Ecosystem Characteristics of Remnant, Headwater Tallgrass Prairie Streams

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North America has lost >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 the 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 with literature values for streams draining agricultural watersheds in the region. We quantified physicochemical and biological characteristics for 2 yr. 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- to 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 probably linked to variable hydrology. We found nine amphibian species using the Osage streams as habitat or breeding sites, but little usage at Konza was probably 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.

Tallgrass prairie and its streams are highly endangered ecosystems; most tallgrass prairies were plowed and converted to row crop agriculture more than 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 the water quality, productivity, and community structure of these remaining systems. Tallgrass prairie streams are understudied, except at the Konza Prairie Biological Station 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, and 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 the resumption of flow or after scouring, they are recolonized 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 to 10 yr (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 N (TN) and NO_3^- concentrations in Konza tallgrass prairie streams can increase as a function of both

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Abbreviations: BOM, benthic organic matter; CPOM, coarse particulate organic matter; CR, community respiration; EPT, Ephemeroptera, Plecoptera, and Trichoptera; FPOM, fine particulate organic matter; GPP, gross primary production; ISS, inorganic suspended solids; NPP, net primary productivity; SRP, soluble reactive phosphorus; TN, total nitrogen; TP, total phosphorus; TSS, total suspended solids; VFPOM, very fine particulate organic matter; VSS, volatile suspended solids.

number of days and years following fire (Dodds et al., 1996); however, the 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 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). The 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 the 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 cycle (Collins and 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*). 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.

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.

Materials and Methods

Osage Streams

The study streams at Osage Prairie Conservation Area are unnamed intermittent tributaries of the Landon Branch in southwestern Missouri (37°44′25.61″ N, 94°20′12.17″ W; Fig. 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-ha remnant prairie owned and managed by the Missouri Department of Conservation and The Nature Conservancy. Soil types on the Osage Prairie consist of Barco loam (a fine-loamy, mixed, active, thermic Humic Hapludult), Barden silt loam (a fine, mixed, active, thermic Aquollic Hapludalf), and Coweta loam (a loamy, siliceous, superactive, thermic, shallow Typic Hapludoll), all well-drained, gently sloping upland soils (Soil Survey Staff, 2004). Past land use includes haying and cattle grazing from the early 1900s to 1987. Current management consists of midsummer triennial haying, a prescribed fire interval of 3 to 5 yr, and mechanical removal of riparian trees >10 cm in 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 (Solecki and Toney, 1986). In early April 2011, a prescribed burn was performed 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 wk following fire.

Fig. 1. The historical range of tallgrass prairie in the United States (shaded gray, replotted from National Environmental Research Parks, 2007). The stars indicate our study sites (Osage and Konza) where the entire watersheds are in native tallgrass prairie.

Konza Streams

Konza is located in the Flint Hills region of northeastern Kansas and is owned and managed jointly by Kansas State University and The Nature Conservancy (39°5′55.65″ N, 96°36′19.91″ W; Fig. 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 (fine-silty, mixed, superactive, mesic Cumulic Hapludolls) dominate the floodplains and are characterized as having deep, moderately well-drained soil interspersed with rock fragments (Knapp et al., 1998). Watersheds N2B and N4D are in the Kings Creek basin and have been grazed by bison (*Bison bison*) 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. Watershed N2B has a burn interval of 2 yr, N4D is burned every 4 yr, and Shane is burned approximately annually. Shane was burned on 12 April 2011 during our study, and we monitored the stream for 3 wk 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 wk following the prescribed prairie fire (raw data can be found at www.konza.ksu.edu). Because 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 the streams were flowing.

