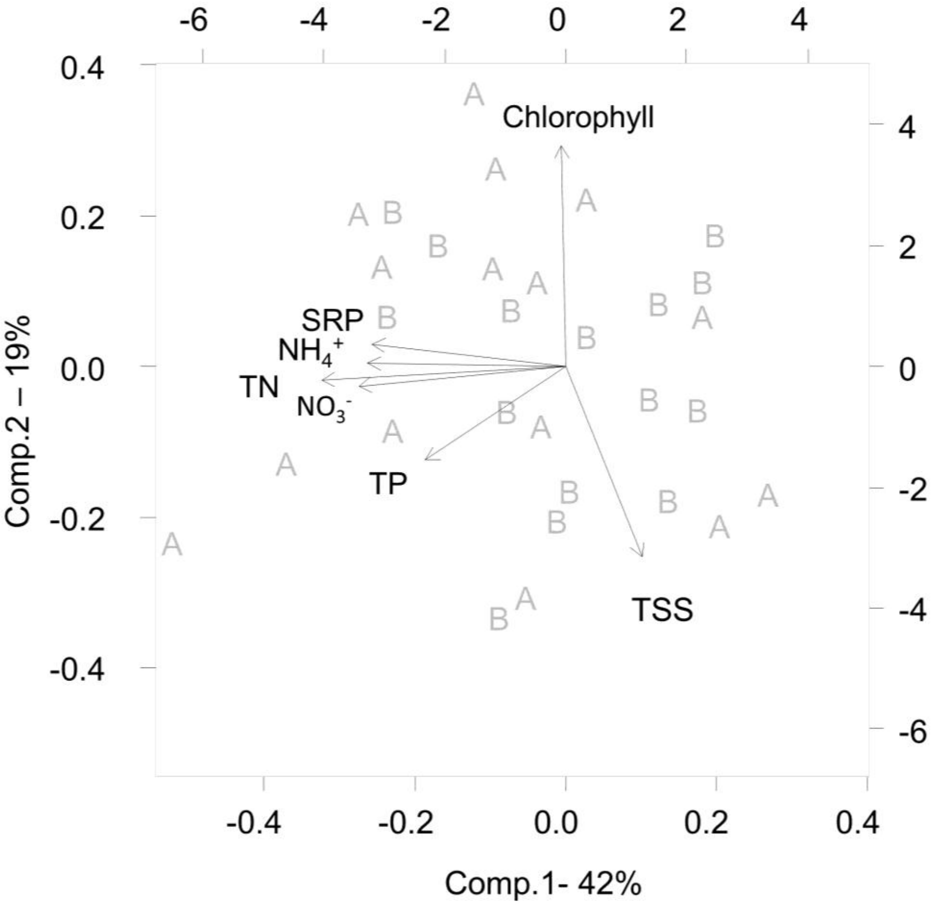

Figure 5.2. Principal components analysis (PCA) showing the relationship of time (before and after) to gradients of several water quality variables (TSS= total suspended solids; SRP=soluble reactive phosphorus; NH_4^+=ammonium; TN=total nitrogen; NO_3^- =nitrate; TP=total phosphorus). Data are from Osage Prairie, MO in 2009-2013 at the control watershed. This plot examines trends for before (“B”) and after (“A”) patch-burning.

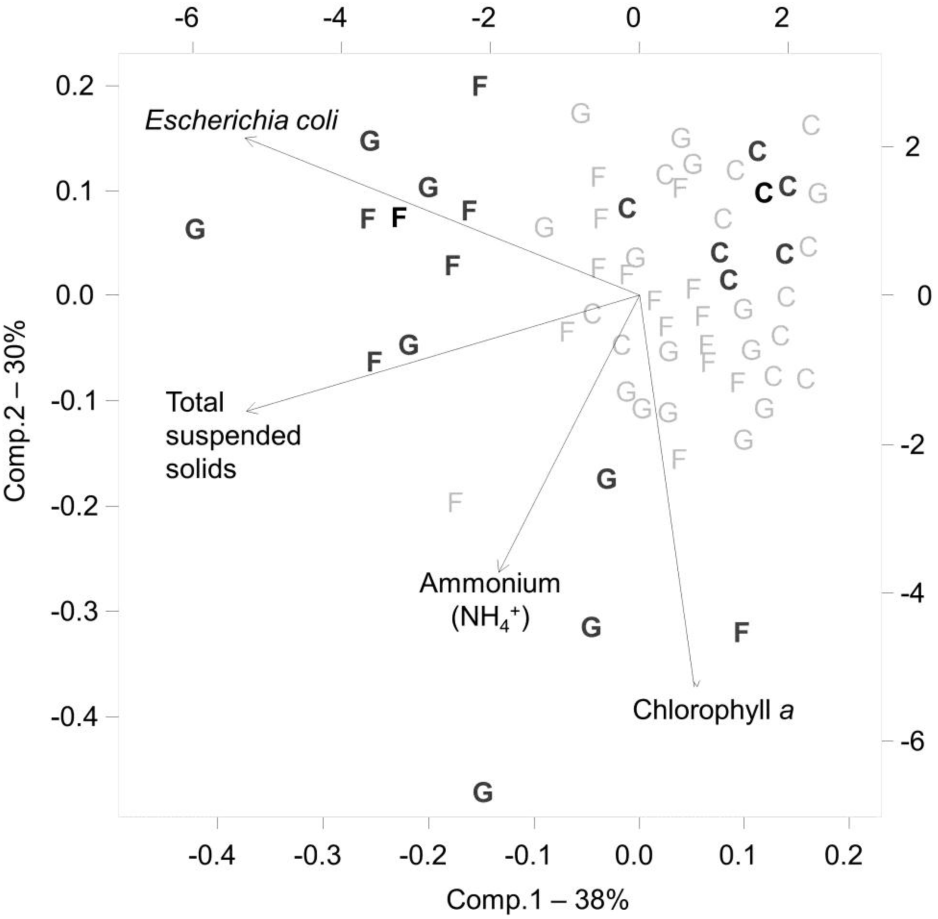

Figure 5.3. A principal components analysis (PCA) shows the relationship of treatments to gradients of several water quality variables. Data are from Osage Prairie, MO in 2011-2013 and include three treatments: Patch-burn grazing with riparian fencing along streams (F), patch-burn grazing with grazer access to streams (G), and control site without grazing (C). The light gray symbols are sample dates when cattle were off pasture, and dark gray symbols indicate when cows were on pasture.

