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ECOSYSTEMS

Removal of Woody Riparian Vegetation Substantially Altered a Stream Ecosystem in an Otherwise Undisturbed Grassland Watershed

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ABSTRACT

Riparian zones are key interfaces between stream and terrestrial ecosystems. Yet, we know of no whole-watershed experiments that cut only woody vegetation in the riparian zone in an otherwise intact watershed to isolate the role of riparian zones on stream ecology. We removed all of the woody riparian vegetation (from 10- and 30-m-wide buffers in headwaters and main channels, respectively) for 5 km of stream in a single watershed while leaving the remainder of the grassland watershed un-impacted. We assessed water chemistry changes 3 years before and 3 years after riparian wood removal and in two neighboring control watersheds with a before–after, control-impact design and analysis. Riparian woody removal caused 10–100-fold increases in mean stream water nitrate concentrations and pulses of high nitrate for 3 years thereafter. Other nutrients and total suspended solids increased 2–25 times for the 3 years of post-removal. In-stream rates of gross primary production, ecosystem respiration, and net ecosystem production had large treatment effect sizes but also high variance among samples. Past studies of whole-watershed deforestations showed similar water quality responses to our riparian deforestation. Riparian zones of grassland streams are sensitive to disturbance and likely impart relatively greater influence on stream structure and function than the upslope of the watershed. Our results further emphasize the role of riparian zones in biogeochemically linking aquatic and terrestrial habitats.

Key words: disturbance; prairie restoration; prairie stream; riparian buffer; water chemistry; whole-stream metabolism; woody encroachment; woody removal.

HIGHLIGHTS

- Stream hydrology (mean daily discharge) did not differ after the riparian wood removal
- Riparian wood removal caused seasonal pulses across several consecutive years for stream water NO_3^-, SRP, TN, and TP

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- The riparian wood removal resulted in large increases in the means and variances of nutrient and sediment concentrations

INTRODUCTION

Riparian zones have distinct hydric vegetation and soils and are an active zone for biogeochemical and hydrological processes at the interface between land and streams (Gregory and others 1991). Scientists obtain understanding of riparian effects on aquatic ecosystems via two ways. First, researchers conduct whole-watershed deforestation experiments in hardwood and coniferous forests and compare those results to removal of all but a riparian buffer strip (for example, Bosch and Hewlett 1982; Castelle and others 1994; Lee and others 2004). A second approach uses correlations between water quality, watershed land-use, and riparian buffer widths (for example, Osborne and Kovacic 1993; Kemp and Dodds 2001; Dodds and Oakes 2004; Huxman and others 2010). However, we know of no study that examined the influence of removing a riparian forest buffer in an entire watershed while maintaining native upland cover to elucidate the influences of riparian vegetation disturbance alone. Therefore, it is unclear if riparian disturbances have greater effects on streams compared to upland disturbances due to proximity to water and/or because riparian zones, which differ in environmental factors and ecosystem processing rates from uplands, are highly sensitive to disturbance.

Our previous work of riparian wood removals at stream reach-scales (a 30-m-wide riparian zone and 35-m-long stream reach) indicate the importance of woody riparian vegetation on prairie stream ecosystem structure and function (Riley and Dodds 2012; Reisinger and others 2013; Vandermyde and Whiles 2015; Veach and others 2015). Specifically, the riparian woody vegetation removal increased stream gross primary production, shifted algal assemblages (Riley and Dodds 2012) and soil bacterial and fungal assemblages (Veach and others 2015), altered invertebrate communities (Vandermyde and Whiles 2015), and increased denitrification potential of stream and riparian sediments (Reisinger and others 2013). Similarly, Wootton (2012) removed riparian wood in 50-m-wide and 300-m-long reaches of mostly forested regions of the Pysht River in Washington, USA, which increased algal production and abundance of most insect taxa and juvenile salmonids. Riparian managers control the invasive *Tamarix* spp. by reach-scale, riparian wood removal, which causes plant and wildlife changes (Shafroth and others 2005). Though insightful, reach-scale wood removal may not address cumulative watershed responses of factors such as water chemistry or discharge. Therefore, we require better understanding of biogeochemical, physical, and hydrologic effects of riparian forest disturbance achieved by watershed-scale experimentation (Hewlett and others 1969).

Woody vegetation (trees and shrubs) is expanding globally in mesic grasslands (Briggs and others 2005), and ''woody encroachment'' occurs along grassland streams (Veach and others 2014, 2015). Managers actively restore grassland streams by riparian woody removal and prescribed fire because grasslands are of high conservation need and grassland streams are highly endangered (Dodds and Oakes 2004). Documenting in-stream impacts may be particularly important because riparian trees and shrubs: (1) provide allochthonous carbon sources (Riley and Dodds 2012); (2) control nutrient concentrations and export (Likens and others 1970; Lyons and others 2000; Dodds and Oakes 2008); (3) control overland and subsurface flow (Wine and Hendrickx 2013), which can either increase or decrease stream water discharge (Rowe 1963; Lyons and others 2000); and (4) reduce water temperature through shading (Pusey and Arthington 2003). We lack watershed experimentation of riparian woody removal that can show how these variables will interact to alter water quality and ecosystem function.