Geomorphology and Physicochemistry

We measured and averaged stream widths (to the point of maximum capacity on the banks) 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 (ESRI). Temperature and O_2 were recorded using YSI 6000 probes at 10-min intervals. Discharge at Osage was measured with an ion-specific Br^- probe (Thermo Orion) as the dilution of a concentrated solution of KBr pumped at a known rate. At Konza, discharge data were compiled for Watersheds N4D and N2B only; measurements were taken at 5-min 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-h period (raw data can be found at 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 −30°C until analysis. Additional water collected from the single-stage US U-59B samplers (Ford, 2007) 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 NO_3^- + NO_2^- (hereafter referred to as simply NO_3), NH_4^+, and soluble reactive P (SRP) concentrations (American Public Health Association, 1995). Unfiltered stream water was analyzed for TN and total P (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 three to five in situ rocks per stream per sampling date for Osage streams only. Rocks were collected and returned to the laboratory frozen. In the laboratory, whole rocks were extracted with hot 95% ethanol (79°C for 5 min, followed by 12 h at 4°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 (Marzolf et al., 1994) 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) in an open area, and temperature and O_2 saturation were recorded using YSI 6150 ROX optical O_2 probes at 10-min intervals. 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 the SF_6 concentration within the study stream reaches (60 m) during base flow (Mulholland et al., 2001). We measured SF_6 concentration and peak area using a Shimadzu GC-2014 gas chromatograph with an electron capture detector. Reaeration rates of SF_6 were calculated as the difference between the natural logarithm 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 the 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 on in-stream temperature. The Solver option in Microsoft 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 base-flow total suspended solids (TSS) concentration analyses in acid-washed bottles from the thalweg when the streams were flowing. The TSS water samples were filtered through precombusted (24 h at 475°C), preweighed glass-fiber filters (GFC Whatman, 1.2-μm retention) within 24 h. Filters with retained material were dried at 60°C, ashed to 475°C (6 h), and reweighed to find the amount of inorganic suspended solids (ISS) and volatile suspended solids (VSS) (American Public Health Association, 1995). Analyses confirmed that wetting and redrying 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 d 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 chosen riffle or run habitats using a Mini-Surber sampler (Wildco) and from pools with a stovepipe corer (three 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 the Mini-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 the Mini-Surber and core samples was estimated visually using a modified Wentworth scale (Wentworth, 1922).

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

We removed all macroinvertebrates from the samples and identified most to the genus level 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 the 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 during the entire study period for that season.

Amphibians

Amphibian sampling occurred every 2 wk from February to June 2011 at Konza and Osage (seven sampling periods). We captured amphibians using a variety of methods to increase the chance of capturing an array of species. Eight small Promar minnow traps were left floating in each stream for 16 to 20 h to capture tadpoles and swimming adults. Two coverboard arrays (one array = 16 boards) were randomly placed within the riparian zone (within 7 m of the channel). The boards (61 by 61 by 1.25 cm; Heyer et al., 1994) were arranged in two rows, with all boards ~61 cm from each other. Once captured, we recorded the 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 min at Streams 2, 3, and 6 between 1600 and 1800 h 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 version 9.2 (SAS Institute) and R 2.14.0 (R Development Core Team, 2011). Water quality data (except temperature and O_2) required logarithmic transformation to meet the assumptions of normality, and macroinvertebrate percentages were arcsine transformed before analyses. For benthic organic matter and invertebrates, we examined seasonal patterns at 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 nonparametric Kruskal–Wallis ANOVA for multiple comparisons to determine if TSS differed among Konza streams and the nonparametric Kendal tau rank correlation to examine relationships between TSS and nutrients. We used Student's t-tests with Bonferroni correction to examine the water quality before and after the fire at each stream. We report median concentrations for water quality data because the 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

Table 1. Summary of the watershed and stream physical characteristics of tallgrass prairie streams at Osage Prairie, MO, and Konza Prairie, KS.

Parameter	Osage Prairie	Konza Prairie
Average watershed area, ha	31 (±18)†	204 (±183)
Average temperature range, °C	−7.2 to 32	−2.7 to 26.6
Average annual total precipitation, mm	1338	835
Strahler stream order	1	3
Stream length range, m	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	NA‡
Burn interval range, yr	3–5	1–4
Grazers, bison	no	yes

† Numbers in parentheses represent 1 standard error.

