ECOSYSTEMS

Impacts of Riparian and Non-riparian Woody Encroachment on Tallgrass Prairie Ecohydrology

Rachel M. Keen,[1]* Jesse B. Nippert,[1] Pamela L. Sullivan,[2] Zak Ratajczak,[1] Brynn Ritchey,[1] Kimberly O'Keefe,[3] and Walter K. Dodds[1]

[1]Division of Biology, Kansas State University, Manhattan, Kansas, USA; [2]College of Earth, Ocean, and Atmospheric Science, Oregon State University, Corvallis, Oregon, USA; [3]Department of Biological Sciences, St. Edward's University, Austin, Texas, USA

ABSTRACT

Woody encroachment has impacted grassland ecohydrology worldwide, prompting management strategies aimed at woody vegetation removal to prevent or mitigate loss of water yield. We measured stream discharge following sustained cutting of riparian trees (2010–2020) in a native tallgrass prairie (northeastern Kansas, USA). Discharge has declined at this site since the 1980's despite a concurrent increase in precipitation. This decline has been previously attributed to increased transpiration of stream water by riparian vegetation. We used water stable isotopes (δ^{18}O and δ^2H) to determine whether riparian grasses, shrubs, and trees primarily used stream/groundwater or soil water. Additionally, we quantified the increase in riparian and non-riparian woody cover (1978–2020) and combined it with sap-flux data to estimate changes in transpirative water loss. Sustained cutting of riparian trees did not result in increased discharge. Rather than stream/groundwater, the largest proportion of water used by riparian trees (*Quercus spp.*) was deep soil water. *Cornus drummondii* (clonal woody shrub) used a higher proportion of stream water and had greater overall variability in water-use. Riparian shrub cover increased about 57% from 1978 to 2020. Over the same time period, shrub cover increased about 20% in areas outside the riparian zone, resulting in an estimated 25% increase in daily transpirative water loss. Although stream water use was less than 50% for all riparian zone species, the total increase in shrub cover on this watershed, coupled with higher transpiration rates of shrubs, suggests that these woody species—within and outside the riparian zone—are key contributors to observed declines in stream flow in this system.

Key words: woody encroachment; grassland hydrology; tallgrass prairie; stable isotopes; land cover; canopy transpiration.

HIGHLIGHTS

- Stream flow did not increase after a decade of repeated annual cutting of riparian trees.
- Shrub cover increased steadily within and outside the riparian zone from 1978 to 2020.
- A 20% increase in shrub cover led to a 25% increase in landscape-scale water loss.

INTRODUCTION

Grasslands and wooded grasslands cover about 30% of the Earth's surface and originate roughly 1/5 of global runoff, making them an important part of stream biogeochemical and hydrologic dynamics globally (Dodds 1997; Dodds and others 2019). The expansion of woody vegetation into grasslands (Knight and others 1994; Briggs and others 2002; Eldridge and others 2011; Ratajczak and others 2012; Veach and others 2014) threatens grassland stream dynamics, as stream hydrology is intricately linked to its contributing terrestrial habitat. For many grasslands, riparian areas in particular have transitioned from primarily herbaceous to woody-dominated, affecting ecosystem dynamics, streamflow, and stream health (Wilcox 2002; Briggs and others 2005; Huxman and others 2005; Scott and others 2006; Veach and others 2014; Honda and Durigan 2016; Larson and others 2019). Consequences of changing riparian species composition and/or density on streamflow dynamics depend upon species-specific rooting patterns, sources of water accessed by those species, and magnitude of water flux via transpiration (Wilcox and others 2005) as well as local climate, geology, geomorphology (Huxman and others 2005) and evaporation of water from the stream channel. However, woody encroachment in grassland ecosystems typically results in an overall increase in evapotranspiration (Acharya and others 2018), particularly in more mesic grasslands (Huxman and others 2005), which could exceed the effects of these other factors.

Woody species often have higher transpiration rates compared to grasses (Scott and others 2006; Wang and others 2018; O'Keefe and others 2020) and can access deeper soil water and stream- or groundwater that would flow into streams, whereas grasses primarily use water in the top 30 cm of soil (Nippert and Knapp 2007). As woody cover increases, these differences in water-use can increase the overall magnitude of water lost through transpiration (Scott and others 2006;

Honda and Durigan 2016; Wang and others 2018; O'Keefe and others 2020) and alter infiltration rates and water flow paths in the soil (Wilcox and others 2005; Huxman and others 2005), potentially depleting deep soil water stores over time (Acharya and others 2017). Depending on the magnitude of these changes, woody encroachment has the potential to reduce streamflow and groundwater recharge (Huxman and others 2005). Although woody encroachment can decrease local water yield (Qiao and others 2017; Honda and Durigan 2016), there are also studies showing that woody encroachment had few impacts on streamflow and cases where mechanical removal of riparian woody vegetation did not promote streamflow recovery (Belsky 1996; Dugas and others 1998; Wilcox 2002; Wilcox and others 2005; Wilcox and Thurow 2006).

In an effort to assess ecosystem consequences of woody riparian expansion in tallgrass prairie, mechanical cutting of riparian woody vegetation was initiated on a section of an intermittent headwater stream (Kings Creek) at the Konza Prairie Biological Station (KPBS; northeastern Kansas, USA) in December of 2010. KPBS has experienced significant and widespread woody encroachment—both within and outside of riparian corridors—over the past several decades (Briggs and others 2005; Ratajczak and others 2014). From 1980 to 2020, mean stream discharge has declined, resulting in an increased number of no flow or ''dry'' days per year, which were not correlated with changes in annual precipitation (Dodds and others 2012). Instead, these changes were assumed to be a consequence of riparian woody encroachment. Following the onset of annual tree cutting, changes in riparian bacterial/fungal communities and stream chemistry occurred (Reisinger and others 2013; Veach and others 2015; Larson and others 2019), but no rebound in streamflow was observed in the first three years of removal (Larson and others 2019), suggesting that aboveground removal of riparian vegetation had little short-term effect on the hydrologic partitioning of water.

One potential explanation for the lack of streamflow recovery following woody removal is that riparian tree species were not directly consuming and transpiring stream water to the magnitude previously presumed. Streamside trees can bypass stream water via deep rooting systems, relying instead on deeper soil water or groundwater sources (Dawson and Ehleringer 1991; Brooks and others 2010). Alternatively, despite the continued cutting of riparian woody vegetation, increased woody cover of shrubs on the broader

watershed may enhance overall evapotranspiration fluxes on the hillslopes, thereby reducing the amount of deep infiltration and subsequent recharge of the stream aquifer. In this scenario, streamflow declines would represent reduced recharge and hydrologic partitioning at the watershed-scale rather than direct uptake of stream- or groundwater by woody plants in the local riparian corridor.