We report the effects of removing all the riparian woody vegetation from a native tallgrass prairie watershed to understand the role of riparian disturbance on streams. Specifically, we removed trees and shrubs along about 5 km of stream channel that encompasses an entire sub-watershed within this region (30-m-wide strips on each side of main channels and 10-m-wide strips along tributaries), which disturbed 21% of the total watershed area. We examined water quantity, quality, and whole-stream metabolism for 3 years before and 3 years after the experimental woody riparian vegetation removal using before–after, control-impact (BACI) design and analyses (Downes and others 2002). We also examined 25 years of prior discharge and water quality data in these watersheds to put the experimental results in a longer temporal context and expand our inferences. We hypothesized that the woody vegetation removal experiment would lead to increased stream discharge due to reduced tree canopy interception and water uptake by trees and shrubs (Bosch and

Hewlett 1982). Further, we expected higher in-stream suspended sediment concentrations due to loss of root stabilization and increased overland flow and higher stream water nutrient concentrations due to loss of riparian vegetation that would intercept nutrients. We also hypothesized that the subsequent increases in nutrients and light would increase gross primary production and ecosystem respiration.

MATERIALS AND METHODS

Site Descriptions

We studied three neighboring treatment watersheds (''N2B'' as the impacted watershed, and ''N4D'' and ''N1B'' as control watersheds) within the Kings Creek watershed on Konza Prairie in northeastern Kansas, USA (39° 5′55.65″N, 96°36′19.91″W; Figure S1). Watershed N4D served as a control for nutrients and sediments and N1B as a control for discharge because each watershed had more complete datasets for these specific variables. The three watersheds were intermittent streams completely encompassed by native tallgrass prairie, except along the streams due to riparian woody encroachment (Veach and others 2014, 2015). The upland flora was grass-dominated (*Andropogon gerardii, Panicum virgatum, Schizachyrium scoparium,* and *Sorghastrum nutans*). Dominant tree species in the riparian zone included *Celtis occidentalis, Cercis canadensis, Gleditsia triacanthos, Quercus macrocarpa, Q. muehlenbergii*, and *Ulmus americana*. Our previous analyses of the impacted and control watersheds indicated that the proportion of stream length with woody vegetation present had increased from about 35% in 1985 to about 80% in 2010 (Veach and others 2014, 2015). *Bison bison* freely grazed all three watersheds since 1992 (density = ~ 0.21 animal units per hectare) but had minimal impacts on water quality (Larson and others 2013b). Prescribed fire occurred with three target frequencies of annually, (N1B), biannually (N2B) and every 4 years (N4D), but fire frequency had modest effects on water quality (Dodds and others 1996; Larson and others 2013a, b). See Table 1 for more watershed characteristics.

The study sites had three water quality collections per week since 1988 while flowing. A 25-year dataset indicated that the controls N4D and N1B behaved similarly with respect to water chemistry, including this 6-year experiment. However, the control N1B behaved more like the impacted watershed N2B with respect to patterns of discharge, probably because the area of N4D was somewhat larger (see datasets at: https://climhy.lternet.edu/).

Woody Removal Experiment

We used a BACI experimental design with repeated samples paired in time (Downes and others 2002). January 2008–October 2010 was the pretreatment phase (''Before''), and February 2011–November 2013 was the post-treatment period following riparian woody removal (''After''). We chose a fixed, 30-m-wide riparian buffer along the main channels and 10-m-wide buffer along the side channels because this range is thought to be sufficient to capture most nonpoint-source runoff in grasslands (Daniels and Gilliam 1996; Lim and others 1998; Lee and others 2004). We cut the riparian wood from October 2010 to February 2011 when the stream channel was dry, the vegetation was dormant, and the ground was frozen. We mechanically removed all woody vegetation in watershed N2B from 30-m-wide strips on each side of the main channel (1.7 km) and 10-m-wide strips on each side of the smaller geomorphologically active stream channels (3.3 km) using brush mowers (151 kg hand-driven), backpack cutters, and chainsaws. In April 2011 and 2013, we removed the woody debris from the stream channel and burned the entire impacted watershed and drip-torched the stream channels to burn remaining debris. We maintained the treatment by brush cutting woody recruitment each winter following the removal and did not apply chemical herbicides. We conducted reach-scale woody removal experiments at one 30-m-wide reach in years 2006–2008 at the control watershed N4D (Riley and Dodds 2012; Reisinger and others 2013), but otherwise the riparian vegetation was unmodified in the two control watersheds.

Stream Sampling

We outfitted each stream with a v-notch weir at the bottom of the watershed to continuously log discharge and routinely sample water chemistry. We sampled water from the thalweg in all watersheds three times weekly during periods of flow. Water was collected by hand in acid-washed bottles, transported to the laboratory in a cooler, and processed within 2 h. Samples returned to the laboratory were either filtered with Whatman GF/C filters and then frozen at − 30°C (for inorganic nutrients and dissolved organic carbon) or frozen whole at − 30°C (for total N and total P). Another subsample was used for total suspended solids (TSS), volatile suspended solids (VSS), and inor-

Table 1. Characteristics of the Controls and Impacted Watersheds at Konza Prairie, Kansas, USA, during the Woody Removal Experiment in Years 2008–2013