‡ NA, not available.

pools with depths up to 0.75 m for amphibian larvae and fish habitat. The streams flowed all year in 2010. In 2011, the streams dried completely in mid-June and did not resume flow until December. Despite the 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 varied significantly 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 the average discharge was lower than at Osage (Table 1). Flow was documented in May 2009 to mid-June 2009, with a median base-flow discharge of 0.004 m^3 s^{-1}. Flow ceased from June to November (at Shane and N2B) and resumed in December 2009. Whereas Shane and N2B dried in the summer months, N4D had low flow with a median discharge value of 0.003 m^3 s^{-1}. Data from historical records at Konza show that these streams can be without flow for more than a year or more or can flow continuously (Dodds et al., 2004) but did not during our study.

Chemical Properties

At Osage, Streams 1 and 2 had greater total nutrient values ($P < 0.001$), and the medians for all Osage streams were 252 μg L^{-1} TN and 37.1 μg 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 during the 2-yr study (Table 2).

At Konza, TN was not different among watersheds ($P = 0.104$), with a median of 392 μg L^{-1} (Fig. 2). Total P was greatest at N4D and Shane ($P = 0.999$) and significantly higher than at 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 ratio was inversely correlated to TSS ($\tau = -0.201$, $P < 0.001$). Storm flows significantly increased TN by 12 times ($P = 0.015$) and 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 ($P < 0.001$) (Fig. 2).

At Osage, inorganic nutrients were highly variable temporally, even at base flow (Table 2). Ammonium 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 ($P = 0.417$) or correlated with TSS ($R^2 = 0.04$). Similar to trends with TSS, the variance of NH_4^+ increased greatly with stage height. The SRP concentrations did not vary by site at base flow ($P = 0.554$) but did increase approximately eightfold during storm-flow events at each site ($P < 0.001$) (Table 2). Nitrate concentrations varied spatially in the Osage streams, with Streams 1 and 3 having slightly higher values ($P = 0.019$). There was no obvious seasonal trend at base flow. Storm flows increased NO_3 (Table 2) but it 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, NO_3 concentrations decreased fourfold following prescribed fire at Streams 2 and 4 ($P = 0.015$), and SRP concentrations decreased by half ($P = 0.014$). Ammonium 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

Table 2. Summary statistics for six headwater streams on Osage Prairie, MO, from 2009 to 2011 (base-flow sample size = 99; storm-flow sample size = 51). Blanks indicate no storm-flow samples. Organic matter values are habitat weighted.

Parameter	Base flow		Storm flow	
	Range	Median	Range	Median
NO_3, μg L^{-1}†	0.4–121	7.7	7.7–657	42.6
NH_4^+, μg L^{-1}†	7.3–228	15.3	1.7–1083	22.4
Soluble reactive P, 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 N, μg L^{-1}	100–803	252.8		
Total P, μg L^{-1}	7–165	20.1		
Total N/total P 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, °C	0–21.5	14		
Dissolved O_2, mg L^{-1}	0.2–12.8	8.1		

† Storm flows significantly increased the median value ($P < 0.05$).

‡ AFDM, ash-free dry mass.