In this study, our main objective was to determine the impacts of riparian and non-riparian woody vegetation on water cycling in a tallgrass prairie watershed. To this end, we assessed where dominant riparian species in this watershed obtain their water and paired this information with a new spatial analysis of woody cover change through time. In addition, existing sap flux data for woody shrubs and dominant grass species at KPBS were used in conjunction with remote sensing of woody cover change over time to produce watershed-scale estimates of transpirative water loss. Our research objectives were to (1) continue reporting whether changes in precipitation and discharge occurred. We then pivot to a mechanistic explanation for declining discharge by: (2) determining whether common riparian woody species use stream water as their primary water source, (3) assessing the magnitude of change in woody cover over the past four decades, both within and outside the riparian corridor of this grassland headwater stream, and (4) combining these changes in plant cover with existing sap-flux data to estimate catchment-scale changes in water flux via estimates of transpiration by woody and herbaceous plants.

MATERIALS AND METHODS

Study Area

Sampling was conducted at Konza Prairie Biological Station (KPBS), a 3487-ha native unplowed tallgrass prairie in northeastern KS, USA (39.1°N, 96.9°W), co-owned by The Nature Conservancy and Kansas State University. KPBS is a Long-Term Ecological Research (LTER) site focused on the dynamics of fire, grazing, and climatic variability as key drivers of change within a temperate mesic grassland. KPBS is divided into watersheds that have varying fire frequencies (1-y, 2-y, 4-y, or 20-y prescribed burns) and grazing treatments (native bison, cattle, or no grazing).

In lowland areas and stream valley bottoms, soils are characterized as silty-clay loams that reach depths of more than 2 m (Ransom and others 1998). KPBS geology can be described as mer-

okarst, where weathering of limestone bedrock layers results in an intricate system of fractures, joints, and perched aquifers (Sullivan and others 2019, 2020). These layers of weathered limestone (with high hydraulic conductivity) are separated by mudstone layers (with low hydraulic conductivity), creating a complex network of below-ground water infiltration and flow (Vero and others 2017). Shallow groundwater tables (~ 5.5 m depth) in this merokarst system appear to be well-connected to the Kings Creek stream system at KPBS, resulting in rapid water table responses to changes in precipitation (Macpherson and others 2008, 2019).

The climate at KPBS is mid-continental with cold, dry winters and warm, wet summers. Long-term mean annual precipitation (1983–2020) is 812 mm, most of which occurs during the growing season (April–September). During the winter (November–February), most vegetation at KPBS is dormant or senesced, allowing precipitation inputs to infiltrate to greater soil depths, avoiding immediate uptake by plants. During the growing season, precipitation inputs are less likely to infiltrate to greater soil depths in grass-dominated areas because herbaceous root density is high (Nippert and others 2012) and water uptake by the herbaceous community is focused on surface soil layers (Nippert and Knapp 2007; O'Keefe and Nippert 2017).

KPBS has high floristic diversity (Collins and Calabrese 2012) consisting of dominant perennial C_4 grasses (*Andropogon gerardii, Schizachyrium scoparium, Panicum virgatum,* and *Sorghastrum nutans),* as well as sub-dominant grass, forb, and woody species. Historically, this region of the Flint Hills was comprised mainly of open grasslands with very little woody vegetation, with the exception of riparian corridors (Abrams 1986). Over the past several decades, native woody vegetation cover has increased at KPBS, particularly in riparian zones and in watersheds with lower fire frequency (Briggs and others 2005; Veach and others 2014).

In this study, we sampled in a watershed (N2B) that is burned every two years and grazed by bison since the early 1990's. The cover of woody riparian vegetation increased from the 1980s through 2010 (Veach and others 2014), and this watershed was selected for a riparian woody removal experiment that began in 2010. To determine the influence of woody riparian removal on streamflow and ecosystem processes, the majority of aboveground woody vegetation was mechanically removed via cutting within 30 m of the Kings Creek streambed in main channels and within 10 m of side channels (Larson and others 2019). Vegetation was cut along 4.8 km of stream channel during winter to mini-

mize soil disturbance, and roughly half the removal area was re-cut each year to minimize woody re-growth. Woody shrubs in particular re-sprouted quickly following cutting, though most trees did not. The removal area comprised roughly 21% of the total watershed area.

Discharge and Climate Data

Daily stream discharge and precipitation amounts for Kings Creek from 1983 to 2020 were obtained through the Konza Prairie LTER database (KNZ LTER datasets ASD05 and ASD06; Dodds 2018). Discharge measurements were taken at five-minute intervals at a triangular throated flume located near the terminus of the N2B catchment. For precipitation and discharge, we computed a five-year running average and then performed a linear regression of each variable. This approach was based on a manuscript exploring more advanced hydrological modelling and temporal auto-correlation in both of these variables (Raihan and others unpublished). Prior to this study, no rebound in streamflow had been seen after the first three years of riparian tree removal (Larson and others 2019).

Stable Isotopic Analysis of Source Water and Stem Xylem Water

Three deep soil cores (2 m length, 5 cm diameter) were collected outside of the riparian corridor in watershed N2B. Cores were extracted with a hy-draulic-push corer (540MT Geoprobe Systems, Salina, KS). After collection, cores were immediately stored in sealed plastic coring tubes in a laboratory refrigerator at 1–2 °C. Cores were subsampled at 10, 20, and 30 cm, then every 25 cm for the remainder of the core. When the core was cut, root-free subsampled soil was immediately placed into exetainer vials (LabCo Ltd, UK) and stored at 1–2 °C. Soil water was extracted from each soil depth for 55–65 min using the cryogenic vacuum distillation method (Ehleringer and Os-mond 1989; modified in Nippert and Knapp 2007). Archived stream water samples (01/01/2010–01/01/2017) from Kings Creek collected on watershed N2B and a nearby watershed (N1B) were subsampled and analyzed for $\delta^{18}O$ and δ^2H. Archived groundwater samples (Edler Spring, KPBS) were also analyzed for $\delta^{18}O$ and δ^2H values over the same time interval.

Plant species of interest for this study included some of the most common species expanding in KPBS riparian areas: Q. macrocarpa (bur oak), Q. muehlenbergii (chinquapin oak), and C. drummondii.