Treatment	Control 1	Control 2	Impacted
Watershed name	N1B	N4D	N2B
Data used for the before–after, control-impact analyses	Discharge	Water chemistry	Discharge and water chemistry
Latitude/longitude (at sampling location)	39°5′6.84″N 96°34′34.23″W	39°5′15.01″N 96°35′5.09″W	39°5′23.05″N
96°35′19.43″W			
Watershed area (ha)	121	135	83
Stream length (km)	6.48	8.86	5.02
Record of hydrology and water chemistry (start year)	1988	1988	1988
Riparian area in woody vegetation prior to removal (ha)	15.27	16.29	17.56
Area of riparian vegetation removed (ha)	0	0	17.56
Watershed area disturbed from riparian woody removal (%)	0	0	21
Prescribed fires during experiment (no wildfires)	April 22, 2008 April 7, 2009 April 3, 2010 April 13, 2011 April 11, 2012 April 3, 2013	April 7, 2009 April 3, 2013	April 7, 2009 April 13, 2011 April 3, 2013

ganic suspended solids (ISS) on Whatman GF/C filters with weighing and ashing at 475°C (APHA 1995). Water was stored at − 30°C until analyzed for nitrate + nitrite (hereafter referred to as nitrate; NO_3^-), ammonium (NH_4^+), soluble reactive total phosphorus (SRP; APHA 1995), and total nitrogen (TN) and phosphorus (TP) concentrations (Ameel and others 1993) using an OI-Analytical Flow Solution IV auto analyzer. Dissolved organic carbon (DOC) samples were adjusted to pH below 2 with 2 N HCl and then analyzed using platinum-catalyzed combustion using a Shimadzu TPC 5000 analyzer.

We measured discharge every 5 min at a triangular-throated flume at the base of each watershed and processed for mean daily discharges. The control site for discharge was watershed N1B because the discharge patterns best matched the impacted site N2B prior to the experiment and had a more complete dataset compared to control N4D.

We used the single-station method to estimate ecosystem respiration (ER), gross primary production (GPP) and net ecosystem production (NEP) rates in each stream (Dodds and others 2013). We modeled 22, 3–7 day sampling periods. Solar radiation values were collected from a micrologger on site. Barometric pressure was collected from the National Oceanic and Atmospheric Administration's Quality Controlled Local Climatological Dataset logged at the Manhattan, KS Regional Airport, approximately 5 km away from the impacted site. We measured water temperature and O_2 saturation during 10 min intervals using YSI 6150 ROX optical O_2 probes (YSI Inc, Yellowsprings, OH) placed just above the weirs. The YSI probes were deployed for 1-week periods and were then replaced with calibrated probes. We modeled daily stream metabolism based on measured total solar radiation, O_2, water temperature, barometric pressure, and the exchange rate of O_2 with the atmosphere (that is, aeration) and calculated a mean daily average for every 3–7-day intervals to reduce temporal autocorrelation. This model used light to scale GPP rates and made both ER and GPP rates dependent upon in-stream temperature. We modeled reaeration as previously described (Riley and Dodds 2012). The ''Solver'' option in Excel found values for GPP and ER that minimized the sum of square of errors between the observed and modeled O_2 concentrations.

Data Analyses

We tested for changes in ecosystem state variables after the riparian woody removal using two analyses (Andersen and others 2009): (1) a principal component analysis (PCA), which was a visualization method to observe changes in multiple variables and (2) BACI analysis with samples paired in time to assess statistical significance of woody removal. We included data from about 276 sampling dates for the following ecosystem state variables: TSS, TN, NH_4^+, NO_3^-, SRP, TP, and mean daily discharge. Sample sizes were smaller for whole-stream metabolism (22 sampling periods) because we removed the sondes during winter to prevent sonde damage and daily data were averaged for every 3–7 days to avoid serial autocorrelation. We performed all statistical analyses using the ''stats'' package in R (version 3.0.2, R Core Team 2013).

We examined the data prior to analyses to test statistical assumptions and ensure the PCA and BACI analyses were appropriate for this dataset. Plotting time series data showed the responses at the control sites were parallel to responses at the impacted sites during the pretreatment phase, which suggested similar temporal trajectories (Smith and others 1993; Stewart-Oaten and Bence 2001). Based on Q–Q plots, the Shapiro–Wilk test of normality (function ''shapiro.test''), and the Bartlett test of homogeneity of variances (function ''bartlett.test''), log-transformation did not conform to normality and equal variance assumptions, so we used nonparametric testing. The raw datasets for water quality and ecosystem metabolism initially did not conform to the independence assumption because of frequent sampling (three times per week or more); so, we computed weekly to biweekly averages, which removed temporal autocorrelation according to the Ljung-Box test (function ''Box.test''). Further, by using the difference value (Control-Impact) as the ecosystem state variable, we minimized serial autocorrelation and common issues with pseudo-replicated data (Downes and others 2002).

We used a PCA as an exploratory visual technique to graphically illustrate the relationships among treatments and water chemistry and to infer change (Andersen and others 2009). The PCA was conducted using the function ''princomp'' in the R stats package. The variables were standardized using a *Z*-score and then log-transformed to meet parametric assumptions. Each point within the ordination (indicated by an ''I'' or a ''C'') is a component score associated with the monthly average for each parameter.

We used a traditional BACI analysis with samples paired in time to test the effects of the riparian woody removal (Downes and others 2002). The BACI design focuses on the change at the impacted site relative to the control, after the experimental treatment is applied. The ecosystem state variable analyzed is the difference value between the control and impact (C-I) for each paired sampling period and is used in a Wilcoxon rank-sum test to compare the before and after period (R function ''wilcox.test''). The *W*-statistic for this test is from a nonparametric Student's *t* test, whereby the difference value (C-I) is compared to time of the experiment (Before and After). We defined the experimental unit as a watershed and the observational unit as a water quality sample. We used biweekly averages for each ecosystem state variable at each site. The model formula was:

$$\begin{aligned}\text{Ecosystem State Variable} = \text{Treatment} + \text{Time} \\ + \text{Treatment} * \text{Time}\end{aligned}$$

where the measurement was the water quality ecosystem state variable; Treatment was either the control (watershed N4D or N1B) or impacted site (watershed N2B); Time was before or after the treatment (Wang and others 2003). A significant interactive term (Treatment*Time) indicated a statistical difference in the before and after period at the impacted site. The statistical information is reported in the results as (*W*-statistic [degrees of freedom] = *X*, *p* value = *X*).