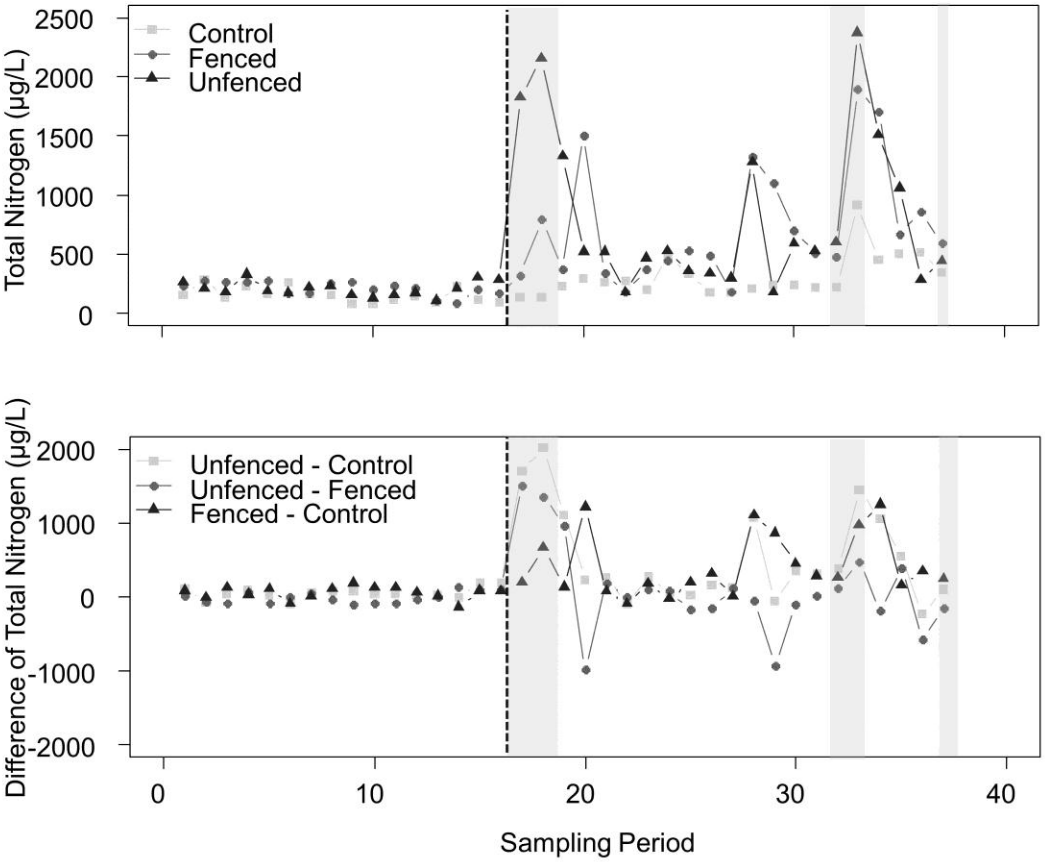

Figure 5.4. Time series plot of total nitrogen from Osage Prairie, Missouri, USA before and after the implementation of a patch-burn grazing experiment in years 2009-2013. The dashed vertical line shows the separation of the before and after periods of PBG. The gray panels indicate sampling dates when cattle were on pasture from 1 May - 31 July. Total nitrogen had a statistically significant increase at fenced and unfenced riparian zones in the after period.