(rough-leaf dogwood). C. drummondii is also expanding beyond the riparian area, comprising as much as 20% of aerial coverage in this watershed (Ratajczak and others unpublished data). Additionally, we collected samples from Andropogon gerardii, the most common perennial C_4 grass in this ecosystem. We chose eight sampling sites directly along Kings Creek (within 5 m from the stream) in watershed N2B, the site of the riparian woody re-moval experiment. At each site, non-photosynthetic tissue was collected from each species in May, June, July, and August of 2016. For each woody individual, 10–15 cm of stem tissue (from stems $\leq$ 1 cm diameter) were collected and immediately placed in an exetainer vial. For grasses, crown tissue was collected and stored in the same way. All samples were immediately put on ice, and then stored at 1–2 °C. Xylem water was extracted using the cryogenic vacuum distillation method (Ehleringer and Osmond 1989; Nippert and Knapp 2007).

All water samples (soil, stream, groundwater, and xylem water) were analyzed for $\delta^{18}O$ and δ^2H on a Picarro WS-CRDS isotopic water analyzer. ChemCorrect software was used to identify if spectral interference by organic contaminants occurred during analysis of soil and plant water samples—contaminated samples were removed from further analysis. Isotopic ratios were expressed in per mil (‰) relative to V-SMOW (Vienna Standard Mean Ocean Water). The long-term precision of this instrument using in-house standards was less than 0.3 ‰ for δ^2H and less than 0.15 ‰ for $\delta^{18}O$. Differences in xylem water $\delta^{18}O$ between species were assessed using a mixed effects model with sampling date and species as fixed effects and sampling site as a random variable to discern differences among several predictor variables on the source water used by these species. Mixed effects models were performed using the nlme package in R (Pinheiro and others 2016).

Source Water Use of Riparian Vegetation

Stable isotopes are often used as a tool to identify plant water sources in riparian ecosystems (Ehler-inger and Osmond 1989; Dawson and Ehleringer 1991; Busch and others 1992; Ehleringer and Dawson 1992). When coupled with robust statistical mixing-model techniques (Parnell and others 2013), water isotope analyses allow for the determination of the proportional reliance on multiple water sources coupled with the associated variability from the prediction. Stable isotope water data (δ^2H and $\delta^{18}O$) were analyzed using the

Bayesian mixing model simmr (stable isotope mixing models in R; Parnell and others 2013) to determine source water use by riparian vegetation growing near Kings Creek. This model was used to analyze proportional water use of woody riparian vegetation—potential sources included stream water, deep soil water (averaged across 50–250 cm), and shallow soil water (averaged across 0–30 cm). For each simmr run, a posterior distribution consisting of 10,000 MCMC (Markov Chain Monte Carlo) iterations was produced that showed the best estimates of source water use for each species. Model summaries included means, standard deviations, and credible intervals for each source.

Expansion of Woody Cover Over Time

We used remote sensed aerial imagery to estimate how the cover of trees and shrubs changed in watershed N2B over time (1978–2020), parsing changes in the riparian and the non-riparian zones. Compared to trees, shrubs are typically more difficult to differentiate from herbaceous vegetation in aerial imagery. At coarse resolutions, like those commonly used in LANDSAT, MODIS, and some USDA NAIP imagery, shrubs and herbaceous species are especially difficult to differentiate. However, with high resolution imagery, tall shrubs can potentially be identified with high accuracy. We combined images from a range of sources [ultimately Google Earth (2021) and NEON (2021)] to identify true color aerial images (red, green, and blue wavelengths) with a resolution of at least 1 m. This search yielded images from 2002, 2003, 2010, 2012, 2014, 2016, 2018, 2019, and 2020 (see Table S1 for the source of each image and related details). An additional black and white image from 1978 was also located, which was derived from a low-altitude flyover and an analog camera. This image had coarser resolution, but long-term data indicates that forb cover was low on this site at that point (Ratajczak and others 2014) and grassy areas are easier to differentiate from shrubs. Therefore, this image was also included in analyses (see Table S1 for details, including citations for Google Earth images).

Within the area of this watershed, we established a network of permanently located plots. Each circular plot was 1256 m² (20 m radius), with 38 plots in the non-riparian zone and 29 plots in the riparian zone. These levels of replication allowed for approximately 50 m between plots, with differences in spacing to account for rare topographic features like bison paths and steep draws in the broader watershed. A larger sample size was nee-

ded for the non-riparian zone because the riparian zone only occupies approximately 1/5 of the watershed.

For each combination of image and plot, we used photo interpretation to outline woody vegetation. At sub-meter accuracy, polygons were drawn around all distinguishable trees, shrubs, grassland, and areas that contained woody vegetation. When trees and shrubs could not be distinguished from each other, these polygons were labelled as ''other woody'', and comprised less than 5% of woody plant cover across images, but a larger portion of woody cover in 1978. Images were co-interpreted by two users (Brynn Ritchey and Zak Ratajczak) to increase accuracy. For each plot, proportion of woody vegetation (tree, shrub, and ''other woody'') was calculated, then values for all riparian and non-riparian plots were averaged to obtain the mean proportion of woody cover in the riparian and non-riparian zones of the watershed for each year. Herbaceous cover was calculated by subtracting total woody proportion (shrub + tree + ''unknown woody'') from 1.

Watershed-scale Transpiration Estimates

Modeled daily canopy transpiration values (E_C; mm day^{-1} per m² ground area) for *A. gerardii* and *C. drummondii* at KPBS were obtained from O'Keefe and others (2020). The State-Space Canopy Conductance (StaCC) model (Bell and others 2015) was used to predict E_C values based on stem sap flow (daytime and nighttime) measured throughout the growing season in 2014 (day of year 140–260). Weather in 2014 was comparable to an average year, with 709 mm of precipitation (compared to a long-term average of 829 mm per year) and a July mean temperature of 31.7 °C (compared to a long-term average of 32.7 °C). Cumulative growing season canopy transpiration was divided by the number of days in the growing season during 2014 to obtain daily values (for more detailed methods, see O'Keefe and others 2020).

In conjunction with woody cover data, daily canopy transpiration rates were used to estimate watershed daily canopy transpiration rates (E_{CW}) that reflect the proportion of herbaceous versus shrub cover in the non-riparian zone of our sample watershed each year. The model can be reduced to the following approach:

$$E_{CW} = S_T * E_{CS} + H_T * E_{CH}$$

where S_T and H_T are mean proportions of shrub and herbaceous cover, respectively, for a given year T. E_{CS} and E_{CH} are modeled shrub (*C. drummondii*;

2.01 mm day^{-1}) and grass (*A. gerardii*; 0.91 mm day^{-1}) daily canopy transpiration rates, respectively, from O'Keefe and others (2020). Calculations assumed average climate conditions for each modeled year.