We used several different and complementary techniques in order to infer change at the impacted site. In Table 2, we report the statistical significance level at $\alpha = 0.05$, the treatment effect size (Cohen 1977), and the relative magnitude of changes. Some biologically significant results can also be viewed as graphical trends (Murtaugh 2002). The conclusions on ''significant changes'' may differ slightly among techniques due to the impact of sample size and treatment of variance of the different techniques. The treatment effect size complements *p* values because effect size is independent of sample size and the data can be easily used in future meta-analyses or comparisons with similar studies (Cohen 1977).

RESULTS

Before the riparian wood removal, the control and impacted streams were similar in hydrology (N1B) and water quality (N4D; Figures 1, 2, 3 and 4). The bound tree roots within the stream channel had created small sediment dams, but shortly after we cut and burned the roots, the spring floods obliterated the in-stream dams. The elimination of riparian woody vegetation at the impacted site was distinctly visible via satellite imagery (Figure 5). We detected significant changes in several ecosystem state variables from the riparian woody removal. The increased means and variances from

Table 2. Statistical Reporting for the Before-After, Control-Impact Analyses of the Riparian Vegetation Removal

Ecosystem parameter	*W*-statistic	DF	*p* value	Magnitude of impact	Cohen's *d*	Treatment effect size
TN (μg N/L)	78	18	0.002	Mean increased 1x; SD increased 2x	0.3	Small
NH_4^+ (μg N/L)	146	18	0.325	NS; Mean increased 1x; SD increased 2x	0.4	Small
NO_3^- (μg N/L)	43	18	< 0.001	Mean increased 25x; SD increased 15x	0.9	Large
SRP (μg P/L)	95	18	0.012	Mean increased 4x; SD increased 8x	0.3	Small
TP (μg P/L)	18	18	0.001	Mean and SD increased 2x	0.3	Small
TSS (mg/L)	43	28	< 0.001	Mean and SD increased 3x	0.1	Small
VSS (mg/L)	57	28	< 0.001	Mean increased 3x; SD increased 2x	0.2	Small
ISS (mg/L)	83	28	< 0.001	Mean increased 5x; SD increased 11x	0.2	Small
DOC (mg/L)	169	18	0.751	NS; Mean increased 2x; SD increased 4x	0.2	Small
Water temperature (°C)	101	20	0.126	NS; Mean and SD increased 1x	0.2	Small
GPP (g O_2 m^{-2} d^{-1})	70	10	0.115	NS; Mean and SD decreased > 375x	0.7	Moderate
ER (g O_2 m^{-2} d^{-1})	60	10	0.496	NS; Mean increased 1x; SD increased 2x	1.6	Large
NEP (g O_2 m^{-2} d^{-1})	60	10	0.481	NS; Mean increased 1x; SD increased 2x	1.6	Large
Mean monthly discharge (m^3/s)	185	18	0.466	NS; Mean decreased 2x; SD increased 1x	0.2	Small

''NS'' stands for no statistical significance at a Type 1 error rate of $\alpha = 0.05$ for paired Wilcoxon rank-sum tests. We also report the treatment effect size (Cohen's d) as an indicator of mean relative differences between the impacted and control sites.

the disturbance could indicate a change in ecosystem state (Scheffer and others 2001; Andersen and others 2009). We were unable to detect significant changes in discharge, but all water column nutrient and sediment concentrations increased 1–100 times in the impacted stream relative to the control stream (N4D; Table 2, Figures 2, 3 and 4; Supplements 2–3). The removal of riparian woody vegetation decreased GPP rates but increased rates of ER and NEP (Table 2; Table S2).

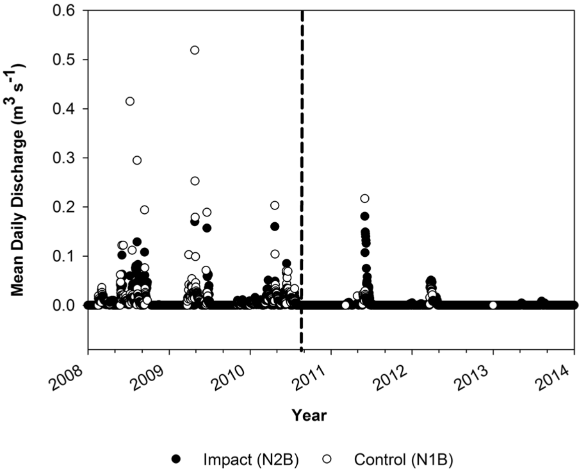

Figure 1. Hydrographs showing average daily discharge (Q) at the control (N1B) and impacted site (N2B). The dashed line separates the before period and the after the riparian removal period. The BACI analyses did not detect an influence of riparian removal on discharge and the treatment effect size (Cohen's *d*) was low.

Water Quantity

Daily discharge was not altered following the woody removal (W[18] = 185, $p = 0.466$; low treatment effect size). The mean discharge and periods of intermittency and flooding at the control (N1B) and impacted sites were generally consistent through time. The post-treatment period experienced mild drought at both watersheds, which resulted in reduced average daily discharge and more no-flow days. After the riparian wood removal, the periods of lowest flows followed rewetting in the spring and had the highest nutrient concentrations (Figure S2).

