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Unexpected hydrologic response to ecosystem state change in tallgrass prairie

R.M. Keen [a,b,c,*], K. Sadayappan [d], K.M. Jarecke [e], L. Li [d], M.F. Kirk [f], P.L. Sullivan [e], J.B. Nippert [a]

[a] Division of Biology, Kansas State University, Manhattan, KS, United States
[b] Kansas Biological Survey and Center for Ecological Research, University of Kansas, Lawrence, KS, United States
[c] Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, KS, United States
[d] Department of Civil and Environmental Engineering, Pennsylvania State University, University Park, PA, United States
[e] College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, Corvallis, OR, United States
[f] Department of Geology, Kansas State University, Manhattan, KS, United States

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ABSTRACT

In grasslands around the world, climate change is occurring in tandem with woody encroachment (the spread of woody vegetation in grass-dominated ecosystems). State transitions from grassland to shrub/woodland have been identified aboveground via changes in species cover and composition, but the hydrological impact of these transitions is not well understood. Shifts from grass- to woody-dominance have the potential to impact evapotranspiration, soil moisture dynamics, and groundwater recharge. Therefore, it is possible that the consequences of aboveground vegetation change may be observable in the hydrological system. We leveraged long-term hydrological records from a tallgrass prairie site in northeastern Kansas, USA, to examine how concurrent changes in climate and land-cover have altered hydrological dynamics over the last century. Stream discharge has declined in recent decades despite > 100 years of climate wetting. The relationship between incoming precipitation and streamflow has weakened over the last 40 years, suggesting that shifts in the physical landscape are altering patterns of hydrological connectivity. Long-term isotope records show a divergence in the isotopic composition of precipitation (no change in $\delta^{18}O$) and stream/groundwater (decreasing $\delta^{18}O$) over the last decade. These results suggest that woody encroachment is accelerating the hydrological cycle, potentially by decreasing groundwater recharge (via increased evapotranspiration) and/or increasing infiltration rates (via creation of macropores). Holistically, these changes illustrate the interdependence of above- and below-ground processes in the local hydrological cycle, and the cascading long-term consequences (decades to centuries) for critical zone function once woody encroachment has occurred.

1. Introduction

Global circulation models predict an intensification of the hydrological cycle as the climate warms, leading to increased precipitation variability and higher frequency of extreme rainfall events (Easterling et al., 2000; Allen and Ingram, 2002; USGCRP, 2018; Jones, 2019; IPCC, 2021). Warming and shifts in precipitation patterns have been recorded in recent decades in many parts of the world (Garbrecht et al., 2004; Dore, 2005; Rahmani et al., 2015; Wu et al., 2020), and these trends are expected to continue to change global carbon, nutrient, and hydrological cycles (IPCC, 2021). In the Great Plains ecoregion of the central United States, projected impacts of climate change on precipitation regimes include (1) no change or slight increases in total annual precipitation, (2) increased precipitation variability, resulting in longer dry periods punctuated by fewer, but larger, rain events, and (3) shifts toward greater winter and / or spring precipitation (USGCRP, 2018; IPCC, 2021). These shifts have the potential to alter local and regional water cycles, as precipitation timing and event sizes can substantially influence runoff and groundwater recharge (Small et al., 2006; Meixner et al., 2016; Pumo et al., 2016), water infiltration dynamics (Loague et al., 2010; Price, 2011), plant available water (Fay et al. 2002, 2003; Heisler-White et al., 2009), and water chemistry and quality (Li et al., 2022; van

* Corresponding author at: Kansas Biological Survey and Center for Ecological Research, University of Kansas, Lawrence, KS, United States.
E-mail address: rmkeen@ku.edu (R.M. Keen).

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Vliet et al, 2023; Li et al. 2024).

In addition to changes in climate, the encroachment of woody vegetation (shrubs and trees) into historically grass-dominated ecosystems is also occurring in the Great Plains ecoregion (Briggs et al., 2005; Archer et al., 2017), as well as in grasslands and savannas around the world (Knapp et al., 2008; Eldridge et al., 2011; Stevens et al., 2017). Woody encroachment can alter water cycling dynamics independent of changes in climate (Huxman et al., 2005; Viglizzo et al., 2015; Acharya et al., 2018; Zou et al., 2018). Woody shrubs and trees are typically more deeply rooted (Canadell et al., 1996; Schenk and Jackson, 2002) and transpire at greater rates than the grasses they replace (Scott et al., 2006; O'Keefe et al., 2020). In mesic grasslands where precipitation generally exceeds evapotranspiration (ET), excess water is stored in deeper soil layers that are recharged each year (Huxman et al., 2005). As woody cover increases in these systems, shrubs and trees can access water stored deeper (>30 cm) in the soil profile, allowing ET to outpace precipitation, particularly during drier years (Logan and Brunsell, 2015; Wilcox et al., 2022). Over time, this can lead to drying of deeper soil layers in infrequently burned watersheds with high woody cover (Craine and Nippert, 2014), decrease the amount of water flow reaching stream and groundwater systems (Acharya et al., 2018; Keen et al., 2022; Dodds et al., 2023a), and possibly shift the relative proportion of shallow and deep groundwater flow paths contributing to streamflow generation (Macpherson and Sullivan, 2019; Sadayappan et al., 2023).

While increasing tree and shrub cover typically increases ET in mesic grasslands (Huxman et al., 2005; Wilcox et al., 2022), shifts in rooting architecture and root depth distributions with woody encroachment can also alter belowground water fluxes, as the rooting systems of woody vegetation impact soil structure differently than the shallow, fibrous rooting systems of grasses (Lu et al., 2020). Shallow rooting zones dominated by fibrous grass roots are expected to facilitate more lateral subsurface flow (Alaoui et al., 2011; Sullivan et al., 2018), while deeper, coarser rooting systems of shrubs and trees tend to facilitate more vertical recharge of water via creation of macropores (Beven and Germann, 1982; Jarvis, 2007; Alaoui et al., 2011; Bargués Tobella et al., 2014). These conflicting impacts of woody encroachment – increased water loss from soils via transpiration, but potentially increased infiltration of water to greater depths in the soil profile – make it difficult to predict the net hydrological effects of woody encroachment and the consequences for grassland water yield, particularly if precipitation dynamics are changing at the same time.