Because tree E_C data were not available for this site and tree cover was more extensive in the riparian zone (likely contributing substantially to total riparian transpiration), only the non-riparian zone was used for estimates of daily water loss in this watershed. Shrub cover and herbaceous cover—which had available E_C data from KPBS—were used in calculations of non-riparian zone E_{CW}, while tree cover and "other woody" cover were excluded. This will likely result in an underestimation of woody cover in the non-riparian zone, leading to a more conservative estimate of water loss via transpiration outside of the riparian corridor.

RESULTS

Stream Discharge

Consistent with Dodds and others (2012) and Macpherson and Sullivan (2019), five-year mean running discharge decreased by about 55% ($r^2 = 0.32$, $p < 0.0001$; Figure 1B), whereas 5 year running cumulative precipitation increased significantly ($r^2 = 0.20$ $p < 0.0001$; Figure 1A) by about 17% between 1987 and 2019 (Figure 1B). From 2010 to 2017, discharge amounts had high interannual variability, and discharge events coincided with periods of high intensity precipitation, as expected (Figure 1). These data suggest about a twofold decrease in runoff efficiency (ratio of annual discharge to inputs of precipitation) across the site.

Source and Xylem Water $\delta^{18}O$

From 2010 to 2017, mean groundwater $\delta^{18}O$ was $-5.6‰$ (± 0.01 SE), which was similar to stream water $\delta^{18}O$ ($-5.48‰ \pm 0.06$ SE) over the same time period (Figure 2). Water from the top 50 cm of soil had greater mean $\delta^{18}O$ values ($-4.9‰ \pm 0.26$ SE) than water from deeper soil (50–250 cm depth; $-7‰ \pm 0.18$ SE). The pattern of lower soil water $\delta^{18}O$ at zones deeper in the soil profile reflects infiltration inputs via winter precipitation (Dansgaard 1964; West and others 2006). Xylem water $\delta^{18}O$ for *A. gerardii* ($-4.56‰ \pm 0.27$ SE) was significantly higher than *C. drummondii*, *Q. muehlenbergii*, and *Q. macrocarpa* $\delta^{18}O$ ($-5.89‰ \pm 0.17$ SE, $-6.45‰ \pm 0.21$ SE, and $-6.54‰ \pm 0.39$ SE, respectively) ($p < 0.001$ for all three species) (Figure 3). *C. drummondii* xylem water $\delta^{18}O$ was slightly higher than *Q. muehlenbergii* and *Q. macrocarpa*, but not significantly different ($p = 0.31$ and $p = 0.33$, respectively) (Figure 3).
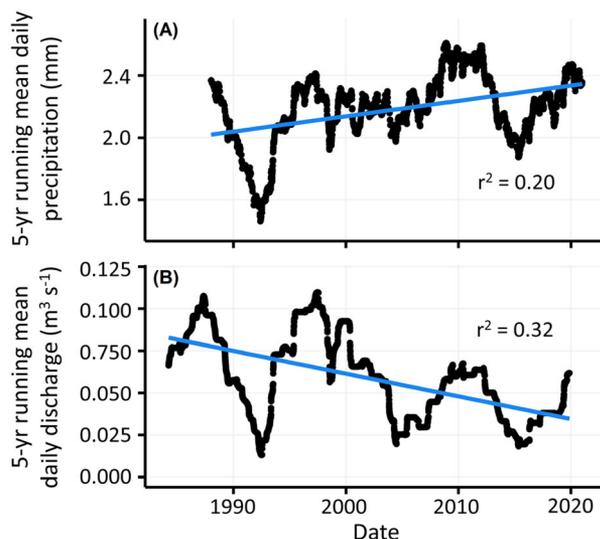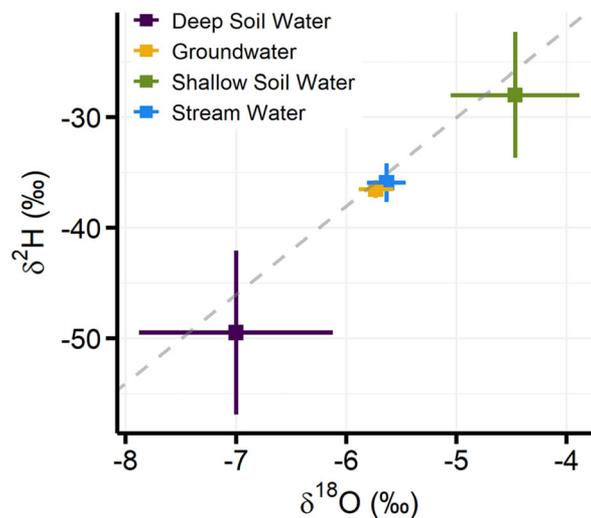

Figure 1. **A** 5-year back-tracked running mean of daily precipitation measured at KPBS headquarters from 12/31/1987 to 12/31/2020. **B** 5-year back-tracked running mean of daily discharge for Kings Creek at KPBS from 4/1/1984 to 11/16/2019. Discharge measurements were taken every five minutes during this time period at the USGS station 06879650 2 km downstream of the woody removal site.

Figure 2. Measured $\delta^{18}O$ and δ^2H values for each water source at KPBS (shallow soil water [0–30 cm], stream water, groundwater, and deep soil water [50–250 cm]). Bars represent standard deviation. Dashed gray line represents the global meteoric water line.