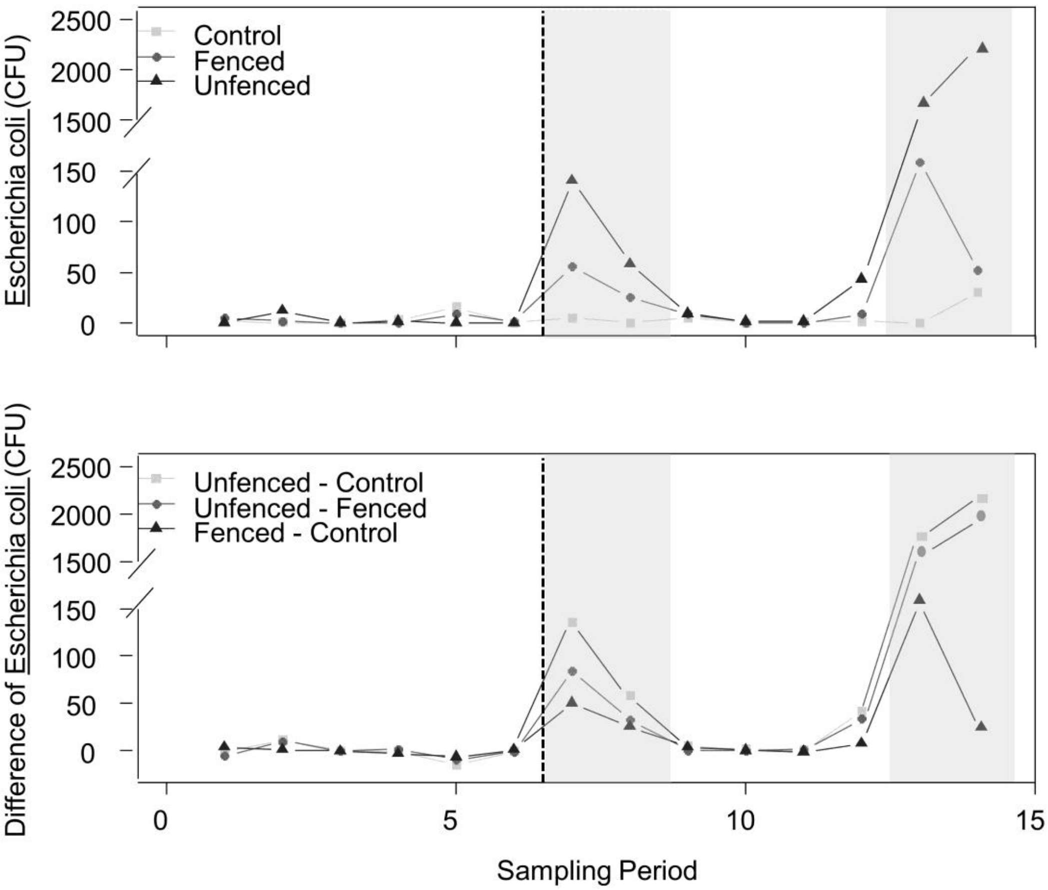

Figure 5.5. Time series plot of *Escherichia coli* from Osage Prairie, Missouri, USA before and after the implementation of a patch-burn grazing experiment in years 2009-2013. The dashed vertical line shows the separation of the before and after periods of PBG. The gray panels indicate sampling dates when cattle were on pasture from 1 May - 31 July. *Escherichia coli* had a statistically significant increase at fenced and unfenced riparian zones in the after period.

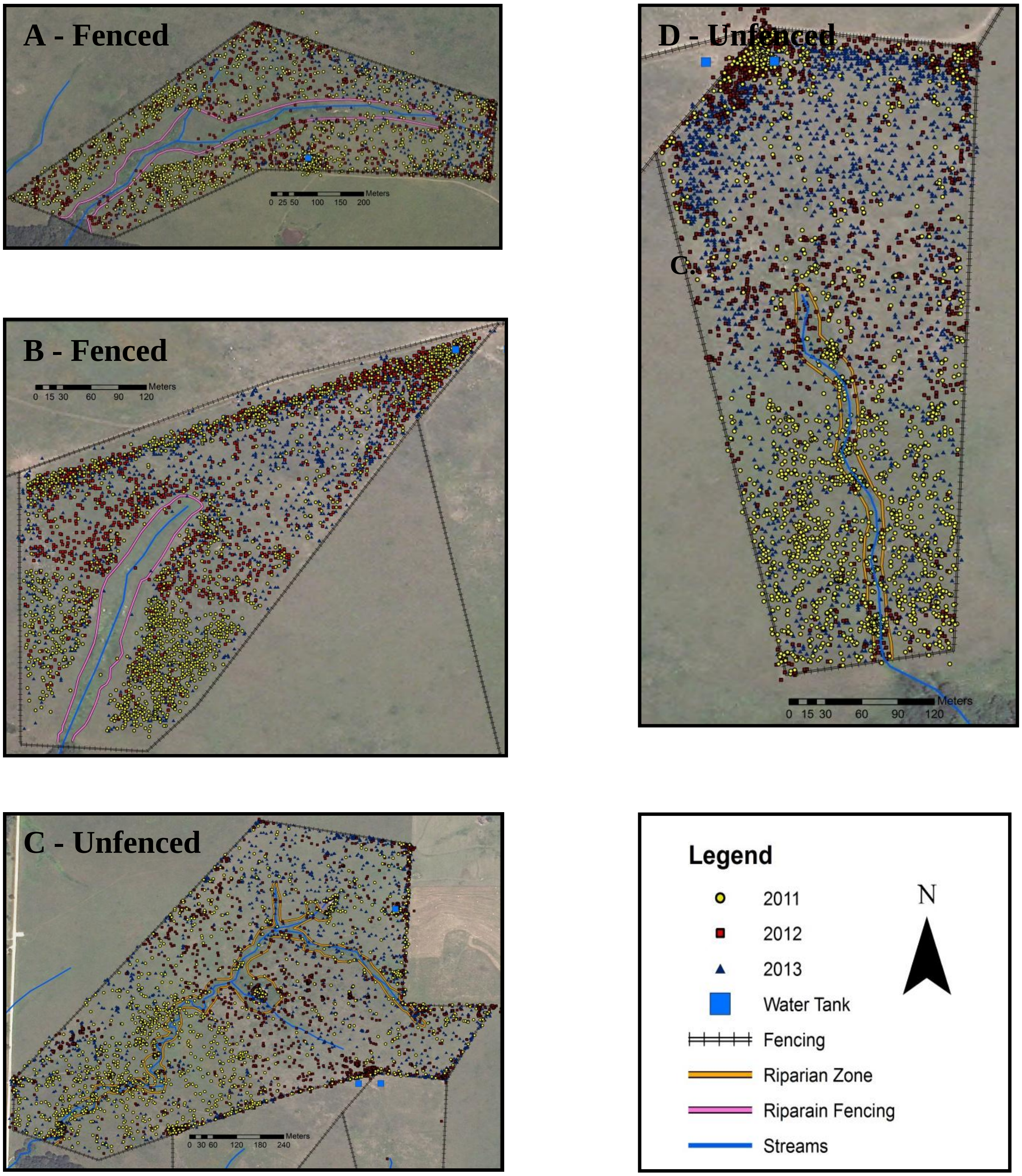
A - Fenced
0 25 50 100 150 200 Meters
B - Fenced
0 15 30 60 90 120 Meters
C - Unfenced
0 30 60 120 180 240 Meters
D - Unfenced
C
0 15 30 60 90 120 Meters
Legend
2011
2012
2013
Water Tank
Fencing
Riparian Zone
Riparain Fencing
Streams
N

Figure 5.6. Cattle positions every 1 hr at Osage Prairie, MO during a three year patch-burn grazing experiment. Treatments include two watersheds under PBG with riparian fencing ((A) and (B)), and two watersheds that allow cattle full access to the riparian areas ((C) and (D)). In riparian fenced watersheds, 2-stranded poly tape electric riparian fence was installed approximately 10 m from the geomorphically-active stream channels.