Previous assessments of the ecosystem state transition from grassland to shrubland or woodland – which often exhibits hysteresis (Beisner et al., 2003; Collins et al., 2021) – have focused primarily on shifts in vegetation cover and species composition through time (Ratajczak et al., 2014b; Collins et al. 2021). Yet, the impact of ecosystem state transitions on belowground structure and, thus, the hydrologic cycle, has received far less attention. In one example, Robinson et al. (2018) reviewed potential environmental changes or disturbances (e.g., severe drought or changes in plant cover) that can lead to shifts in soil structure, chemical properties, and ultimately soil moisture dynamics that may be irreversible or very slow to recover to the original state. Recent work has shown that shifts in soil structure as a result of climate and land-cover change are occurring at decadal scales and can have substantial effects on critical zone function (Sullivan et al., 2022). Knowing that shifts in plant functional type dominance with woody encroachment (i.e., grasses to shrubs) have the potential to impact ET (Zhang et al., 2001; Huxman et al., 2005; Scott et al., 2006; Logan and Brunsell, 2015), long-term soil moisture dynamics (Craine and Nippert, 2014), and groundwater recharge (Acharya et al., 2018), it is possible that ecosystem state transitions could be observable in the hydrological cycle and subsurface structure as well as in vegetation communities in mesic grasslands.

To examine how changes in climate and land-cover have altered the hydrological cycle over time, we leveraged a mesic grassland site that has experienced woody encroachment over the last three decades (Briggs et al., 2005; Ratajczak et al., 2014a). At this site (Konza Prairie Biological Station; KPBS; northeastern, KS, USA), long-term data shows that stream flow has declined, and the number of no-flow days have increased, despite an increase in annual precipitation over the last 30–40 years (Dodds et al., 2012; Keen et al., 2022; Sadayappan et al., 2023). Extensive temporal hydrological records (precipitation, stream flow, groundwater) and vegetation cover at KPBS allowed us to assess the impacts of changes in climate (inter- and intra-annual precipitation dynamics) and land-cover on grassland ecohydrology. Specifically, we analyzed the long-term precipitation record from the nearby city of Manhattan, KS (1898–2022) as well as a shorter-term precipitation record from KPBS (1984–2022) to ask whether precipitation total amounts, variability, seasonality, or event sizes have changed over the last 40–120 years. We then examined the relationship between precipitation and stream flow to understand the degree to which coherence among these two variables may have changed over the last four decades. Finally, we used a 10 + year record of water stable isotopes ($\delta^{18}O$ and $\delta^{2}H$) of precipitation, stream flow, and groundwater at KPBS to assess whether connectivity between these water pools has changed.

2. Methods

2.1. Site description

This study occurs in northeastern Kansas, which is located on the western edge of the tallgrass prairie portion of the Great Plains (Samson et al., 2004). Tallgrass prairie ecosystems are dominated by warm-season C_4 grasses (primarily *Andropogon gerardii*, *Panicum virgatum*, *Sorghastrum nutans*, and *Schizachyrium scoparium*), but also contain a high diversity of subdominant grasses (C_3 and C_4), forbs, and shrub / sub-shrub species (Collins and Calabrese, 2012). The climate in northeastern Kansas is mid-continental, with warm, wet summers and cold, dry winters. This region receives ~ 830 mm of precipitation each year, with ~ 75 % of precipitation occurring during the growing season (April – September; Hayden, 1998; Goodin and Fay, 2003). Growing season precipitation is primarily derived from warm air masses moving north out of the Gulf of Mexico, while dormant season precipitation is primarily derived from cold air masses moving south out of Canada (Sullivan et al., 2019).

Konza Prairie Biological Station (KPBS; 39.1°N, 96.9°W), a 3,487-hectare tallgrass prairie south of Manhattan, KS, is intensively monitored and has multi-decadal records of precipitation and stream flow, in addition to long-term water stable isotope records (precipitation, stream water, groundwater). KPBS is located within the Flint Hills, a ~ 2.5 million hectare region in the western-portion of the tallgrass prairie characterized by rolling hills underlain by alternating limestone and shale bedrock layers (Vero et al., 2018). This site is co-owned by Kansas State University and The Nature Conservancy and is a Long-Term Ecological Research (LTER) site that was established in 1980. KPBS is divided into replicated, experimental watersheds that have varying grazing (ungrazed, grazed by cattle (*Bos taurus*), or grazed by bison (*Bison bison*)) and fire (1-, 2-, 4-, and 20-year burn frequency) treatments. These treatments provide a range of severity of woody encroachment, with a greater degree of woody cover in watersheds that are burned less frequently (Briggs et al., 2005). In this study, we leveraged data from four bison-grazed watersheds: N1B (1-year burn frequency, 120.9 ha), N2B (2-year burn frequency, 78.2 ha), N4D (4-year burn frequency, 120.4 ha), and N20B (20-year burn frequency, 84.4 ha). These watersheds were chosen because they all have long-term stream discharge records, and three of them (N1B, N4D, and N20B) have long-term records of plant cover. Non-riparian woody cover ranges from ~ 20 % (N1B) to > 50 % (N20B) on these watersheds as a result of the range in burn frequencies (Hartnett et al., 2023). The primary encroaching woody species at this site are clonal shrubs – *Cornus drummondii* (rough leaf dogwood) in particular has rapidly spread in cover over the last 3–4 decades, but other encroaching clonal shrubs include *Rhus glabra* and *Prunus americana* among others (Briggs et al.

2005; Ratajczak et al. 2014a). Eastern redcedar (*Juniperus virginiana*) is also encroaching at this site, but primarily in ungrazed, infrequently burned watersheds (Ratajczak et al. 2014a). Eastern redcedar is almost entirely absent from bison-grazed watersheds because bison frequently kill seedlings and prevent establishment of mature redcedars (Hoch 2000).

In all four watersheds included in this study, upland soils are shallow and rocky and are classified as cherty silty clay loams (Benfield-Florence and Clime-Sogn complexes), while lowland soils can reach depths of > 2 m and are classified as silty clay loams (Ivan silt loams; Ransom et al., 1998; Ratajczak, 2023). Stream flow at KPBS is intermittent, largely due to high rates of evapotranspiration during the spring and summer months that can outpace precipitation inputs (Sullivan et al. 2019). Declining stream discharge and an increase in the number of no-flow days have been observed at KPBS since the 1980′s (Dodds et al., 2012). Stream discharge at this site is primarily driven by groundwater supply – past studies have determined that well-developed connections exist between the groundwater and stream systems, evidenced by rapid water-table responses following rainfall events (Brookfield et al., 2017) and isotopic signatures of stream and groundwater (Keen et al., 2022; Hatley et al., 2023).