Water Quality and Ecosystem Metabolism Responses

The NO_3^- concentrations increased significantly after woody vegetation was removed from the riparian zone (W[18] = 43; $p < 0.001$; large treatment effect size). The arithmetic mean and standard deviation of NO_3^- concentrations increased more than an order of magnitude after the woody removal and the natural log response ratio increased fourfold. Following the riparian woody removal, 30% of NO_3^- samples had greater concentrations than the pretreatment period maxi-

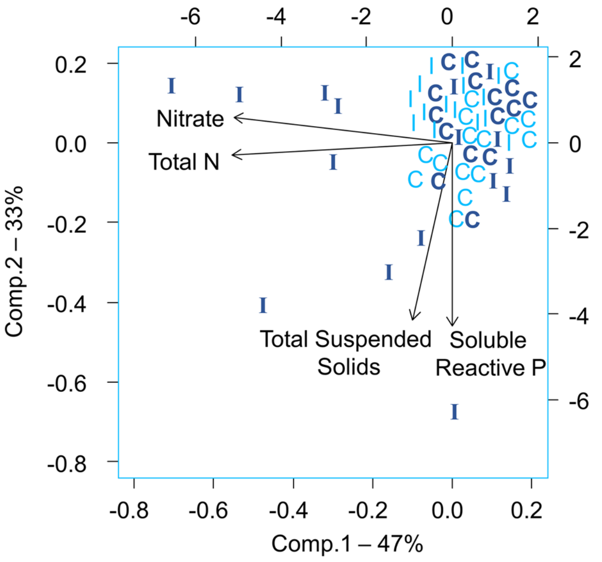

Figure 2. A principal component analysis (PCA) of nutrient data before and after the woody removal. *Light blue* samples were the before period (*n* = 25; monthly average) and *dark blue* samples were the after period (*n* = 25; monthly average). The stream nutrients and sediments at the impacted (I) site N2B were generally greater than the control site N4D (C). The *right* and *top* axis scales corresponded to sample scores and the *bottom* and *left* axis scales matched the variable loadings.

mum concentration (103 µg NO_3^-–N/L). For historical context, the maximum concentration within 25 years prior to woody removal at N2B was 490 µg NO_3^-–N/L; the concentration has never been recorded at the control (N4D) (*n* = 1000 samples per site; Figure S3). The maximum after removal at N2B was detected up to 2082 µg NO_3^-–N/L, in addition to 9 samples above the historical high of 490 µg NO_3^-–N/L. Rewetting of the intermittent streams each spring caused high NO_3^- pulses but the NO_3^-concentrations declined toward control conditions over the course of several weeks as baseflow resumed (Figure 2A–B, Figure S2). The greatest NO_3^- pulse occurred the second spring after the wood removal. Similar magnitude pulses of NO_3^- did not occur in either of the control watersheds (N1B or N4D). Storm flows did not increase NO_3^- concentrations (Figure S2).

Additionally, TN, TP, and SRP increased significantly following riparian wood removal and pulsed seasonally with rewetting in spring (Table 2, Figures 2, 3). The arithmetic mean of SRP increased as much as fivefold after the removal (Figures 2, 3C–D). Prior to woody removal, we did not measure any SRP value greater than 38 µg P/L; following removal, the maximum detected was 554 µg P/L. The arithmetic means and standard deviations of TN and TP concentrations doubled (Figure 2E–H).

The amount of VSS (organic particulates), ISS (inorganic particulates), and TSS (inorganic + organic) increased significantly. All suspended solids at least tripled their mean and standard deviation following the riparian woody removal (Table 2, Figure 4). Although the control (N4D) often had higher VSS and ISS concentrations throughout the experiment, the log response ratio revealed the impacted site had increased sediment supply after the riparian woody removal while the control's sediment concentrations remained stable. Sediment concentrations were highly correlated with phosphorus concentrations, but not nitrogen concentrations. We did not detect significant changes in the DOC concentrations (Table 2).

We detected moderate to large treatment effect sizes for whole-stream metabolism rates, but the variance among samples was large, making graphical trends modest and statistical relations not significant (Table 2, Table S2). GPP averaged about 375 times lower after the woody removal, whereas ER and NEP were about 1.5 times greater after riparian woody vegetation removal. The disparity of statistical significance and treatment effect sizes for metabolism are likely due to differences in Cohen's *d* (a standardized measure of relative differences) and BACI calculations, the latter being dependent on Wilcoxon rank-sum tests which have low statistical power with low replication (*n* = 11 for this study's metabolism data; Wang and others 2003). We find the decrease in GPP worthy of remark, but express caution in interpreting this result given high variance. Water temperature did not increase despite more light exposure after tree canopy removal (W[20] = 10, *p* = 0.13).

DISCUSSION

Our whole-watershed, riparian woody vegetation removal experiment provided unique information because small-scale riparian manipulations may not cause cumulative or scalable, whole-watershed responses. Our experiment reversed the typical experimental approach to testing watershed disturbance; rather than comparing watersheds with complete deforestation to those with a maintained riparian buffer strip, we cut only the riparian zone in an otherwise intact, native grassland watershed. This experiment underscored the disproportionate role of riparian disturbance on stream biogeochemistry in a grassland watershed, which could potentially have broad ramifications for watershed science across biomes.