Source Water Use of Riparian Vegetation

Due to the substantial isotopic overlap between stream and groundwater sources at this site (Figure 2), we considered groundwater and stream water to be the same source to avoid source redundancy in the model. KPBS is known to have a strong stream-groundwater connection (Vero and others 2017; Brookfield and others 2017), further validating the decision to combine stream- and groundwater sources in the mixing model. From here on, we refer to this combined source as stream/groundwater. The simmr model using $\delta^2 H$ and $\delta^{18}O$ from xylem water produced frequency distributions that showed the proportional contribution of each source–stream/groundwater, deep soil water (50–250 cm), and shallow soil water (0–30 cm)—to water use by each species. Model results for *Q. macrocarpa* showed that deep soil water made up the largest proportion of source water used (55.9% ± 9.4 SD) followed by stream/groundwater (26.7% ± 13.2 SD) and shallow soil water (17.4% ± 9.4 SD) (Figure 3B). Source water use by *Q. muehlenbergii* was similar, with deep soil water making up 60.2% (± 8.8 SD) of the source water used followed by stream/groundwater (23.8% ± 12.9 SD) and shallow soil water (16% ± 7.7 SD) (Figure 3C). Stream/groundwater and shallow soil water made up the largest proportion of source water use by *C. drummondii* (37.1% ± 20.5 SD and 38.1% ± 10 SD, respectively), but the variability associated with the model prediction for stream/groundwater use was higher in comparison to the oak species. Deep soil water contributed 24.8% (± 12.3 SD) of source water used by *C. drummondii* (Figure 3D). *A. gerardii*, the only C_4 grass species measured, primarily used shallow soil water (78.3% ± 10.4 SD) and showed relatively low proportional water use of both stream/groundwater (13.8% ± 10.2 SD) and deep soil water (7.8% ± 4.5 SD) (Figure 3A).

Expansion of Woody Cover Through Time

From 1978 to 2010 (prior to riparian woody plant removal), total woody cover increased to 67.5% in the riparian zone and to 14.9% in the non-riparian zone. In the riparian zone, trees accounted for most of this expansion (45.3% increase in tree cover), whereas woody plant expansion in the non-riparian zones was primarily by shrubs (14.5% increase in shrub coverage). The effects of tree removal in the riparian zone were evident from 2010 to 2012,
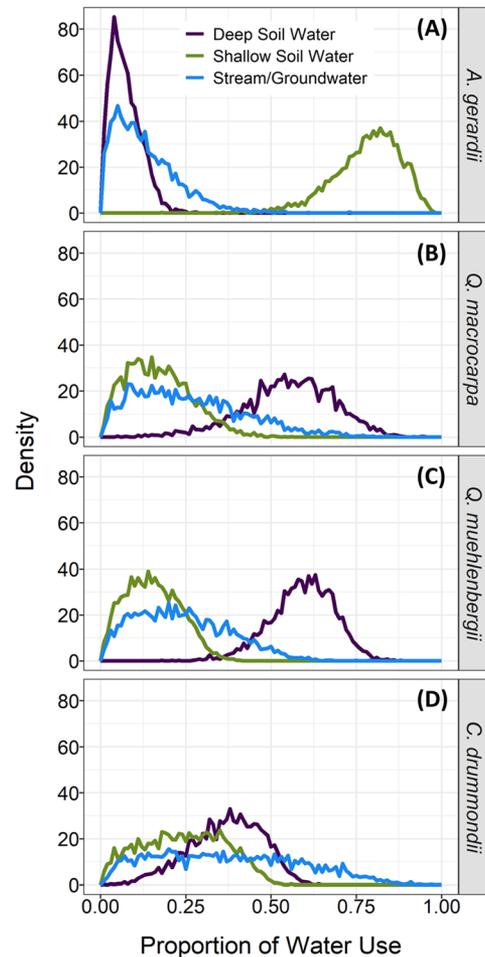
Figure 3. Mixing model output of proportional source water use for *A. gerardii, Q. macrocarpa, Q. muehlenbergii,* and *C. drummondii*. Density values from the simmr model were averaged for each source and species to produce density histograms.

with a sharp decrease in tree cover and an increase in shrub cover (Figure 4). Tree cover remained low (< 11%) in the riparian zone after the onset of the riparian tree removal project, but riparian shrub cover increased rapidly from 2010 to 2020, reaching 58.9% cover by the final year (Figure 4). Across the broader watershed, shrub cover steadily increased from 2010 to 2020, reaching 20.8% in the final year, and tree cover remained low (< 1%) throughout the entire time period. See Table S2 for cover proportions and area values for each year.

Watershed-scale Transpiration Estimates

In 1978, E_{CW} (estimated watershed daily canopy transpiration rate) was 0.91 mm day^{-1}, reflecting
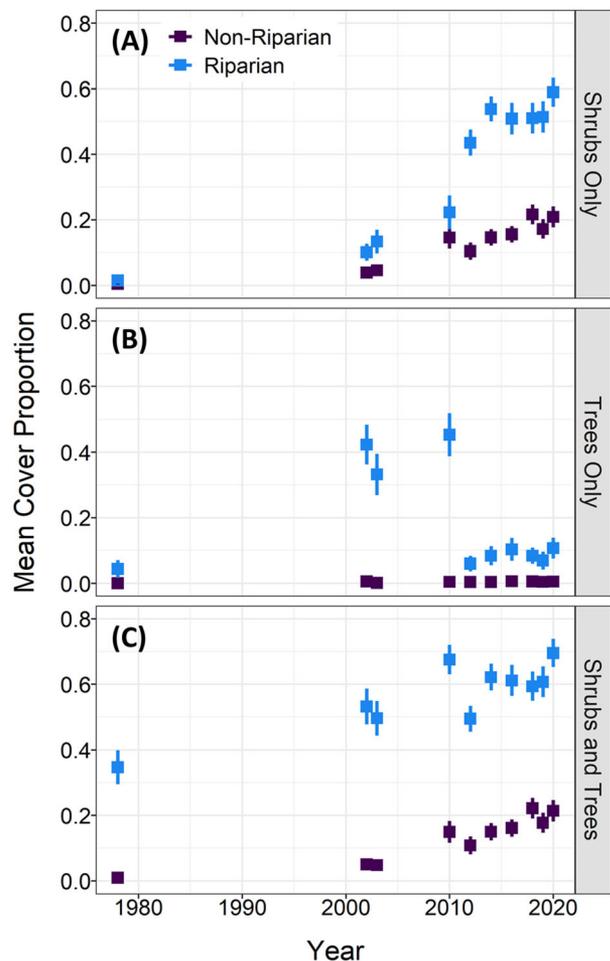
Figure 4. Proportion of **A** shrub cover, **B** tree cover and **C** total woody cover in the riparian and non-riparian zones for the years 1978, 2002, 2003, 2010, 2012, 2014, 2016, 2018, 2019, and 2020. Note that for 1978 we were unable to distinguish between shrubs and trees, which is why the value in the bottom panel is not the sum of the top two panels.
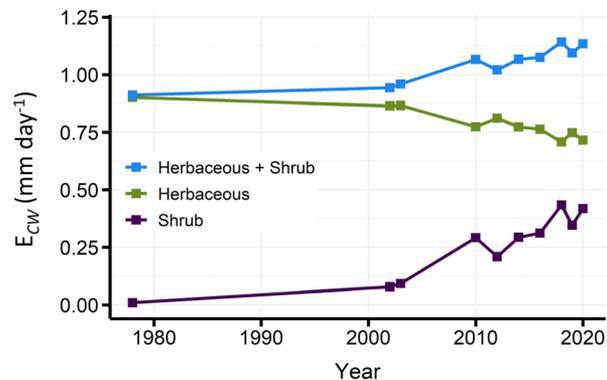