2.2. Long-term hydrological records

A long-term record of daily precipitation (1898 to 2022) for Manhattan, KS was obtained through the National Climate Data Center's Global Historical Climatology Network (station ID: USC00144972; https://www.ncdc.noaa.gov/cdo-web/datasets/). Daily precipitation and stream discharge records (1983 to 2022) for KPBS were obtained through the Konza Prairie LTER database. Stream discharge measurements were taken every five minutes at a triangular-throated flume on watersheds N1B, N2B, N4D, and N20B (Dodds, 2023b-e; datasets: ASD02, ASD04, ASD05, ASD06), and precipitation amounts were measured at KPBS headquarters using a Belfort weighing rain gauge from January 1983 to April 2010, and an Ott Pluvio2 rain gauge from March 2010 to December 2022 (Nippert, 2023; datasets: APT01).

Co-located wet deposition collectors, deployed as part of the National Atmospheric Deposition Program (NADP), collected precipitation samples used to assess precipitation water chemistry. Precipitation was collected from the wet deposition collectors every Tuesday morning (when water was available), following the NADP protocol. These subsamples were then used for water isotope analysis ($\delta^{18}O$ and $\delta^{2}H$) – each sample collected for isotope analysis therefore integrates the signatures of events from the previous seven days. The wet deposition collectors were sealed in the closed position except during active precipitation events, eliminating the potential for evaporative isotopic enrichment of the precipitation samples (more detail on the wet deposition sensor can be found in the metadata of Blair, 2019). Groundwater samples were collected weekly from the Edler Spring well at KPBS, and stream water samples were collected weekly from the weirs at each watershed (N1B, N2B, N4D, and N20B) when water was present. After collection, all water samples were stored in sealed vials in a −20 °C freezer and archived at Kansas State University. Archived precipitation (2001 to 2022), stream water (2007 to 2021), and groundwater (2010 to 2022) samples were subsampled and analyzed for $\delta^{18}O$ and $\delta^{2}H$ to develop long-term water stable isotope records.

Water samples were analyzed for $\delta^{18}O$ and $\delta^{2}H$ using a Picarro WS-CRDS isotopic water analyzer at Kansas State University. Isotopic ratios were expressed in per mil (‰) relative to the international standard V-SMOW (Vienna Standard Mean Ocean Water). The long-term precision of water isotope analyses was assessed using three in-house standards to calculate a calibration curve, along with a laboratory working standard ($n = 16$ per run) used for within-run drift correction. More information on our water isotope methodology can be found in Appendix 2 of Keen et al. (2024). Assessed as standard deviation, the precision across and within runs was < 0.3 ‰ for $\delta^{2}H$ and < 0.15 ‰ for $\delta^{18}O$.

2.3. Changes in precipitation dynamics through time

2.3.1. Precipitation amounts and variability

Changes in mean annual precipitation and precipitation variability through time were assessed using running mean, standard deviation (SD), and coefficient of variation (CV). The long-term Manhattan, KS precipitation record (122 years; hereafter referred to as the 'MHK record') and the shorter-term KPBS precipitation record (37 years; hereafter referred to as the 'KPBS record') were analyzed separately. For both records, a 10-year moving window was used to remove substantial inter-annual variability in precipitation and observe long-term precipitation trends. Trends in running mean, standard deviation (SD), and coefficient of variation (CV) were assessed using modified Mann Kendall trends tests with trend-free pre-whitening (Kendall, 1948; Mann, 1945; Von Storch, 1999) using the tfpwmk function in the modifiedmk package (Patakamuri et al., 2020) in R (version 4.3.0).

2.3.2. Seasonality of precipitation

In all seasonal analyses in this study, the growing season includes April – September and the dormant season includes October – March. Changes in the amount of growing and dormant season precipitation, as well as the proportion of annual precipitation occurring in the growing vs. dormant seasons, were assessed for both precipitation records using 10-year moving windows. These trends were also assessed using modified Mann Kendall trends tests with trend-free pre-whitening.

2.3.3. Sizes and number of precipitation events

Changes in the number of precipitation events – both annual number of events and number of events during the growing vs. dormant seasons – were assessed using 10-year moving windows and analyzed using modified Mann Kendall trends tests with trend-free pre-whitening. We defined a precipitation event as an individual day with precipitation > 5 mm, since both records contained daily precipitation amounts. This 5 mm cutoff was established to isolate 'ecologically significant' precipitation events that would not be completely intercepted and / or evaporated before reaching the soil surface. These smallest events (<5 mm) have historically been ignored in ecological studies (Coupland, 1950; Sala and Lauenroth, 1982; Hao et al., 2012). In addition, measurement accuracy of the smallest precipitation events has likely improved over the last century, so removing the smallest event sizes is also expected to reduce measurement error associated with older precipitation records, particularly for the longer MHK dataset. Changes in mean event size – both annually and in the growing and dormant seasons – were also assessed using 10-year moving windows for both records. Again, precipitation events were defined as individual days with precipitation > 5 mm.

2.4. Shifts in precipitation-discharge relationship

2.4.1. Precipitation–discharge relationship through time

To determine how precipitation and stream discharge dynamics have shifted over time, annual and monthly relationships between discharge (Q) and precipitation (P) were assessed. Annual Q/P ratios were calculated using stream discharge from four watersheds at KPBS (N1B=120.9, N2B=79.2, N4D=120.4, N20B=84.4 ha). To account for differences in watershed size, annual mean specific discharge was calculated by dividing daily discharge values (m^3/day) by watershed size (m^2) before summing across each year (m $year^{-1}$). A 10-year moving window was used to remove substantial inter-annual variability and assess long-term trends in annual Q/P. Changes in annual Q/P ratios, as well as 10-year moving window mean annual Q/P ratios, were assessed using modified Mann Kendall trends tests with trend-free pre-whitening.

Monthly mean specific discharge was also calculated by dividing daily discharge values (m^3/day) by watershed size (m^2) before summing across each month (m $month^{-1}$). We assessed the relationship between monthly mean specific discharge and monthly precipitation amounts using a moving-window correlation analysis to assess changes in correlation strength through time. Pearson's correlation coefficients were calculated for monthly mean specific discharge and monthly precipitation using a 10-year moving window for the years 1987–2020. Results from additional moving-window lengths (5-, 7-, and 9-years) can be found in Fig. S1.