Tables

Table 5.1. A comparison of the water quality values before and after implementation of patch-burn grazing (PBG) at Osage Prairie, USA in 2009-2013. Treatments include all streams prior to PBG, and unfenced and fenced riparian watersheds. Data presented are means (±2SD), and maximum values. An * indicates a statistically significant difference in the means before and after PBG (compared to a control) at alpha=0.10.

Water quality parameter	**Before PBG (all streams)**	**During PBG (fenced)**	**During PBG (unfenced)**
Total suspended solids (mg/L)	11 (10) 40	18 (17) 75	16 (16)* 59
Total nitrogen (μg/L)	192 (65) 330	301 (183)* 919	705 (498)* 1892
Total phosphorus (μg/L)	15 (19) 128	155 (278)* 769	207 (384)* 1497
Ammonium (μg/L)	24 (31) 191	56 (31) 113	82 (137) 627
Nitrate (μg/L)	20 (19) 70	375 (616)* 2569	536 (859)* 3310
Soluble Reactive Phosphorus (μg/L)	7 (5) 22	11 (16) 71	11 (14) 58
***Escherichia coli* (colony forming units)**	3 (5) 15	39 (53)* 159	514 (887)* 2,213
Benthic chlorophyll *a* (μg/cm^2)	7 (3) 16	6 (3) 15	9 (3)* 22
Gross Primary Production (g O_2 m^{-2} d^{-1})	0.61(0.42) 1.62	0.43 (0.09)* 0.53	0.67 (0.27)* 0.9
Community Respiration (g O_2 m^{-2} d^{-1})	-0.74 (0.38) -1.23	-2.24 (0.39) -2.68	-2.04 (1.18) -3.79
Net Ecosystem Production (g O_2 m^{-2} d^{-1})	-1.98 (-2.24) -7.73	-2.24 (0.38) -2.68	-2.04 (1.18) -3.79

Table 5.2. A summary of the changes in water quality following patch-burn grazing (PBG) at Osage Prairie, USA from 2009-2013. Treatments included fenced and unfenced riparian watersheds, compared against a control. The response types were the changes before and after implementation of PBG (Before/After), as well as immediately before and after cattle were on pastures using a reduced dataset (Immediate). The statistical test used a before-after, control-impact design (Downes 2002). The NA indicates data was not sufficient for statistics. An * indicates a statistically significant difference at alpha=0.10.

Water quality parameter	**Treatment**	**Response Type**	**t-statistic**	**Degrees of Freedom**	**p-value**
Total suspended solids (mg/L)	Fenced	Before/After	-0.91	29	0.372
	Fenced	Immediate	0.99	12	0.352
	Unfenced	Before/After	-2.41	29	0.024*
	Unfenced	Immediate	2.43	12	0.032*
Total nitrogen (µg/L)	Fenced	Before/After	-2.35	33	0.025*
	Fenced	Immediate	0.91	7	0.391
	Unfenced	Before/After	-2.56	29	0.016*
	Unfenced	Immediate	1.88	10	0.090*
Total phosphorus (µg/L)	Fenced	Before/After	-4.13	23	<0.001*
	Fenced	Immediate	1.83	8	0.104*
	Unfenced	Before/After	-4.96	23	<0.001*
	Unfenced	Immediate	2.57	8	0.032*
Ammonium (µg/L)	Fenced	Before/After	0.62	28	0.541
	Fenced	Immediate	-1.39	8	0.203
	Unfenced	Before/After	0.60	27	0.552
	Unfenced	Immediate	1.11	7	0.307
Nitrate (µg/L)	Fenced	Before/After	-3.05	13	0.009*
	Fenced	Immediate	NA	NA	NA
	Unfenced	Before/After	-3.16	13	0.007*
	Unfenced	Immediate	NA	NA	NA
Soluble Reactive Phosphorus (µg/L)	Fenced	Before/After	0.29	30	0.773
	Fenced	Immediate	0.28	10	0.786
	Unfenced	Before/After	1.73	30	0.094*
	Unfenced	Immediate	0.44	10	0.670
***Escherichia coli* (colony forming units)**	Fenced	Before/After	-1.94	12	0.078*
	Fenced	Immediate	2.16	5	0.087*
	Unfenced	Before/After	-2.97	12	0.012*
	Unfenced	Immediate	2.67	5	0.046*
Benthic chlorophyll *a* (µg/cm^2)	Fenced	Before/After	-0.16	26	0.874
	Fenced	Immediate	2.48	11	0.030*

	Unfenced	Before/After	-2.65	26	0.014*
	Unfenced	Immediate	4.02	11	0.003*
Gross Primary Production (g O$_2$ m^{-2} d^{-1})	Fenced	Before/After	2.16	5	0.087*
	Fenced	Immediate	NA	NA	NA
	Unfenced	Before/After	2.67	5	0.046*
	Unfenced	Immediate	NA	NA	NA
Community Respiration (g O$_2$ m^{-2} d^{-1})	Fenced	Before/After	-0.149	6	0.887
	Fenced	Immediate	NA	NA	NA
	Unfenced	Before/After	0.08	5	0.937
	Unfenced	Immediate	NA	NA	NA
Net Ecosystem Production (g O$_2$ m^{-2} d^{-1})	Fenced	Before/After	0.67	5	0.538
	Fenced	Immediate	NA	NA	NA
	Unfenced	Before/After	-1.20	5	0.274
	Unfenced	Immediate	NA	NA	NA