Figure 5. Estimated watershed daily canopy transpiration rates (E_{CW}) for shrubs only (purple), herbaceous species only (green), and combined shrub and herbaceous E_{CW} (blue) for the years 1978, 2002, 2003, 2010, 2012, 2014, 2016, 2018, 2019, and 2020. Transpiration estimates were calculated using proportional woody and herbaceous cover data for each year in conjunction with modeled woody and herbaceous canopy transpiration rates from O'Keefe and others (2020). Estimates were made for the non-riparian zone of the watershed only.

DISCUSSION

The impacts of woody vegetation on grassland streamflow and groundwater recharge depend on a variety of factors, including magnitude of water flux via transpiration, species-specific rooting patterns, and local climate and geomorphology (Wilcox and others 2005). Similarity in $\delta^{18}O$ between groundwater and stream water (Figure 2) reflect the shallow groundwater at KPBS (~ 5.5 m below ground level; Macpherson and others 2008; Sullivan and others 2020) and the connection to the Kings Creek stream system (Vero and others 2017). Declines in stream discharge over the past several decades at KPBS (Figure 1) were not correlated with changes in precipitation or temperature but were previously correlated with a gradual (but extensive) increase in woody cover along the riparian corridor (Dodds and others 2012). Results from this study support the hypothesis that riparian woody vegetation likely has a negative impact on stream discharge in this tallgrass prairie watershed, but also suggests that woody plant expansion outside of the riparian zone could account for a substantial portion of declining streamflow.

The lack of stream flow recovery following a decade of mechanical cutting of riparian trees suggests that observed declines in streamflow are not solely attributable to transpiration of groundwater and stream water by large riparian trees. Results from the stable isotope mixing model

the fact that herbaceous cover in the non-riparian zone was nearly 100% during this year (Figure 5; Table S2). An approximate 20% increase in shrub cover in the non-riparian zone between 1978 and 2020 led to an increase of about 25% in E_{CW}, reflecting the higher transpiration rate of *C. drummondii* relative to the C_4 grasses they replaced. Small increases in E_{CW} (calculated per m^2 ground area) translate to substantial magnitudes of water when scaled up to the entire non-riparian zone of this watershed (538,966 m^2)—from about 490,000 L of water per day to more than 600,000 L of water per day.

indicate that riparian trees were using groundwater and stream water in this watershed, but that these sources made up a relatively small proportion of overall water use (Figure 3). A dendrochronology study performed in the same watershed at KPBS reported that the rate of riparian tree establishment had been increasing since the 1970's (Weihs and others 2016). Therefore, it is possible that this gradual increase in tree cover over several decades, presumably associated with an overall increase in magnitude of stream- and groundwater usage, could have contributed to observed declines in streamflow. However, we would have expected to see a rebound in streamflow following removal if transpiration of stream- and groundwater by riparian trees was the primary cause of this decline.

Compared to *Q. macrocarpa* and *Q. muehlenbergii*, *C. drummondii* in the riparian zone was more variable in its source water use and showed a higher proportion of stream water use than the two oak species (Figure 3). This suggests that transpiration of stream water by *C. drummondii* could have been substantial during portions of the growing season. Additionally, shrub cover in the riparian corridor increased rapidly, particularly in the past 20 years (Figure 4). A higher proportion of stream water use by *C. drummondii* compared to the oak species, coupled with high transpiration rates (O'Keefe and others 2020) and a rapid increase in riparian cover by *C. drummondii*, makes it likely that the magnitude of stream water use by riparian woody shrubs increased substantially in recent decades. Along with gradual increases in tree cover since the 1970's, this more recent increase in shrub cover could be contributing to declines in stream flow via direct consumption of stream water.

In addition to increasing shrub cover in the riparian zone, shrub cover has also increased in the broader watershed since 2002, although this trend is more modest compared to average rate of encroachment in the riparian corridor. Although these shrubs are less directly connected to the stream corridor, an increase in whole-watershed woody cover could increase total evapotranspiration and have cascading impacts on interflow, deep soil water recharge, and streamflow generation. Due to the higher magnitude of water-use by dominant woody shrubs compared to C_4 grasses (O'Keefe and others 2020), the observed 20% increase in shrub cover on the broader watershed from 1978 to 2020 (Figure 4; Table S2) corresponds to an approximate 25% increase in daily transpirative water-loss over this time period (Figure 5). In addition, eddy covariance measurements at KPBS suggest that this effect of shrub expansion on transpiration fluxes may be enhanced when transpiration outpaces precipitation inputs in a given growing season—a phenomenon observed at KPBS during dry years in woody-encroached areas (Logan and Brunsell 2015). Results from this study and Logan and Brunsell (2015) suggest that the expansion of woody cover at the catchment-scale may be more critical in determining streamflow dynamics than previously considered. Assuming that deep soil moisture would historically contribute to recharge if it was not taken up by woody vegetation, this trend will likely become more pronounced as shrub cover increases—particularly if summer drought events become more frequent in an altered future climate.

Based on these results, we argue that increased tree and shrub cover, both in riparian and non-riparian zones, contributed to declining stream flow in this watershed via increased transpiration of stream/groundwater directly, and declining deep soil water that would otherwise recharge stream/groundwater. We note that it is possible that the area of riparian tree-removal compared to total watershed area in this study could have been too small to detect an impact on streamflow. However, the removal encompassed about 21% of the total watershed area (Larson and others 2019), which was found to be sufficient to elicit a detectable response in streamflow in many paired watershed studies (Bosch and Hewlett 1982; Brown and others 2005). The lack of post-removal recovery of stream discharge could also be attributed to (1) rapid increases in riparian shrub cover after the onset of tree-removal (Figure 4A, B), likely due to increased availability of light, and (2) continued increases in woody cover on the broader watershed after the onset of riparian tree removal. The lack of continuous sap-flux data for riparian vegetation limits our ability to quantify the magnitude of transpirative water-use from deep soil water vs. stream/groundwater sources throughout the growing season, particularly for trees, but does not alter the significance of shrub water use both within the riparian area and across the watershed more broadly.