2.4.2. Shrub cover and grassland-to-shrubland transitions

To compare trends in woody encroachment to shifts in the precipitation–discharge relationship, we also updated and modified a figure from Ratajczak et al. (2014b) showing changes in woody cover over time. We obtained long-term shrub cover data for KPBS for watersheds N1B (1-year burn frequency), N4D (4-year burn frequency), and N20B (20-year burn frequency; Hartnett et al., 2023). These watersheds were selected because they contain permanent species cover plots that have been maintained since 1983 (Hartnett et al., 2023; dataset: PVC02) as well as long-term records of stream discharge (Dodds, 2023b–e). Four 50-m transects for species cover were established in each watershed, with five 10 m2 plots established along each transect. At each plot, species cover was measured annually using a modified Daubenmire scale based on percent cover (0–1 %, 4–5 %, 5–25 %, 25–50 %, 50–75 %, 75–90 %, and 95–100 %) for each species, and the midpoint of each range was used to calculate cover (as in Ratajczak et al., 2011; Collins and Calabrese, 2012). For this study, we included shrub and tree species that can grow higher than the grass canopy and that are actively encroaching outside of the riparian corridor; short-statured sub-shrub species were excluded (e.g., *Amorpha canescens*). Table S1 contains a list of woody species included in this analysis. Changes in cover for each watershed were calculated separately. In addition, an average weighted by watershed size (N1B=120.9, N4D=120.4, N20B=84.4 ha) was calculated to determine the overall trend across fire frequencies.

2.5. Stable isotope trends in precipitation, stream water, and groundwater

2.5.1. Long-term water isotope trends

The precipitation isotope record spanned from 1/30/2001 to 11/29/2022. Amount-weighted least squares regressions were used to assess changes in precipitation $\delta^{18}O$ over this time period. Note that, since each isotope sample represents an integrated signature from the previous seven days (see Section 2.2), total weekly precipitation amounts were used as weights in the regressions. Precipitation $\delta^{18}O$ was also split into growing (March – September) and dormant seasons (October – February) to assess whether temporal trends occurred within either season. Amount-weighted least squares regressions were performed for each season separately over the same time period. The stream water isotope record spanned from 2/19/2007 to 8/10/2020, and the groundwater isotope record spanned from 1/13/2010 to 12/28/2022. Trends in stream water and groundwater $\delta^{18}O$ were assessed using linear regression analyses.

3. Results

3.1. Mean and variability of precipitation

In the MHK record, results from the modified Mann-Kendall trends tests showed that annual precipitation increased from 1898 to 2021. This trend was not significant for raw annual precipitation values ($p = 0.112$, $\tau = 0.097$), but the 10-year running mean value increased significantly ($p < 0.001$, $\tau = 0.517$; Fig. 1a). Variability in annual precipitation increased from 1898 until the 1960′s, and then declined through 2022 (Fig. 1b,c). Over the entire time period, there was a significant increase in 10-year running SD ($p < 0.001$, $\tau = 0.281$; Fig. 1b) and 10-year running CV ($p = 0.045$, $\tau = 0.127$; Fig. 1c; Table S2). In the KPBS record, precipitation also increased over the last ~ 40 years. This trend was not significant for raw annual precipitation values ($p = 0.961$, $\tau = 0.007$), but there was a marginally significant increase in the 10-year running mean ($p = 0.074$, $\tau = 0.232$). Variability (both 10-year running SD and CV) decreased significantly during the same period (SD: $p < 0.001$, $\tau = -0.674$; CV: $p < 0.001$, $\tau = -0.697$; Fig. 1b,c; Table S3).

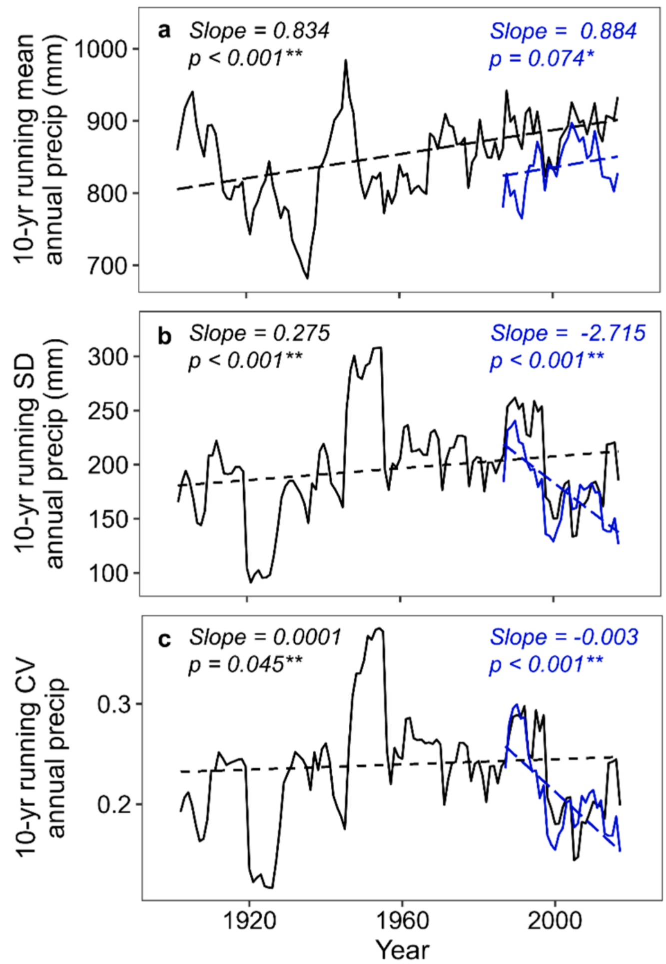

Fig. 1. Changes in mean annual precipitation and precipitation variability through time. (A) 10-year running mean annual precipitation, (B) 10-year running standard deviation (SD), and (C) 10-year running coefficient of variation (CV) for the Manhattan, Kansas (MHK; 1898–2021; black) and Konza Prairie Biological Station (KPBS; 1983–2021; blue) records. Sen's slope and p-values from modified Mann-Kendall trends tests with trend-free pre-whitening are provided in each panel. Asterisks represent significant trends (**$p < 0.05$ and *$p < 0.1$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.2. Seasonality of precipitation

In this region, a greater proportion of precipitation occurs in the growing season compared to the dormant season, and this trend was apparent in both the MHK and KPBS records (Fig. S2). In the MHK record, there have been significant increases in 10-year running mean growing season ($p < 0.001$, $\tau = 0.414$) and dormant season ($p < 0.001$, $\tau = 0.478$) precipitation. In the KPBS record, there has been a significant increase in 10-year running mean dormant season precipitation ($p = 0.011$, $\tau = 0.239$), but not growing season precipitation ($p = 0.412$, $\tau = 0.108$; Fig. S2a; Tables S2, S3). In both records, there has been a significant increase in the 10-yr running mean proportion of annual precipitation occurring during the dormant season (MHK: $p < 0.001$, $\tau = 0.229$; KPBS: $p = 0.019$, $\tau = 0.306$; Fig. S2c, Table S2, Table S3).