Table 5.3. A comparison of Osage Prairie, Missouri stream nutrient concentrations with and without patch-burn grazing (PBG) to suggested reference values for regional tallgrass prairie streams under various land treatments (*Bison grazing* or *Row-crop agriculture*). Treatments at Osage Prairie were streams with no grazing (*Control*), fenced riparian watersheds with PBG (*PBG, fenced riparian*), and unfenced riparian watersheds with PBG (*PBG, unfenced riparian*).

	Reference	**Control & Fire**	**Bison grazing**	**PBG, fenced riparian**	**PBG, unfenced riparian**	**Row-crop agriculture**
Avg. total nitrogen (µg/L)	430	300	350	705	800	2,150
Avg. total phosphorus (µg/L)	47	20	10	155	207	270
Avg. total suspended solids (mg/L)	Data not available	10	2	17	17	200
Citations	U.S. EPA 1998 Smith et al. 2003 Dodds & Oakes 2004	This paper	Larson et al. 2013b	This paper	This paper	Dodds & Whiles 2004 Dodds et al. 2009

Chapter 6 - Conclusions

Tallgrass prairie stream ecology

Spatial and temporal variability

Tallgrass prairie streams exhibited variability in both water chemistry and biological assemblages from Kansas to Missouri (Ch. 2). Future study could examine the latitudinal gradient of tallgrass prairie that extends from Minnesota to Texas, because this gradient may have different plant species composition, geology, temperature regimes, and management schemes that can influence streams (Matthews 1988, Rabeni 1996). The large variability across sampling times and seasons indicates that multiple sampling dates are required to adequately characterize tallgrass prairie streams (Ch. 2). Further, to detect statistically significant changes across treatment means or variance components in a tallgrass prairie stream experiment, large sample sizes will likely be required unless the treatments vary dramatically. By capturing this intra- and inter-annual stream variability, we hope this information can be useful in aiding states (like Missouri) to establish reference conditions and develop water quality criteria.

Fire and grazing are measurable disturbances

Fire and grazing are natural processes in tallgrass prairie, and this dissertation documented that they are also quantifiable disturbances to streams (Ch. 2, 3, 4, 5). The impacts of fire showed interesting short-term effects on nutrient dynamics at both Osage and Konza Prairies, but these effects never exceeded recommended reference conditions for the region (U.S.

EPA 1998, Smith et al. 2003, Dodds and Oakes 2004). In contrast, the effects of cattle on pasture were drastic and more than doubled the recommended reference conditions (Ch. 5). When cattle were taken off pasture, water quality concentrations were reduced but not to pre-treatment conditions. A post-treatment phase at Osage for years 2013-2014 will determine if the absence of PBG will return streams to the pre-treatment state and will closely examine disturbance recovery dynamics.

Comparison of bison and cattle

Currently, there are two opposing hypotheses regarding the equivalency of cattle as comparable surrogates for bison. One view is that cattle would not influence water quality more than bison; therefore, cattle grazed watersheds will match reference conditions. Others argue bison and cattle differ behaviorally and physiologically (Christopherson et al. 1979, Allred et al. 2011b), and therefore will impact streams differently. These conflicting hypotheses sparked my research interest.

This dissertation suggests that bison at Konza Prairie rarely inhabited riparian areas (<5% time), and therefore minimally influenced water quality export (Ch. 3). In contrast, cattle regularly occupied riparian zones at Osage Prairie (~20% time), and had measurable impact on water quality (Ch. 5). Therefore, watersheds with bison and those without cattle matched suggested reference values for tallgrass prairie streams (U.S. EPA 1998, Smith et al. 2003, Dodds and Oakes 2004). Despite the difficulty in managing bison, bison may be a good surrogate to cattle stocking on pastures where riparian and water quality protection take precedence.

I acknowledge these comparisons of bison and cattle are currently circumstantial evidence. The data collected to compare the animals were taken from two study locations, Osage and Konza Prairies, which differed in many respects (Ch. 2) that could influence results of animal behavior and stream impacts. Additionally, the densities of bison were moderately low (~0.21 AU/ha) and the cattle densities were higher (~0.4 AU/ha). My dissertation indicates that further study where the experimental units are controlled for animal density, watershed size, past land uses, etc. is needed to make direct comparison of ungulate behavior and stream impacts.

Management suggestions

Land management objectives will ultimately dictate how fire and grazing is applied. Common management goals are cattle production (i.e., maximizing cattle weight gains), enhancing prairie diversity, and protecting water quality. Land management will need to prioritize these goals because each will require trade-offs. For example, maximizing cattle production (in the short-term) will likely entail annual fire and heavy grazing, but at costs of reduced diversity and water quality (Sovell et al. 2000). Alternatively, if the primary goal is the creating habitat diversity, fire and grazing in moderation will satisfy (Ch. 4, Howe 1994, Collins et al. 1998) but may require trade-offs for water quality (Ch. 5). Patch-burn grazing (with moderate cattle densities and riparian fencing) is likely a balance across these three management objectives; PBG can have cattle weight gains comparable to traditional management regimes (Fuhlendorf and Engle 2004), enhance habitat structure for wildlife (Ch. 4), and reduce water quality impacts by protecting the riparian zone (Ch. 5).