CONCLUSION

These results illustrate the importance of combining fine scale ecohydrology, experimental manipulations, and quantification of broader vegetation changes to understand the influence of woody encroachment on grassland ecohydrology. Changes in soil water infiltration, transport, and use by vegetation represent key fluxes within grassland

ecosystems, and alterations to these fluxes as a result of woody encroachment could prevent alluvial aquifers from rebounding to pre-disturbance levels following riparian woody removal (Vero and others 2017). Taken together, this long-term study clearly illustrates the complex impacts of woody encroachment on the ecohydrology of grassland ecosystems and underscores the utility of a critical zone observatory (CZO) framework that links aboveground and belowground processes at multiple scales to understand the consequences of ongoing landscape change (Dawson and others 2020).

ACKNOWLEDGEMENTS

DATA AVAILABILITY

Data will be made available through the KPBS Long-Term Ecological Research (LTER) website (http://lter.konza.ksu.edu/data).

REFERENCES

Abrams MD. 1986. Historical development of gallery forests in northeast Kansas. Vegetatio 65(1):29–37.

Acharya BS, Hao Y, Ochsner TE, Zou CB. 2017. Woody plant encroachment alters soil hydrological properties and reduces downward flux of water in tallgrass prairie. Plant and Soil 414:379–391.

Acharya BS, Kharel G, Zou CB, Wilcox BP, Halihan T. 2018. Woody plant encroachment impacts on groundwater recharge: A review. Water 10(10):1466.

Bell DM, Ward EJ, Oishi AC, Oren R, Flikkema PG, Clark JS. 2015. A state-space modeling approach to estimating canopy conductance and associated uncertainties from sap flux density data. Tree Physiology 35(7):792–802.

Belsky AJ. 1996. Western juniper expansion: Is it a threat to arid northwestern ecosystems? Journal of Range Management 49:53–59.

Bosch JM, Hewlett JD. 1982. A review of catchment experiments to determine the effect of vegetation changes on water yield and evapotranspiration. Journal of Hydrology 55(1–4):3–23.

Briggs JM, Knapp AK, Brock BL. 2002. Expansion of woody plants in tallgrass prairie: A fifteen-year study of fire and fire-grazing interactions. The American Midland Naturalist 147(2):287–294.

Briggs JM, Knapp AK, Blair JM, Heisler JL, Hoch GA, Lett MS, McCarron JK. 2005. An ecosystem in transition: Causes and consequences of the conversion of mesic grassland to shrubland. BioScience 3:243–254.

Brookfield AE, Macpherson GL, Covington MD. 2017. Effects of changing meteoric precipitation patterns on groundwater temperature in karst environments. Groundwater 55(2):227–236.

Brooks JR, Barnard HR, Coulombe R, McDonnell JJ. 2010. Ecohydrological separation of water between trees and streams in a Mediterranean climate. Nature Geoscience 3:100–104.

Brown AE, Zhang L, McMahon TA, Western AW, Vertessy RA. 2005. A review of paired catchment studies for determining changes in water yield resulting from alterations in vegetation. Journal of Hydrology 310(1–4):28–61.

Busch DE, Ingraham NL, Smith SD. 1992. Water uptake in woody riparian phreatophytes of the southwestern United States: A stable isotope study. Ecological Applications 2(4):450–459.

Collins SL, Calabrese LB. 2011. Effects of fire, grazing, and topographic variation on vegetation structure in tallgrass prairie. Journal of Vegetation Science 23:563–575.

Dansgaard W. 1964. Stable isotopes in precipitation. Tellus 16(4):436–468.

Dawson TE, Ehleringer JR. 1991. Streamside trees that do not use stream water. Nature 350:335–337.

Dawson TE, Hahm WJ, Crutchfield-Peters K. 2020. Digging deeper: what the critical zone perspective adds to the study of plant ecophysiology. New Phytologist 226(3):666–671.

Dodds WK. 1997. Distribution of runoff and rivers related to vegetative characteristics, latitude, and slope: a global perspective. The North American Benthological Society 16(1):162–168.

Dodds WK. 2018. ASD05 Stream discharge measured at the flumes on watershed N01B at Konza Prairie. Environmental Data Initiative. https://doi.org/10.6073/pasta/32e97c5c437f5 4799f11d7ba41ea9053.

Dodds WK, Robinson CT, Gaiser EE, Hansen GJA, Powell H, Smith JM, Morse NB, Johnson SL, Gregory SV, Bell T, Kratz TK, McDowell WH. 2012. Surprises and insights from long-term aquatic data sets and experiments. Bioscience 62(8):709–721.

Dodds WK, Bruckerhoff L, Batzer D, Schechner A, Pennock C, Renner E, Tromboni F, Bigham K, Grieger S. 2019. The freshwater biome gradient framework: predicting macroscale properties based on latitude, altitude, and precipitation. Ecosphere 10: e02786.

Dugas WA, Hicks RA, Wright P. 1998. Effect of removal of Juniperus ashei on evapotranspiration and runoff in the Seco Creek watershed. Water Resources Research 34:1499–1506.

Ehleringer JR, Osmond CB. 1989. Stable Isotopes. Pearcy RW, Ehleringer JR, Mooney HA, Rundel PW, editors. Plant phys-

iological ecology: field methods and instrumentation. New York: Springer, New York. p281–300.

Ehleringer JR, Dawson TE. 1992. Water uptake by plants: perspectives from stable isotope composition. Plant, Cell & Environment 15:1073–1082.

Eldridge DJ, Bowker MA, Maestre FT, Roger E, Reynolds JF, Whitford WG. 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecology Letters 14(7):709–722.

Google earth(a) 7.3.4.8248. (July 16, 2021). Riley County, Kansas U.S.A. 39° 04′ 58.21′′S, 96° 35′ 21.22′′W, Eye alt 9937 feet. See Table S1 for all image citations.

Honda EA, Durigan G. 2016. Woody encroachment and its consequences on hydrological processes in the savannah. Philosophical Transactions of the Royal Society B 371(1703):20150313.

Huxman TE, Wilcox BP, Breshears DD, Scott RL, Snyder KA, Small EE, Hultine K, Pockman WT, Jackson RB. 2005. Ecohydrological implications of woody plant encroachment. Ecology 86(2):308–319.

Knight CL, Briggs JM, Nellis MD. 1994. Expansion of gallery forest on Konza Prairie Research Natural Area, Kansas, USA. Landscape Ecology 9(2):117–125.