3.3. Number and size of precipitation events

Both records show a significant increase in 10-year running mean event size (MHK: $p < 0.001$, $\tau = 0.571$; KPBS: $p = 0.005$, $\tau = 0.366$; Fig. 2b, Table S2, Table S3). In the MHK record, there have been significant increases in 10-year running mean event size in both the growing season ($p < 0.001$, $\tau = 0.465$) and dormant season ($p < 0.001$, $\tau = 0.562$; Table S2). In the KPBS record, there has been a marginally significant increase in 10-year running mean event size in the growing season ($p = 0.054$, $\tau = 0.251$) but not the dormant season ($p = 0.116$, $\tau = 0.205$; Table S3). There has been an increase in the number of precipitation events annually in the KPBS record ($p = 0.002$, $\tau = 0.398$; Table S3) – this trend is driven by an increasing number of events in both the dormant ($p = 0.014$, $\tau = 0.32$) and growing seasons (marginally significant; $p = 0.064$, $\tau = 0.241$). In the MHK record, there was no significant trend in annual number of events ($p = 0.108$, $\tau = -0.101$; Table S2), but there was a significant decrease in the number of growing season events per year ($p = 0.005$, $\tau = -0.178$).

3.4. Shifts in precipitation-discharge relationship

Modified Mann-Kendall tests showed that there was no trend in raw specific Q values over time ($p = 0.722$, $\tau = -0.045$) when values were averaged across all four watersheds, but 10-year running mean specific Q declined significantly ($p < 0.001$, $\tau = -0.754$; Fig. S4). The 10-year running mean specific Q also declined significantly in each watershed separately (Fig. S5, Table S4). Similarly, raw Q/P values did not change significantly through time when values were averaged across all four watersheds ($p = 0.676$, $\tau = -0.053$), but 10-year running mean Q/P did decline significantly ($p < 0.001$, $\tau = -0.812$; Fig. 3c). The 10-year running mean Q/P also declined significantly in N1B ($p < 0.001$, $\tau = -0.804$), N2B ($p < 0.001$, $\tau = -0.558$), and N4D ($p < 0.001$, $\tau = -0.768$), and the decline was marginally significant in N20B ($p = 0.097$, $\tau = -0.246$).

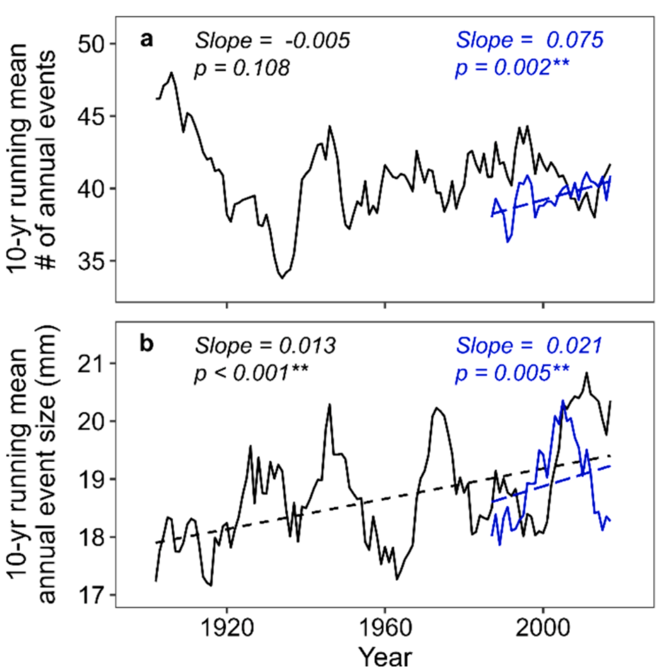

Fig. 2. Changes in the number and size of precipitation events through time. (A) 10-year running mean number of annual precipitation events and (B) 10-year running mean annual precipitation event size for the Manhattan, Kansas (MHK; 1898–2021; black) and Konza Prairie Biological Station (KPBS; 1983–2021; blue) records. Sen's slope and p-values from modified Mann-Kendall trends tests with trend-free pre-whitening are provided in each panel. Asterisks represent significant trends (**$p < 0.05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