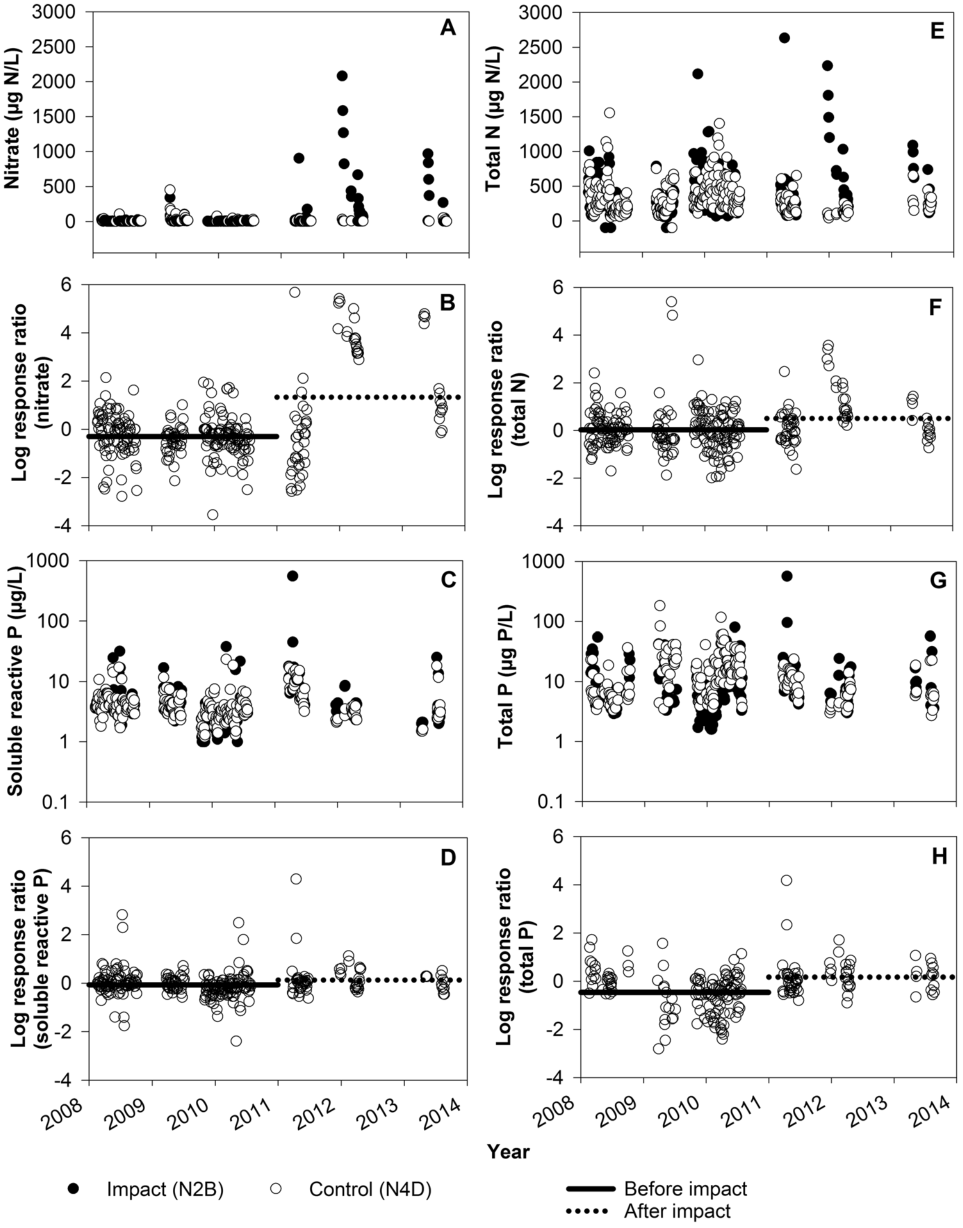

Figure 3. Time series plots of water chemistry before (years 2008–2010) and after the woody riparian removal (years 2011–2013). Panels showed the raw data values and the log response ratio (that is, the difference value) among treatments for nitrate (panels **A** and **B**; *n* = 291 dates), soluble reactive phosphorus (panels **C** and **D**; *n* = 290 dates), total nitrogen (panels **E** and **F**; *n* = 291 dates), and total phosphorus (panels **G** and **H**; *n* = 228 dates). The *lines* showed the average response ratio before (*solid line*) and after (*dashed line*) riparian removal. Water samples were taken thrice weekly and empty spaces indicate periods of no flow.

Riparian Woody Vegetation Removal did Not Affect Stream Discharge

Contrary to our hypothesis, discharge did not increase in the impacted watershed. Many studies of woody encroachment effects on stream flow found that increased woody transpiration led to decreased stream discharge or no change (Wilcox and others 2005; Huxman and others 2010). Most tree removal experiments used whole-watershed deforestation and found minimal change in discharge despite lower canopy interception and higher evaporation as reviewed by (Bosch and Hewlett 1982). Syntheses of past watershed studies from the USA Great Plains suggested that at least 20–50% of vegetative cover needs to be removed from the entire watershed before a statistically signifi-