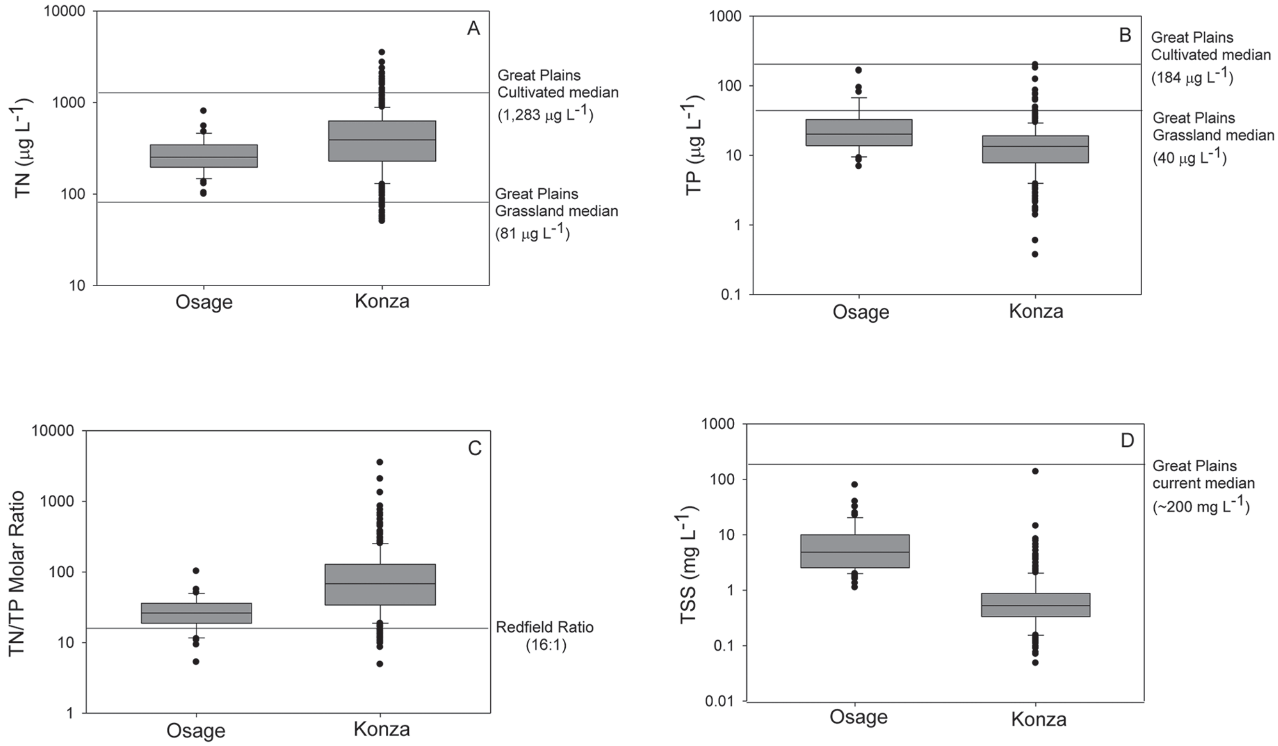

Fig. 2. Box plots (on a logarithmic scale) comparing the values of (A) total N (TN), (B) total P (TP), (C) TN/TP molar ratios, and (D) total suspended solids (TSS) from Osage Prairie, MO, and Konza Prairie, KS. The sites were statistically significantly different from each other in each parameter, yet both sites typically display low values. The Great Plains Grassland and Great Plains Cultivated values are EPA Ecoregion Level 1 criteria, 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.

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 wk following the fire but only at Streams 2 and 4 (where we also detected changes in nutrients). For all streams, the median chlorophyll *a* concentration was 0.67 µg 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 µg 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, which averaged 0.4 µg cm^{-1}.

Osage streams were net heterotrophic overall (GPP < CR). Stream 2 was net autotrophic (GPP > CR) in May 2010, with a net primary productivity (NPP) of 0.11 g O_2 m^{-2} d^{-1}. The 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 (<8 mg L^{-1}), with little variability across sampling periods (Table 2). Increases in TSS from storm flow spanned orders of magnitude (Fig. 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 10-fold greater at Osage that Konza (Fig. 2, $P < 0.001$), yet both regions had low values, with an overall median of 4.85 mg L^{-1}. Furthermore, 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 three- to 12-fold compared with base-flow TSS values at both sites ($P < 0.001$). The prescribed fire did not significantly influence TSS concentrations ($P = 0.196$) 3 wk 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 benthic organic matter (BOM) values in Osage Prairie streams had no significant seasonal patterns. On average, across streams and seasons, the total BOM composition in Osage streams was ~50% CPOM, ~10% FPOM, and ~40% VFPOM (Table 2). Standing stocks of VFPOM in the spring were ~1.7 times higher than winter standing stocks. In contrast to total BOM and VFPOM, CPOM and FPOM were generally higher in fall and winter than spring, but these trends were not statistically significant.