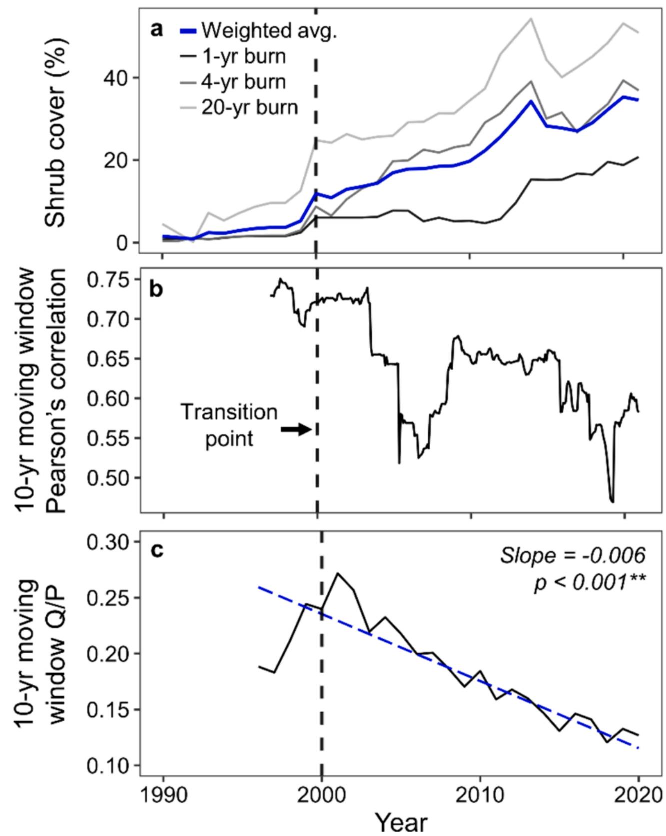

Fig. 3. Changes in shrub cover and discharge-precipitation relationships through time. (a) Change in shrub cover from 1983 to 2021 in 1-year (black), 4-year (dark gray), and 20-year (light gray) burn watersheds. The solid blue line represents average shrub cover from these three watersheds weighted by watershed size. The black dashed line that extends through all three panels represents the transition point (~2000) identified by Ratajczak et al. (2014), when the rate of shrub encroachment rapidly increased – this point is associated with an ecosystem state transition, where the system began moving toward a woody-dominated state. (b) 10-year moving window Pearson's correlation values for the relationship between monthly precipitation and mean monthly specific discharge. (c) 10-year moving window mean annual Q/P for watersheds N1B, N4D, and N20B (watershed N2B was removed since no long-term woody cover data is available for that watershed). Discharge values were standardized by watershed area prior to calculating Q/P and averaging across watersheds. In panel (c), the Sen's slope and p-value from the modified Mann-Kendall trends test with trend-free pre-whitening are provided (asterisks represent significant trends; **$p < 0.05$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Across the entire time period (1987 – 2020), the Pearson's correlation between precipitation and discharge was 0.63 (Fig. S6). The 10-year moving window Pearson's correlations were calculated over the same period. Correlations were highest in the late 1990′s and early 2000′s, but declined after ~ 2003, reaching a minimum value of 0.47 (Fig. 3b). Changes in woody cover through time were also calculated for watersheds with long-term vegetation monitoring (N1B, N4D, and N20B). Mean woody cover was calculated and weighted by watershed size to determine overall changes in woody cover from 1983 to 2021 (Fig. 3a). Woody cover was highest and increased most rapidly in the watershed with a 20-year burn frequency, while the watershed with a 4-year burn frequency had an intermediate rate of increase, and the annually burned watershed had the lowest overall woody cover and slowest rate of increase through time (Fig. 3a). In all three watersheds, the rate of change in woody cover increased sharply around the year 2000.

3.5. Stable isotope trends in precipitation, stream water, and groundwater

Precipitation stable isotopes ($\delta^{18}O$ and $\delta^{2}H$) were more variable than either stream water or groundwater $\delta^{18}O$ and $\delta^{2}H$ (Fig. 4; Fig. S7). Precipitation and stream / groundwater stable isotopes showed consistent and diverging trends through time at KPBS. Linear regression results showed that stream and groundwater $\delta^{18}O$ and $\delta^{2}H$ have both declined significantly through time ($p < 0.001$ in all cases; Fig. 4b,c; Fig. S8; Table S5). In contrast, there has been no change in amount-weighted precipitation $\delta^{18}O$ overall ($p = 0.213$), or during the growing season

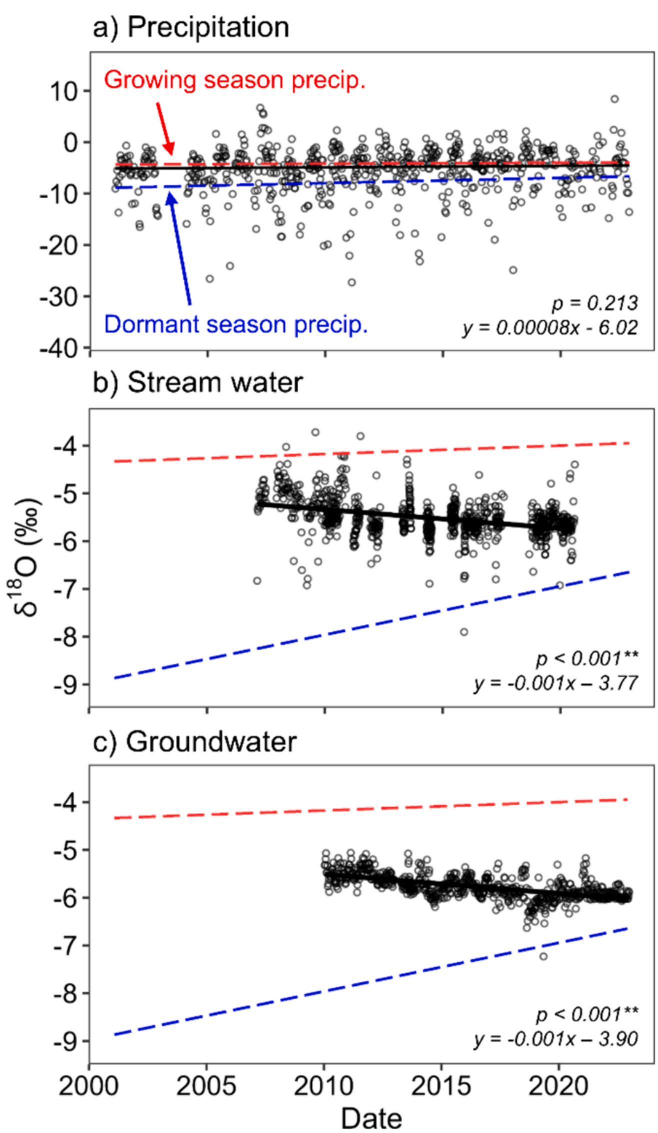

Fig. 4. Changes in precipitation, stream water, and groundwater $\delta^{18}O$ through time. $\delta^{18}O$ of (a) precipitation, (b) stream water, and (c) groundwater collected at KPBS through time. The amount-weighted regression line, equation, and p-value for precipitation $\delta^{18}O$ are shown on panel (a). Linear regression equations and p-values are provided for stream water and groundwater in panels (b) and (c). Asterisks represent significant trends; $^{**}p < 0.05$. Colored dashed lines on each panel are amount-weighted regression lines for growing season (red; March – September) and dormant season (blue; October – February) precipitation $\delta^{18}O$. Corresponding amount-weighted regression equations and p-values for growing and dormant precipitation $\delta^{18}O$ can be found in Fig. S9. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

($p = 0.412$). However, dormant season precipitation $\delta^{18}O$ had a marginally significant increasing trend ($p = 0.06$; Table S4). There has been no change in amount-weighted precipitation of $\delta^{2}H$ overall ($p = 0.201$) or in either season (growing season: $p = 0.095$; dormant season: $p = 0.753$; Table S5).