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Appendices

Appendix A - Detailed methodology for Chapter 4

Additional information on the methodology used to capture herpetofauna, to analyze sediment and nutrient concentrations, and to conduct statistical analyses for the herpetofauna study at Osage Prairie in 2011-2012.

Animal surveys

To ensure dispersal was not simply an artifact of the breeding season or seasonal succession of vegetation structure, I monitored Control patches throughout time to compare to estimates from treated patches. Each sampling date, the sites were randomly ordered for sampling to reduce the "time of day" effect. To eliminate observer bias in herpetofaunal detection, I was the sole person conducting the surveys. I used three capture methods. First, two minnow traps were deployed in streams in each patch for 16-20 hours to capture tadpoles, salamander larvae, and any swimming adults. Second, coverboard arrays of sixteen boards (61 cm x 61 cm x 0.75 cm [Heyer et al. 1994]) were arranged in 2 rows as artificial refugia. At least 3 months prior to sampling, the boards were weathered (Dodd Jr. 2010). I removed boards from the burn zone immediately before the burn and replaced them shortly following the burn in the original location. The coverboards were left to rest for 2 days before sampling to allow recolonization. Finally, visual encounter surveys (VES) were conducted along three permanent transect lines of 40 m each (Heyer et al 1994). The VES transects were placed 0 m (water's edge), 2 m, and 9 m parallel to the streamside.

Water samples

Since 209, monthly water samples were collected at the base of each watershed in acid-washed bottles from the thalweg and stored on ice. The NH_4^+ samples were filtered within 24 h (Whatman GFF, 0.7 µm retention) and then frozen at -30ºC until analyzed for NH_4^+ (APHA 1995). Three independent runs were performed using an OI-Analytical Flow Solution IV autoanalyzer (Xylem Inc., White Plains, USA) and values were averaged. For TSS, 1 L water samples were filtered through pre-combusted, pre-weighed glass-fiber filters (GFC Whatman, 1.2 µm retention) within 24 hours. Filters with retained material were dried at 60°C and weighed to calculate TSS (APHA 1995).

Redundancy analysis

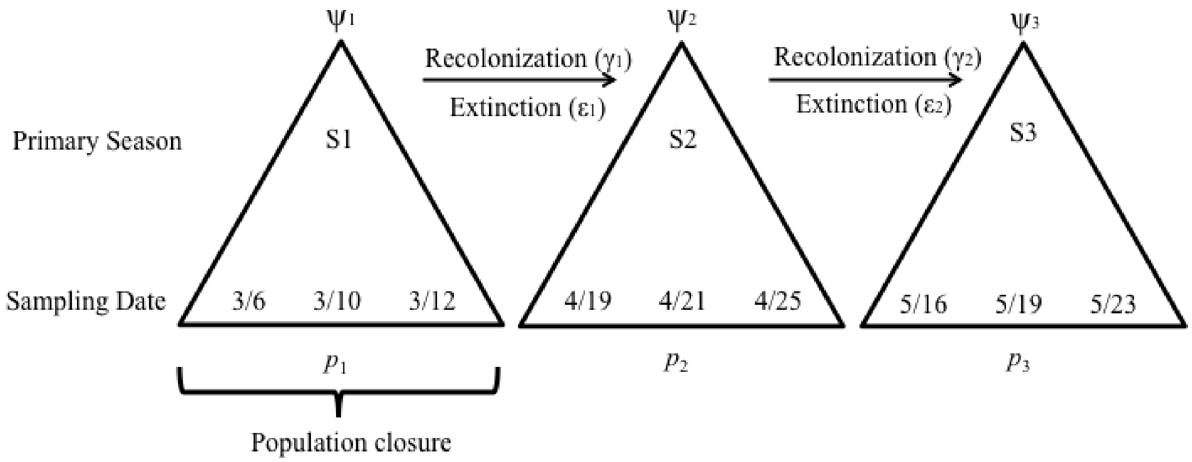
I ran a redundancy analysis (RDA) because the environmental gradients of interest are short (e.g., often categorical and the distance between patches were <2 km; Legendre & Legendre 1998). The measured environmental variables (i.e., the RDA terms) for the riparian community included *year* (categorical; 2011 or 2012), *patch type* (categorical; Fire, F+G, Lt Grazing, Control, Fire-Legacy, or F+G-Legacy), *grass height* (continuous), *% grass cover* (continuous), *ground cover type* (categorical; bare or grass), and *litter depth* (continuous). The aquatic environmental factors included *year* (categorical; 2011 and 2012), *patch type* (same as reptiles), *watershed* (categorical: stream 1, 2, 3, or 4), *water depth* (continuous), *% in-stream vegetation cover* (continuous), *% riparian canopy cover* (continuous), *TSS* (total suspended solids; continuous), and NH_4^+ (ammonium; continuous). The variance inflation factors found no redundancy in either model, so all predictor variables were kept.

Robust-design occupancy modeling

The encounter history matrix pooled all reptile species, capture methods, and patches of the same type, but was separated by sample years 2011 and 2012, to increase the degrees of freedom and obtain more precise parameter estimates. This pooling tactic was required to run the model and assumes no heterogeneity between taxonomic groups (e.g., all reptiles respond similarly to the treatments). Occasionally, program MARK yielded nonsense parameters due to low numbers of animals for this "data hungry" modeling approach. Nonsensical parameter estimates and those in which the standard error was greater than the estimate are excluded from the Results section and indicated by NA on Figures. Further, I attempted to use the robust-design occupancy model for two species with the greatest abundance (*Scincella lateralis* and *Terrapene ornata*) and for each the three taxonomic groups (turtles, lizards, and snakes) but the models contained many inestimable parameters, signifying that data must be pooled into one guild (reptiles) for occupancy analysis. No formal goodness-of-fit test exists (MacKenzie et al. 2003), so I assumed overdispersion was negligible and proceeded with model selection according to Akaike's Information Criterion adjusted for small sample size (AIC_c). The top models were considered parsimonious if $AIC_c < 2$ and did not contain uninformative parameters (Arnold 2010). Parameter estimates were taken from the minimum AIC_c model.