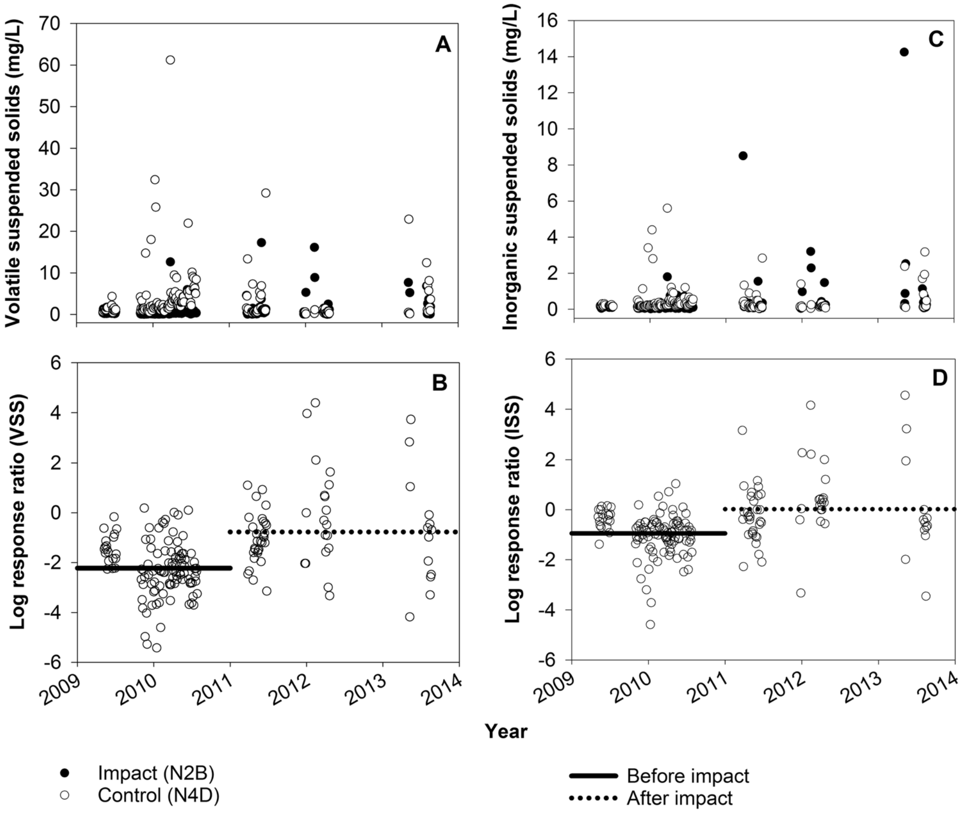

Figure 4. Time series plots of suspended sediments before (years 2008–2010) and after the woody riparian removal (years 2011–2013). Panels represented the raw data values and the log response ratio (that is, the difference value) among treatments for volatile suspended solids (panels **A** and **B**; n = 175 dates), and inorganic suspended solids (panels **C** and **D**; n = 175 dates). The lines showed the average response ratio before (solid line) and after (dashed line) riparian removal. Water samples were taken thrice weekly and empty spaces indicate periods of no flow.

cant discharge response is observed (Bosch and Hewlett 1982; Stednick 1996); however, we only disturbed 21% of the watershed area. This leads us to ask, was the lack of detectable change in discharge related to not meeting a minimal watershed disturbance threshold, or, did naturally high variance confound the statistics? Previously, we have only been able to detect significant hydrologic changes in this system with 5–10 year running means over 30 + years of record (Dodds and others 2012).

Riparian Wood Removal Increased Nutrients and Sediments

We have identified several potential, and not mutually exclusive, explanations as to why woody riparian removal strongly increased in-stream nutrients and suspended sediments: (1) The temporary increase in bare soil from the removal process destabilized riparian soil, which then transported sediments and nutrients bound to them; (2) the nutrient demand of plants and symbionts decreased and released soil-bound nutrients; (3) woody loss caused reductions of ammonium assimilation by plants and their mycorrhizal symbionts (Marschner and Dell 1994), causing increases in soil ammonium, thereby adding to a substantial increase in riparian soil nitrification and leaching of nitrate (Dalgren and Driscoll 1991; Reisinger and others 2013); (4) decreased carbon litter input to the stream lowered nutrient uptake by stream microbes (Webster and others 2000; Bernhardt and others 2003); (5) increased light availability from canopy loss increased suspended algae, and thus the volatile suspended solids (Figure 3); and (6) the in-stream processing of nutrients decreased from geomorphic habitat alterations (Sweeney and others 2004). The first three explanations would represent short-term effects from the initial disturbance itself. The final three explanations would result in ongoing, long-term changes and could represent positive feedback mechanisms that maintain the system in a new ecological state. We will eventually be able to test

Figure 5. Satellite imagery of the Konza Prairie impacted watershed (N2B) before (year 2009) and after (year 2012) the riparian deforestation experiment. We removed 100% of woody riparian vegetation 10–30 m on each side of the stream channels, which disturbed 21% of the total watershed area and led to a visible stream channel. Channels to the left and right of impacted watershed remained woody. Images courtesy of Google Earth.

these hypotheses directly with additional long-term monitoring.

We suspected that overland transport of sediments and particle-bound nutrients to streams (explanation 1, above) was minimal based on several lines of evidence. First, nitrate and suspended solids were not correlated (Figure 2). Also, bison trampling in these watersheds caused large bare patches of disturbed riparian soil that totaled approximately 40% of the riparian area but did not significantly influence stream sedimentation or nutrients (Larson and others 2013b). Recent studies by (Wilcox and others 2005; Ponette-Gonzalez and others 2014) on shrubland-to-grassland transitions found little increase in runoff, as did our study, so increased hydrologic transport is unlikely. Finally, we saw maximum effects the second year after riparian wood removal. The first year had a spring burn and therefore had greater areas of open ground than the second year after the removal. Therefore, we suspect that increased sediments and nutrients were not due to overland transport but were more likely from localized changes of nutrient cycling and demand in the riparian and stream sediments or altered geomorphological processes, such as the loss of sediment dams from rotting tree roots (Zimnierman and Goodlett 1967).