4. Discussion

The physical and biogeochemical changes associated with ecosystem state transitions co-evolve to control the trajectory of water cycling and partitioning across landscapes (e.g., Harman & Troch, 2014; Troch et al., 2015). However, such linkages and feedbacks have rarely been explored and quantified (Troch et al., 2013; 2015; Wagener et al., 2007; Wagener et al. 2010). Exploring changes in the water cycle following ecosystem state transitions has great potential to propel new theories and frameworks in hydrological science and further identify linkages in critical zone processes (e.g., Wilcox et al., 2022). Here, we used long-term records of precipitation, stream discharge, and water stable isotopes in a woody encroached mesic grassland system to explore why significant increases in annual precipitation over the last century have not been mirrored by an increase in stream discharge (Dodds et al., 2012; Keen et al., 2022, Dodds et al., 2023a) and explore why modeling results suggest that groundwater is playing an increasing role in streamflow generation (Sadayappan et al., 2023). Our results show diverging trends in the isotopic composition of precipitation compared to streamflow and groundwater through time at KPBS (Fig. 4), as well as a rapid decrease in correlation between monthly precipitation and stream discharge (Fig. 3b) and declining annual Q/P ratios (Fig. 3c). Together, these results suggest that either changes in intra-annual delivery of precipitation or shifts in the physical landscape following a replacement of grasses by woody plants are altering patterns of connectivity between incoming precipitation and stream discharge. Below, we discuss these two possible mechanisms in detail.

4.1. Changes in precipitation patterns do not explain changes in streamflow generation, but may contribute to changes in stream and groundwater isotopic signatures

In recent decades, increasing precipitation has been documented for multiple sites in the central Great Plains (Garbrecht et al., 2004; Dore, 2005; Rahmani et al., 2015). However, greater annual precipitation is typically associated with sizable increases in streamflow, and these responses are often non-linear. For example, Garbrecht et al. (2004) reported that an increase in precipitation of just 10 % typically leads to an increase of ~ 60 % in streamflow and a more modest increase in ET (~5%) across sites in Nebraska, Kansas, and Oklahoma, yet this is not what has been observed at KPBS. According to climate projections, northeastern Kansas is expected to experience increased precipitation variability in the future, leading to fewer, but larger rainfall events (Easterling et al., 2000; USGCRP, 2018; Jones, 2019; IPCC, 2021) – this would likely result in decreased surface soil moisture as time between rainfall events increases (Fay et al., 2002, 2003; Heisler-White et al., 2009), and could alter patterns of runoff and groundwater recharge (Huxman et al., 2005; Acharya et al., 2018). However, this trend is not yet apparent in the MHK and KPBS precipitation records. Although we have seen a shift toward larger rain events in the MHK record (Fig. 2b; Table S2), there has been no accompanying reduction in the total number of rainfall events over the past century (Fig. 2a; Fig. S3), leading to an overall increase in annual precipitation (Fig. 1a).

The observed patterns in the stable isotope records of stream water and groundwater could be partially attributed to an increasing proportion of precipitation falling in the dormant season, resulting in lower stream and groundwater $\delta^{18}O$ and $\delta^{2}H$ signatures over time (Fig. 4; Table S5). Dormant season precipitation is typically depleted in ^{18}O compared to growing season precipitation in temperate systems (as seen in Fig. 5 and Fig. S9), leading to clear seasonal patterns in precipitation

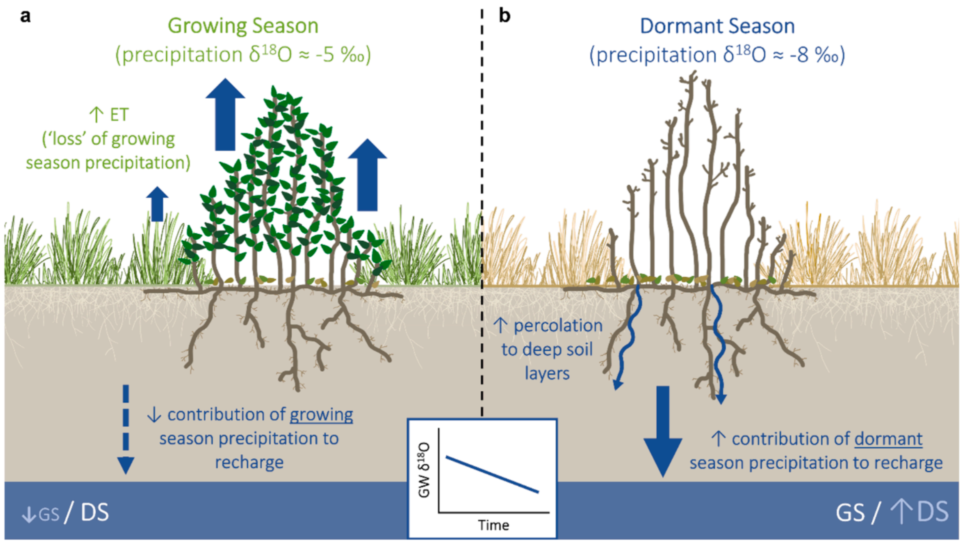

Fig. 5. Potential impacts of woody encroachment on contributions of growing season (GS) and dormant season (DS) precipitation to groundwater recharge. Woody vegetation typically has higher rates of water use compared to grasses, which can lead to increased evapotranspiration as woody cover increases in mesic grasslands. Belowground, the deep, coarse root systems of woody shrubs and trees can alter soil structure (e.g., increased macropore abundance) and increase the occurrence of preferential flow of water to greater soil depths. (a) During the growing season, increased evapotranspiration decreases the amount of growing season precipitation available to contribute to groundwater recharge. This results in a decrease in the proportion of groundwater recharge coming from growing season precipitation relative to the dormant season (↓GS/DS). (b) During the dormant season when most vegetation is not actively taking up water, increased percolation of water to greater soil depths could increase the amount of dormant season precipitation reaching the stream / groundwater system. This would result in an increase in the amount of groundwater recharge coming from dormant season precipitation relative to the growing season (GS/↑DS). Both of these scenarios would increase the proportional contribution of dormant season precipitation to groundwater recharge, which in turn would decrease the groundwater $\delta^{18}O$ signature through time (inset panel), even if the relative magnitudes of growing and dormant season precipitation did not change.

$\delta^{18}O$ and $\delta^{2}H$ (McGuire and McDonnell, 2007; Sprenger et al., 2016; Bowen et al., 2019). An increase in dormant season precipitation (lower $\delta^{18}O$), therefore, could contribute to a decline in stream and groundwater $\delta^{18}O$ over time. Both the longer-term MHK record and shorter-term KPBS record show a small but significant increase in the proportion of precipitation occurring during the dormant season (Fig. S2c). However, over the last two decades, $\delta^{18}O$ of amount-weighted dormant season precipitation has increased slightly, becoming more similar to the signature of growing season precipitation (Fig. S9). We suggest that, in addition to these small shifts in precipitation seasonality, the contribution of dormant season precipitation to groundwater recharge has increased due to physical changes to the system.