Appendix B - Conceptual model

A conceptual diagram for robust-design occupancy modeling. Estimates of occupancy (ψ) and detection probability (*p*) are obtained for each primary season (S1, S2, or S3), where the season corresponds to the successional application of various treatments of fire and/or grazing. Dispersal estimates of recolonization (γ) and extinction (ε) are transition probabilities between primary seasons. This image is based on Pollock (1982) and MacKenzie et al. (2006).



Appendix C – Herpetofuana species list

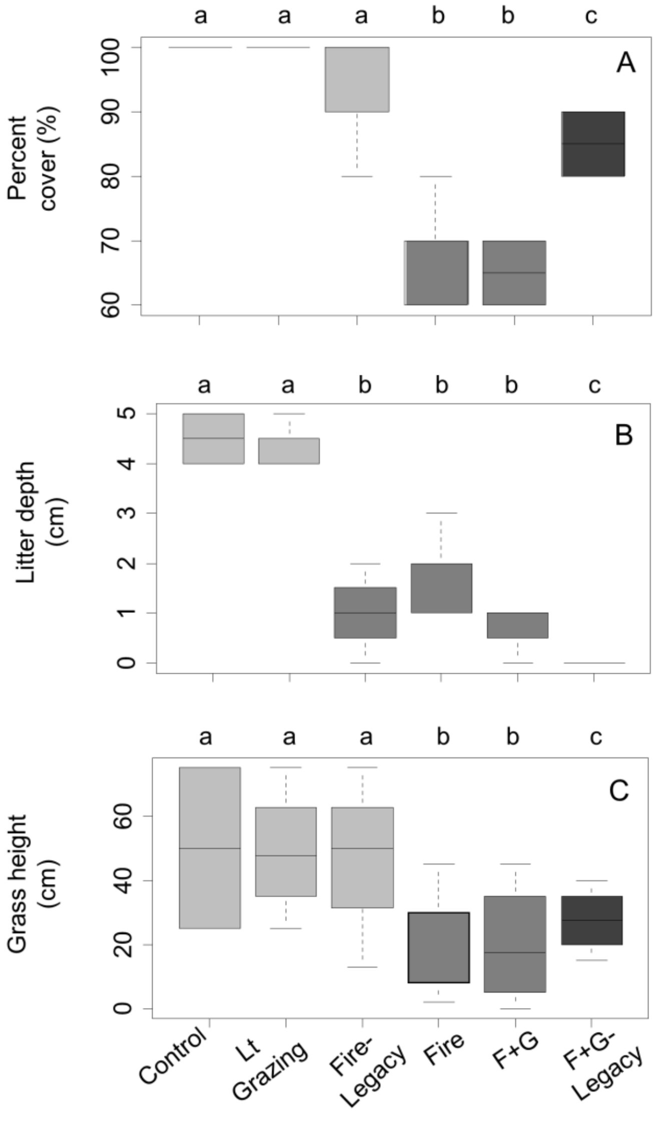
A list of species captured at Osage Prairie, MO in 2011 and 2012 from multiple patch types, including those with fire, cattle grazing, and legacy effects.

Taxonomic Group	**Common Name**	**Species**	**Count**
REPTILES			
Lizard	Slender Glass Lizard	*Ophisaurus attenuatus*	2
Lizard	Little Brown or Ground Skink	*Scincella lateralis*	82
Snake	Eastern Yellow Bellied Racer	*Coluber constrictor flaviventris*	3
Snake	Prairie Ringed Neck Snake	*Diadophis punctatus arnyi*	4
Snake	Black Rat Snake	*Elaphe obsoleta obsoleta*	3
Snake	Prairie Kingsnake	*Lampropeltis calligaster*	1
Snake	Speckled Kingsnake	*Lampropeltis getula holbrooki*	1
Snake	Graham's Crayfish Snake	*Regina grahamii*	1
Snake	Unknown	Unknown	11
Snake	Rough Earth Snake	*Virginia striatula*	1
Snake	Common Garter Snake	*Thamnophis sirtalis*	10
Turtle	Common Snapping Turtle	*Chelydra serpentina serpentina*	8
Turtle	Western Painted Turtle	*Chrysemys picta bellii*	4
Turtle	Three-Toed Box Turtle	*Terrapene carolina triunguis*	2
Turtle	Ornate or Western Box Turtle	*Terrapene ornata ornata*	13
Turtle	Unknown (burned and unidentifiable)	Unknown	4
TOTAL			150

AMPHIBIANS			
A. texanus	Small-mouth Salamander	*Ambystoma texanum* (larvae)	67
B. americanus	American Toad	*Bufo americanus* (tadpoles)	331
R. sphenocephala	Southern Leopard Frog	*Rana (Lithobates) sphenocephala* (tadpoles)	541
Eggs (masses)	varies	varies	23
Adult	Spring Peeper	*Pseudacris crucifer*	1
Adult	Chorus Frog	*Pseudacris triseriata*	2
Adult	American Bullfrog	*Rana (Lithobates) catesbeiana*	3
Adult	Southern Leopard Frog	*Rana (Lithobates) sphenocephala*	20
Adult	Unknown	unknown	23
Adult	Blanchard's Cricket Frog	*Acris crepitans blanchardi*	18
Adult	Small-mouth Salamander	*Ambystoma texanum*	2
Adult	Northern Crawfish Frog	*Rana (Lithobates) areolata circulosa*	6
Adult	Gray Treefrog	*Hyla chrysoscelis-versicolor*	1
Adult	Plains Leopard Frog	*Rana (Lithobates) blairi*	3
	Blanchard’s Cricket Frog	*Acris crepitans blanchardi* (tadpoles)	4
TOTAL			1045