The average total macroinvertebrate abundance in Osage Prairie streams ranged from 28,000 to 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 the 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 the highest values in winter and spring (Table 3). Diversity of macroinvertebrates was lowest during the winter. Collector-gatherers were dominant in terms of abundance and biomass during all seasons, and the collector-gatherer contribution to total abundance was significantly greater in fall than winter and spring (Fig. 3). The 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 (Fig. 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 nine species (Table 4). Most individuals were American toad (*Bufo americanus*;, $n = 231$) and southern leopard frog (*Rana sphenocephala*, $n = 484$) tadpoles. Some southern leopard frog 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 approximately six times higher tadpole counts.

Konza streams were primarily dry during the spring amphibian breeding season. We captured 14 adult amphibians representing two species from February to June 2011 at Konza (Table 4). 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 that 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 4). 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.

Table 3. Macroinvertebrate community characteristics in headwater streams at Osage Prairie, MO, during 2009 to 2011. Values are habitat-weighted averages for samples from six study streams.

Parameter	Fall	Winter	Spring
Abundance, no. m^{-2}	28,020 (1117) a†	102,065 (3482) b	71,841 (2342) b
Biomass, mg AFDM‡ m^{-2}	3,656 (234)	8,306 (439)	13,121 (1380)
Shannon diversity index	2.0 (0.02) ab	1.8 (0.02) b	2.1 (0.01) a
Richness	28.0 (0.1)	31.0 (0.3)	30.9 (0.2)
EPT index§	3.6 (0.3) a	8.1 (0.2) b	6.3 (0.1) b

† Numbers in parentheses represent 1 standard error. Across rows, values followed by different superscript letters are significantly different ($P < 0.05$).

‡ AFDM, ash-free dry mass.

§ Number of taxa within the orders Ephemeroptera, Plecoptera, and Trichoptera.

Discussion

Overall, our results suggest that good water quality, high spatial and temporal variability, and moderate animal diversity characterize both sites. While there was considerable within-site variation in many of the variables we measured, we compared means and ranges with regional published reference data to put these 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

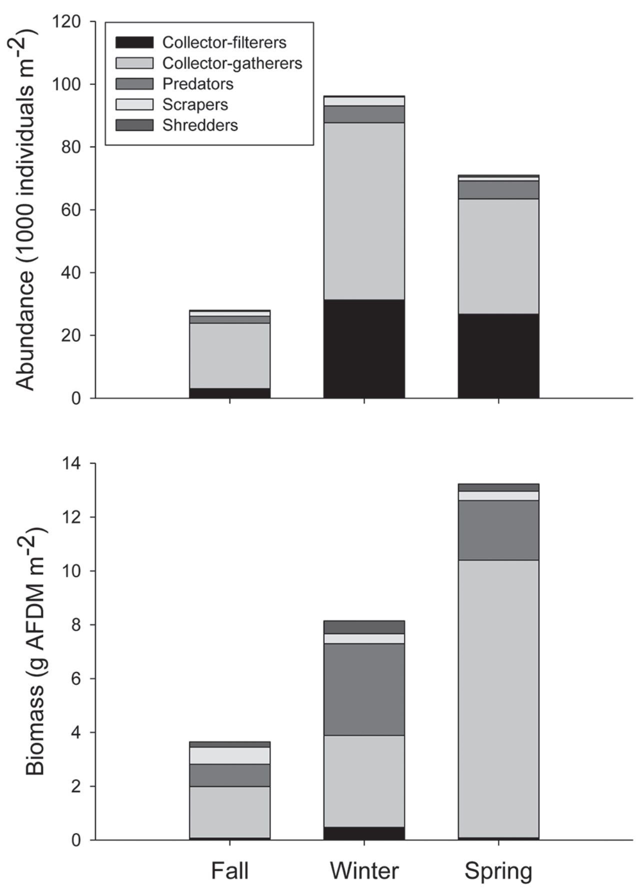

Fig. 3. Habitat-weighted average abundance and biomass of macroinvertebrate functional feeding groups across three seasons at Osage Prairie, MO, during 2009 to 2011 (nine sample dates). Seasons are categorized as: fall (September–November), winter (December–February), and spring (March–May). The summer (June–August) had no flow, so samples were not collected; AFDM is ash-free dry mass.