4.2. Grassland-to-shrubland state transition further drives an increase in dormant season contribution to groundwater recharge

Vegetation cover is one of the primary determinants of groundwater recharge dynamics in many terrestrial systems (Kim and Jackson, 2012; Jasechko et al., 2014), and changes in land-cover can substantially impact groundwater recharge dynamics. In Great Plains grasslands, woody encroachment has been proposed as a likely mechanism for observed declines in groundwater recharge (Huxman et al., 2005; Acharya et al., 2017; Acharya et al., 2018), particularly in more mesic systems (Wilcox et al., 2022). Higher woody cover has the potential to increase ET substantially in mesic grasslands (Huxman et al., 2005), and ET has been shown to outpace precipitation in encroached portions of tallgrass prairie during dry years (Logan and Brunsell, 2015). Woody shrubs and trees typically have higher canopy transpiration rates compared to grasses (O'Keefe et al., 2020), or the ability to continue gas exchange into the dormant season in the case of evergreen Juniperus species (the primary encroacher in the southern Great Plains; Awada et al., 2013; Caterina et al., 2014). Increased cover of woody species at the expense of grasses, therefore, leads to an increase in vegetation water-use at the watershed- or landscape-scale during the growing season in mesic grasslands (Huxman et al., 2005; Keen et al., 2022).

Over the last four decades, there has also been an increase in 10-year running mean vapor pressure deficit (VPD; $p < 0.001$, $\tau = 0.596$; Table S6). It is possible that increasing VPD could contribute to reductions in water yield since higher VPD increases atmospheric demand for water, which can increase evaporation and transpiration rates. However, it is likely that these trends in VPD also exacerbate the effects of woody encroachment on ET – previous work has shown that canopy transpiration of woody shrubs increases more rapidly with increasing VPD compared to grasses and forbs in tallgrass prairie (O'Keefe et al., 2020). In short, increased water-use by woody vegetation during the growing season (particularly under higher VPD conditions) could decrease the amount of growing season precipitation available to contribute to groundwater recharge (Fig. 5a), leading to a proportional increase in the contribution of dormant season precipitation. Due to the seasonal differences in precipitation $\delta^{18}O$, a decline in the contribution of growing season precipitation to groundwater recharge over time could drive reductions in stream and groundwater $\delta^{18}O$.

Woody encroachment could also potentially increase the contribution of dormant season precipitation to groundwater recharge by altering soil water infiltration pathways (Fig. 5b). Coarse rooting systems of shrubs and trees can modify soil water infiltration pathways by creating macropores and increasing preferential flow of water to greater depths (Beven and Germann, 1982; Jarvis, 2007; Alaoui et al., 2011). Greater preferential flow may increase deep infiltration of dormant season precipitation, as most plants are not actively taking up water during the dormant season. Both of these scenarios – decreased contribution of growing season precipitation to groundwater recharge as a result of greater ET (Fig. 5a) and / or increased contribution of dormant season precipitation to groundwater recharge as a result of altered soil water infiltration pathways (Fig. 5b) – are physical consequences of woody encroachment that have the potential to drive, or contribute to, the observed declines in stream and groundwater $\delta^{18}O$ over time.

4.3. Implications of ecosystem state transitions on water cycling in tallgrass prairie

While aboveground evidence for ecosystem state transitions and hysteresis in mesic grasslands has been building over the last decade (Ratajczak et al., 2014b; Collins et al., 2021), we do not have a solid understanding of how these transitions impact the hydrological systems to which they are intricately linked. We do know that hydrological systems can exhibit threshold behaviors – for example, recent work in tallgrass prairie groundwater systems has found that stream discharge occurs only when thresholds of groundwater storage have been reached (Hatley et al., 2023). This threshold behavior indicates that decreasing groundwater recharge due to woody encroachment may have non-linear effects on stream discharge, and that restoration of stream flow by removal of woody vegetation may have substantial lag-effects depending on the degree to which groundwater has decreased (Dodds et al., 2023a). As such, these results have implications for management strategies aimed at restoring streamflow or groundwater levels by mechanically removing woody vegetation. The timing of the observed 'breakdown' in connectivity between precipitation and stream discharge at KPBS corresponds temporally with the rapid increase in woody cover that occurred in ~ 2000 (Fig. 3a,b; Ratajczak et al., 2014b; also documented in Macpherson et al., 2019). This linkage is not evidence of direct causation, but it does illustrate that declining stream discharge is more closely linked with changes in woody cover than with changes in precipitation dynamics over the last ~ 40 years (Sadayappan et al., 2023).

In addition, our results show that stream discharge has declined in all of the watersheds observed in this study, not just the infrequently burned watersheds (Fig. S5) – we do not currently know the extent to which stream discharge and groundwater recharge in one watershed are impacted by encroachment across the broader landscape (i.e., upstream or in neighboring watersheds). Groundwater dye tracer studies at this site have demonstrated that groundwater can enter and leave a watershed without ever showing up in the stream (Barry, 2018) and geophysical data suggest a high degree of connectivity across this merokarst system (Sullivan et al. 2019). Therefore, it is presumable that groundwater flow does not strictly follow watershed boundaries, and extensive woody encroachment in one watershed could have implications for water yield beyond the boundaries of that specific watershed. While the consequences of woody encroachment on hydrological fluxes in tallgrass prairie are becoming evident (e.g., increasing ET, declining streamflow), identifying mechanisms responsible for alterations to the whole hydrological system requires decadal-scale observations. Changes in hydrological functioning, or potentially a shift to an alternative hydrological state, as a result of woody encroachment could take decades or centuries to reverse. Understanding the hydrological impacts of land-cover change, particularly within the context of changing climate conditions, is vital to predicting how these ecosystems will change and transform in the future.

CRediT authorship contribution statement

R.M. Keen: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **K. Sadayappan:** Writing – review & editing. **K. M. Jarecke:** Writing – review & editing. **L. Li:** Writing – review & editing. **M.F. Kirk:** Writing – review & editing. **P.L. Sullivan:** Writing – review & editing, Project administration, Funding acquisition. **J.B. Nippert:** Writing – review & editing, Resources, Project administration, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data records from the Konza Prairie Biological Station are publicly available in the Environmental Data Initiative (EDI) data portal and are cited in the methods.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jhydrol.2024.131937.

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