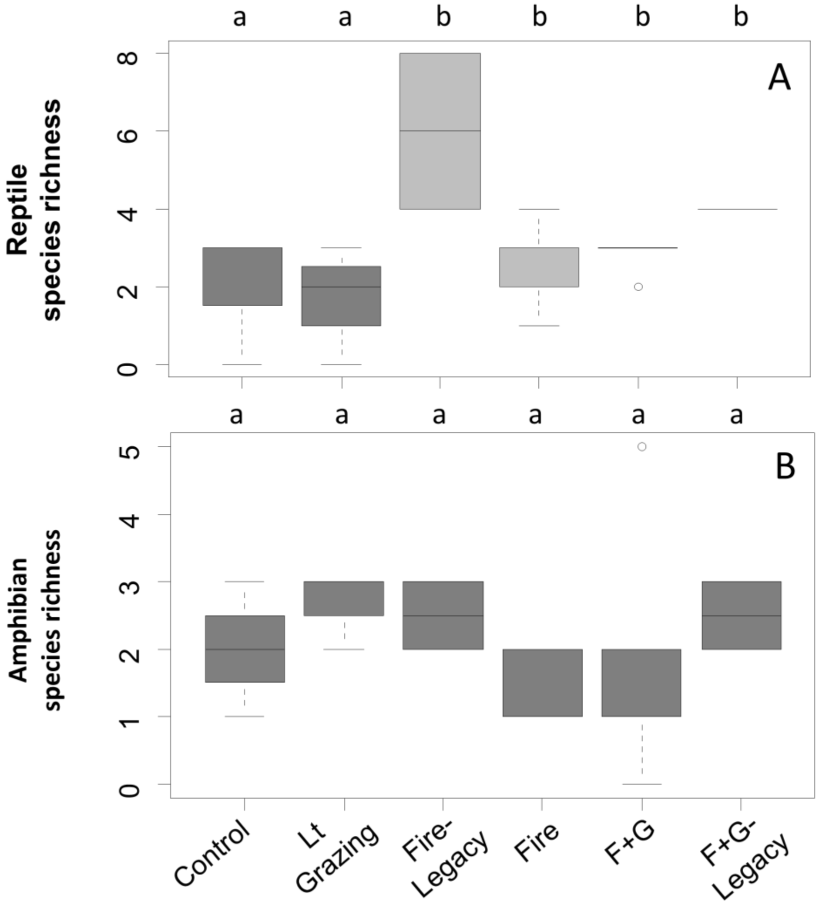
Appendix D – Vegetation structure for patch-burn grazing

Vegetation structures of percent cover (A), litter depth (B), and grass height (C) for 6 patch types (n=6 patches each) at Osage Prairie, MO, USA in March-May of 2011 and 2012. The boxplots are shaded differently and contain different letters above if found statistically different (ANOVA followed by Tukey's HSD test; alpha <0.05). Boxplots show the 25th, 50th, and 75th quartiles and the whiskers are 95% confidence intervals.



Appendix E – Species richness

Reptile (A) and amphibian (B) species richness in 6 patch types from Osage Prairie, MO, USA. The boxplots are shaded differently and contain different letters above if found statistically different (ANOVA followed by Tukey's HSD test; alpha <0.05). Boxplots show the 25th, 50th, and 75th quartiles, the whiskers are 95% confidence intervals, and circles are statistical outliers.



Appendix F – ANOVA table for the herpetofuana community

A permuted multivariate analysis of variance (PERMANOVA) determined the predictors of riparian and aquatic community structures at Osage Prairie, MO in 2011 and 2012.

Factor	**Degrees of Freedom (n,d)**	**Variance**	**F Statistic**	***P*-value**
Riparian Community				
Patch type	5,22	0.185	4.59	<0.001
Grass height	1,26	0.025	3.11	0.048
Year	1,26	0.018	2.25	0.112
Ground cover	1,26	0.007	0.90	0.417
Percent cover	1,26	0.011	1.46	0.247
Litter depth	1,26	0.006	0.69	0.514
Aquatic Community				
Year	1,55	0.113	27.90	<0.001
Watershed	1,55	0.047	11.70	0.002
In-stream cover	1,55	0.019	4.91	0.007
Substrate	3,53	0.028	1.17	0.029
Patch type	5,51	0.031	1.55	0.101
Depth (water)	1,55	0.003	0.07	0.503
Riparian cover	1,55	0.006	0.69	0.514
Total suspended solids	1,55	0.013	2.13	0.103
Ammonium (NH_4^+)	1,55	0.005	0.90	0.405

Appendix G – Candidate models

Top candidate models using Akaike's Information Criterion corrected for small sample size (AIC$_c$) regarding reptile occupancy (ψ), detection (p), recolonization (γ), and extinction (ε) for treated patches at Osage Prairie in 2011 and 2012.

Model	**No. Parameters (K)**	**Deviation**	**ΔAIC$_c$**	**AIC$_c$ Weight (w$_i$)**
*Ψ(g*t) ϵ(g*t) γ(t) ρ1(t) ρ2(t) ρ3(t)*	20	519.2	0.00	0.89
Ψ(t) ϵ(g*t) γ(t) ρ1(t) ρ2(t) ρ3(t)	17	515.1	6.67	0.03
Ψ(g) ϵ(g) γ(g) ρ1(.) ρ2(.) ρ3(.)	19	512.4	8.46	0.01
Ψ(g*t) ϵ(g) γ(g) ρ1(t) ρ2(t) ρ3(t)	19	512.4	8.46	0.00