In-stream nutrient concentrations had dramatic and repeated spikes for several years after riparian woody vegetation removal (Figure 2). Several experiments of whole-watershed deforestations showed increased stream water nitrate export over multiple growing seasons after the disturbance, similar to our observed nutrient pulses (Likens and others 1970; Dalgren and Driscoll 1991; Bernhardt and others 2003, 2005; Yeakley and others 2003). Other studies reported increased available soil pore-water NO_3^- and nitrification following riparian woody removals across many ecosystem types, which led to soil leaching of N to streams (Hamilton and King 1983; Dalgren and Driscoll 1991; Neill and others 2006). A literature review concluded that severe stream N increases occurred with complete watershed deforestations, but less so with select-harvest practices (Rhoades and others 2013). However, we were surprised that disturbing only 21% of watershed caused dramatic increases in stream nitrate that were comparable to nitrate effects from some whole-watershed deforestations (Dalgren and Driscoll 1991; Rhoades and others 2013). Therefore, the results from these past studies could be attributed primarily to the riparian disturbance (although it is also possible forested systems behave differently from tallgrass prairie in this respect). Future studies could test the role of riparian zones on nutrient dynamics in forested systems by using a similar experimental design that removes only the riparian woody vegetation.

Ecological Regime Shift?

The riparian vegetation disturbance initiated a strong system response as detected by two common methods (Andersen and others 2009): the PCA (Figure 2) and the BACI analyses (Figures 3 and 4). We also conducted an ANCOVA with time as an independent variable, which gave similar results

(Table S1). The impacted stream demonstrated sensitivity to woody vegetation removal by the increased means and variances of water quality concentrations and ecosystem metabolism, which could indicate a new ecosystem state (Scheffer and others 2001; Carpenter and Brock 2006). Removing riparian woody plants had apparently destabilized the system, allowing for repeated spikes in sediments and nutrients years after the disturbance. It is possible the stream is resilient to the disturbance of woody vegetation removal because many of the increased concentrations were temporary and often returned to near pretreatment conditions before pulsing again the following year (Figure 3).

The long-term stability of this ecological state and whether this is an alternative stable state is uncertain (Beisner and others 2003). To determine if the system is in an alternative stable state, we would need to show more data that identifies feedbacks maintaining a new state (Scheffer and others 2001; Carpenter and Brock 2006). Our prior research where we conducted reach-scale riparian woody removal showed heterotrophic and autotrophic processes (Riley and Dodds 2012) and invertebrate production and community structure (Vandermyde and Whiles 2015) more closely resembled stream reaches with naturally open grassy riparian zones than forested areas within the Kings Creek watershed. Therefore, we presume that the food web aspects of the Kings Creek watershed had moved to a different ecological state following woody removal. Our future research will focus on identifying the mechanisms responsible for periods of strongly elevated nutrient concentrations, determine the duration of effects, and identify positive feedbacks maintaining those seasonal pulses. We cannot fully assess resilience, test hysteresis, or conclude an alternative *stable* state change without longer-term data and mechanistic understanding of nutrient dynamics.

Riparian Woody Removal as a Stream Restoration Tool

At Konza Prairie, woody expansion has occurred over the last 80 years (Bragg and Hulbert 1976; Knight and others 1994; Veach and others 2014; Weihs and others 2016) and woody riparian encroachment is an emergent phenomenon in grasslands worldwide (Archer and others 1995; Briggs and others 2005). Tree and shrub removal can reduce woody encroachment in grasslands and other semi-arid and arid environments (Lyons and others 2000). Returning grass dominance along prairie streams requires the mechanical and/or chemical removal of shrubs and trees because reintroduction of fire and grazing is often not sufficient to halt woody expansion (Briggs and others 2005). For example, Veach and others (2014, 2015) demonstrated that expansion of woody riparian vegetation continued in annually burned watersheds on Konza Prairie. Maintaining the presumptive pre-European ecological state of grasslands through regular burning and/or bison grazing tends to have minimal effects on water quality compared to the riparian wood removal (Dodds and others 1996; Kemp and Dodds 2001; Larson and others 2013a, 2013b).

Purposefully shifting the aquatic ecosystem from closed-canopy forests to open-canopy grassland by woody removal to approximate historical conditions is a type of riparian restoration. Removal of woody vegetation along Konza Prairie streams allows local processes such as primary and secondary production to approximate those found in grassy reaches (Riley and Dodds 2012; Vandermyde and Whiles 2015). We removed all the woody riparian vegetation over an entire stream network that led to an open-canopy system and significant biogeochemical consequences; so, although woody removal creates an open-canopy system that visually resembles native grassland streams, the water chemistry was different. Larson and others (2013a) found that grassland streams in Missouri with repeated cutting of lesser amounts of woody riparian vegetation did not exhibit such elevated levels of nutrient concentrations. Our future work will reveal longer-term system responses to riparian restoration.

CONCLUSIONS

The removal of woody riparian vegetation had a disproportionately large, short-term influence on sediment and nutrient dynamics and transport relative to its small total areal cover, even though our experimental system was relatively natural and not subjected to whole-watershed disturbance. Our study provides further support for the popular concept that protection of riparian zones is particularly important to uphold water quantity, quality, and ecosystem functions (Gregory and others 1991; Lee and others 2004; Sweeney and Newbold 2014). Protecting naturally open-canopy streams in grassland biomes is critical, because restoration via removal of woody riparian vegetation is costly and has strong impacts to water quality. The protection of riparian zones should be a high priority, regardless of biome.

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