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 TSS concentrations were almost 10 times greater at Osage than at Konza. This difference was probably driven by geology (deeper soils at Osage) because 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 sites. We found inconsistent relationships between the TSS concentration and stage height in our study streams. About 20% of stations in a continental study demonstrated insignificant exponential relationships between TSS 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 or high retention and is reflected in an 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). Konza, however, had a median TN/TP molar ratio of 68:1, and experiments showed colimitation of autotrophic periphyton in those streams (Tank and Dodds, 2003). By comparing benthic chlorophyll *a*, TN, and TP concentrations with the range of reference values from Dodds (2006), we could classify our streams as oligotrophic during 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 seasons demonstrates 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.

Base-flow nutrient and TSS concentrations were considerably lower than most other streams in the ecoregions, which undergo intense agriculture (cropland or grazing). Base-flow 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), probably due to 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 with 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 tall grasses 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 from 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

Table 4. Survey data from six tallgrass prairie streams on Osage Prairie, MO, in spring 2011 (seven sample periods) and three streams on Konza Prairie, KS, in spring 2011 (seven sample periods). Methods of capture included cover boards, minnow traps, and netting. Blanks indicate no captures.

Common name	Scientific name	Osage Prairie			Konza Prairie		
		Adults and juveniles	Tadpoles and larvae	Call index†	Adults and juveniles	Tadpoles and 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			
Plains leopard frog	*Rana blairi*	1		2	1		
Small-mouthed salamander	*Ambystoma texanum*		8	NA‡			
Total		15	774		14	0	

† 1, individual caller; 2, multiple individuals calling but calls distinct; 3, full chorus (Dodd, 2010).

‡ NA, not applicable.

water velocity. This wetland stream was the only Osage stream to exhibit a net positive NPP, probably 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 compared with streams draining cropland (Dodds and Oakes, 2004; Dodds et al., 2009). Wetland prairie streams were probably historically common in mesic regions of the United States, but many have been drained through extensive 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 tallgrass 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 tall grasses 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 the results at Konza. Interestingly, these data show no change in stream TSS concentrations following fire; this supports a former study at Konza that suggested that 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 the 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 at Konza in the western extent of the tallgrass prairie (e.g., Fritz and Dodds, 2002; Stagliano and Whiles, 2002; Whiting et al., 2011). 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 at Osage and other grassland streams is probably linked to the lack of forest canopy, which reduces allochthonous inputs and enhances primary production compared with 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 that pollution-intolerant taxa (e.g., EPT taxa) are not abundant in headwater tallgrass prairie streams compared with similar-sized streams in forested regions. For example, Wallace et al. (1996) reported an EPT index of $\sim$20 for first-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 probably linked to the lower EPT index and overall taxonomic richness compared with headwaters in wetter regions (Fritz and Dodds, 2005). Some degree of hydrologic disturbance may enhance regional diversity, however, 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 two to four 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).

The 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 have focused 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 to spring and then emerge as adults in spring to summer. Our results suggest that biological assessments that focus on late winter and early spring sampling periods will capture the 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 probably 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 that we captured and heard was highly variable in space and time, and this was probably related to variability in the prevailing conditions during the surveys (Dodd, 2010). Thus, if proper sampling techniques are used for multiple sampling events, amphibians could be an important monitoring tool for tallgrass prairie streams. Given the variability that we found, the 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 prairies are simply too small and intermittent to maintain substantial densities of predatory fish. Given the greater abundance of amphibians at Osage, the loss of tallgrass prairie habitat in wetter regions will probably 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 to be higher because of a strong precipitation gradient between sites (PRISM Climate Group, prism.oregonstate.edu, accessed 29 Feb. 2012). 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 probably dominated by burning and grazing. We did observe higher diversity and higher relative abundance with amphibian sampling at Osage compared with Konza, probably due to more hospitable habitat related to the 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 under more mesic conditions (at Osage Prairie, Missouri) compared with Konza, the site with the 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 across small spatial scales, this study suggests that good water quality, moderate heterotrophic conditions, and the occurrence of some sensitive animal species are common traits of tallgrass prairie streams.

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