Larson DM, Dodds WK, Veach AM. 2019. Removal of Woody Riparian Vegetation Substantially Altered a Stream Ecosystem in an Otherwise Undisturbed Grassland Watershed. Ecosystems 22:64–76.

Logan KE, Brunsell NA. 2015. Influence of drought on growing season carbon and water cycling with changing land cover. Agricultural and Forest Meteorology 213:217–225.

Macpherson GL, Roberts JA, Blair JM, Townsend MA, Fowle DA, Beisner KR. 2008. Increasing shallow groundwater CO_2 and limestone weathering, Konza Prairie, USA. Geochimica Et Cosmochimica Acta 72:5581–5599.

Macpherson GL, Sullivan PL. 2019. Watershed-scale chemical weathering in a merokarst terrain, northeastern Kansas, USA. Chemical Geology 527: 118988.

Macpherson GL, Sullivan PL, Stotler RL, Norwood BS. 2019. Increasing groundwater CO_2 in a mid-continent tallgrass prairie: Controlling factors. 16th International Symposium on Water-Rock Interaction. doi: https://doi.org/10.1051/e3sconf/20199806008.

NEON (National Ecological Observatory Network). High-resolution orthorectified camera imagery (DP1.30010.001). https://data.neonscience.org (accessed January 21, 2021)

Nippert JB, Knapp AK. 2007. Linking water uptake with rooting patterns in grassland species. Oecologia 153:261–272.

Nippert JB, Wieme RA, Ocheltree TW, Craine JM. 2012. Root characteristics of C4 grasses limit reliance on deep soil water in tallgrass prairie. Plant and Soil 355(1–2):385–394.

O'Keefe K, Nippert JB. 2017. An assessment of diurnal water uptake in a mesic prairie: evidence for hydraulic lift? Oecologia 183(4):963–975.

O'Keefe K, Bell DM, McCulloh KA, Nippert JB. 2020. Bridging the Flux Gap: Sap Flow Measurements Reveal Species-Specific Patterns of Water Use in a Tallgrass Prairie. Journal of Geophysical Research: Biogeosciences 125(2): e2019JG005446.

Parnell AC, Phillips DL, Bearhop S, Semmens BX, Ward EJ, Moore JW, Jackson AL, Grey J, Kelly DJ, Inger R. 2013. Bayesian stable isotope mixing models. Environmetrics 24(6):387–399.

Pinheiro J, Bates D, DebRoy S, Sarkar D. 2016. NLME: linear and nonlinear mixed effects models. R package version 3.1–53. (http://www.stats.bris.ac.uk/R/src/contrib/2.0.1-patched/ Recommended/nlme_3.1–56.tar.gz)

Qiao L, Zou CB, Stebler E, Will RE. 2017. Woody plant encroachment reduces annual runoff and shifts runoff mechanisms in the tallgrass prairie, USA. Water Resources Research 53(6):4838–4849.

Ransom MD, Rice CW, Todd TC, Wehmueller WA. 1998. Soils and soil biota. Knapp AK, Briggs JM, Hartnett DC, Collins SL, editors. Grassland Dynamics – Long-Term Ecological Research in Tallgrass Prairie. Oxford University Press, New York. p48–66.

Ratajczak Z, Nippert JB, Collins SL. 2012. Woody encroachment decreases diversity across North American grasslands and savannas. Ecology 93(4):697–703.

Ratajczak Z, Nippert JB, Ocheltree TW. 2014. Abrupt transition of mesic grassland to shrubland: evidence for thresholds, alternative attractors, and regime shifts. Ecology 95(9):2633–2645.

Reisinger AJ, Blair JM, Rice CW, Dodds WK. 2013. Woody vegetation removal stimulates riparian and benthic denitrification in tallgrass prairie. Ecosystems 16:547–560.

Scott RL, Huxman TE, Williams DG, Goodrich DC. 2006. Ecohydrological impacts of woody-plant encroachment: Seasonal patterns of water and carbon dioxide exchange within a semiarid riparian environment. Global Change Biology 12(2):311–324.

Sullivan PL, Zhang C, Behm M, Zhang F, Macpherson GL. 2020. Toward a new conceptual model for groundwater flow in merokarst systems: Insights from multiple geophysical approaches. Hydrological Processes 34(24):4697–4711.

Sullivan PL, Stops MW, Macpherson GL, Li L, Hirmas DR, Dodds WK. 2019. How landscape heterogeneity governs stream water concentration-discharge behavior in carbonate terrains (Konza Prairie, USA). Chemical Geology 527: 118989.

Veach AM, Dodds WK, Skibbe A. 2014. Fire and grazing influences on rates of riparian woody plant expansion along grassland streams. PLoS One 9(9): doi:https://doi.org/10.1371/journal.pone.0106922.

Veach AM, Dodds WK, Jumpponen A. 2015. Woody plant encroachment, and its removal, impact bacterial and fungal communities across stream and terrestrial habitats in a tallgrass prairie ecosystem. FEMS Microbiology Ecology 91(10): doi: https://doi.org/10.1093/femsec/fiv109.

Vero SE, Macpherson GL, Sullivan PL, Brookfield AE, Nippert JB, Kirk MF, Datta S, Kempton P. 2017. Developing a Conceptual Framework of Landscape and Hydrology on Tallgrass Prairie: A Critical Zone Approach. Vadose Zone Journal 17(1):1–11.

Wang J, Xiao X, Zhang Y, Qin Y, Doughty RB, Wu X, Bajgain R, Du L. 2018. Enhanced gross primary production and evapotranspiration in juniper-encroached grasslands. Global Change Biology 24(12):5655–5667.

Weihs B, Bergstrom R, Ruffing C, McLauchlan K. 2016. Woody encroachment of a riparian corridor in a tallgrass prairie: dendrochronological evidence from Kansas. Papers in Applied Geography 2(1):1–8.

West JB, Bowen GJ, Cerling TE, Ehleringer JR. 2006. Stable isotopes as one of nature's ecological recorders. Trends in Ecology and Evolution 21(7):408–414.

Wilcox BP. 2002. Shrub control and streamflow on rangelands: A process-based viewpoint. Journal of Range Management 55:318–326.

Wilcox BP, Thurow TL. 2006. Emerging issues in rangeland ecohydrology: vegetation change and the water cycle. Rangeland Ecology & Management 59(2):220–224.

Wilcox BP, Owens MK, Knight RW, Lyons RK. 2005. Do woody plants affect streamflow on semiarid karst rangelands? Ecological Applications 15(1):127–136.