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# Controls on Discharge and Drying in an Intermittent Grassland Stream: Temporal and Network Variability

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## ABSTRACT

Intermittent streams are prevalent worldwide, yet the understanding of drivers of their changing flow patterns remains incomplete. We examined hydrological changes spanning four decades (1982–2020) in Kings Creek, an intermittent grassland stream within the Konza Prairie Biological Station in Kansas, USA. We analysed streamflow data from a US Geological Survey gauge on Kings Creek and three upstream Long Term Ecological Reasearch (LTER) sub-watersheds with annual, biennial or quadrennial burn frequencies and linked trajectories of woody encroachment to increased evapotranspiration and changes in streamflow. Riparian woody cover doubled in the annually and biannually burned sub-watersheds and sevenfold in the quadrennially burned watersheds. We observed significant decreases (84%) in daily discharge and number of annual flow days (55%) at the downstream USGS Kings Creek gauge, with similar changes in the LTER sub-watersheds. The changing riparian cover, propelled by the regional expansion of woody plants, contributed to decreased streamflow by amplifying actual evapotranspiration (ET). Seasonal assessments underscored the critical influence of late summer conditions (July–September), under which increases in ET were linked to rising temperatures and increased evapotranspiration by riparian cover. Our results highlight the significant hydrological impacts of woody encroachment in grasslands and emphasize the importance of long-term ecohydrological monitoring in unravelling the interplay between climate and vegetation as controls on the hyper-variable flow patterns in this intermittent stream. Predicting and managing hydrological impacts on the flow of intermittent grassland rivers and streams worldwide requires accounting for the effects of accelerating woody encroachment.

## 1 | Introduction

Non-perennial streams are common in the majority of river networks worldwide (Messager et al. 2021) and are under-studied and under-monitored with respect to hydrology (Krabbenhoft et al. 2022). Recent studies have begun quantifying the intermittency of stream networks (Leigh et al. 2016; Shanafield et al. 2020), though less is known about changes in intermittency over time, particularly as related to global change (Sauquet et al. 2021; Tramblay et al. 2021). Zipper et al. (2021) documented changes in intermittency in US streams over time using long-term United States Geological Survey (USGS) gauging station data and identified increased aridity as a primary factor driving increased stream drying. Across 540 sites, they demonstrated that streams in more arid regions exhibited trends towards longer dry periods over the past ~40 years. Their analysis controlled for watershed characteristics and land use changes, allowing them to isolate climate aridity as the dominant driver of increasing intermittency trends across the continental United States. However, other potential drivers of temporal change in stream intermittency, particularly the effect of vegetation mediated by evapotranspiration (ET), are not as well studied (McCabe and Wolock 2002; Rodgers et al. 2020).

The timing and rate of stream drying have strong policy implications and heavily influence biogeochemical cycles (Von Schiller et al. 2011), as well as ecological characteristics (Price et al. 2024). Therefore, the timing and duration of 'zero flow' (periods when water discharge is not measurable or falls below detection thresholds in otherwise flowing channels) are commonly used in studying intermittent water bodies (Zimmer et al. 2020). Understanding the patterns and causes of intermittent stream flow is important since drying is becoming more prevalent, and drying patterns vary in both space and time (Allen et al. 2020; Jaeger et al. 2014; Perkin et al. 2017). Although climate is a key factor influencing non-perennial stream flow regimes (Dodds 1997; Hammond et al. 2021), other factors can also lead to stream drying, including anthropogenic activities (Datry et al. 2023; Eng et al. 2019) and human water use (Datry et al. 2014; Zipper et al. 2022).

Grassland rivers and streams are vital components of the Great Plains ecosystem and other grasslands worldwide and are dominated by intermittent streams (Dodds et al. 2004). The Great Plains is well suited for understanding drivers of stream drying due to its extensive stream network, long-term hydrological records, well-documented woody encroachment and natural climate gradient that creates conditions ideal for examining interactions between changing vegetation and hydrology. However, woody plant encroachment is occurring in grasslands globally, altering infiltration rates, soil water storage and streamflow, which can lead to reduced water availability and streamflow duration (Zou et al. 2014). The Kings Creek gauge at the Konza Prairie Biological Station (KPBS) is the only 'benchmark' gauging station in the USGS network with its entire watershed in a relatively pristine grassland. It therefore represents an important sentinel gauge for estimating wider changes across grassland ecosystems.

Kings Creek has experienced the expansion of woody vegetation in its watershed (Veach et al. 2014, 2015) as well as changes in hydrology over the past four decades. Riparian shrub cover increased by about 57% from 1978 to 2020 (Keen et al. 2023), while mean discharge and the number of flow days decreased from 1980 to 2010, with no concomitant decrease in annual precipitation (PPT) and a modest increase in temperature (Dodds et al. 2012). However, it remains unknown to what extent increasing stream intermittency can be attributed to vegetation changes and during which seasons these effects are most pronounced, largely because few datasets simultaneously track both vegetation dynamics and hydrological metrics at appropriate scales and timeframes to capture these gradual ecological transitions.

Our overarching research goal was to investigate the relative importance of changes in vegetation and climate as controls over the changing hydrology in the Kings Creek watershed from 1982 to 2020. We hypothesized that discharge can be impacted within this watershed by interrelated changes in PPT, temperature and vegetative cover, with variable impacts as a function of position in the watershed (Figure 1). We base our study on one USGS discharge measurement station at the bottom of the watershed and discharge measurements at three upstream sub-watersheds (N1B, N2B and N4D) with different historical trajectories of woody vegetation encroachment. We also used additional long-term data on environmental factors collected by the Konza Long-Term Ecological Research programme. We hypothesized that along with the PPT and temperature, the variation in the vegetation composition of these upstream sub-watersheds would influence ET and flow regimes (defined in terms of annual or seasonal mean discharge and number of zero flow days). As woody vegetation increases, we predict that higher ET will lead to decreased discharge and fewer flow days in a year. Our research objectives were to (1) characterize changing discharge patterns and identify during which seasonal meteorological factors have the greatest impact on changes in discharge; (2) assess changes in meteorological factors that could influence the hydrology; and (3) link changes in meteorology and vegetative cover to discharge at the watershed outlet and upstream sub-watersheds.

## 2 | Methods

### 2.1 | Study Area Description

Kings Creek has a 10.6-km$^2$ drainage area entirely within KPBS. KPBS is a 3487-ha tallgrass prairie located in the northern part of the Flint Hills region near the city of Manhattan, Kansas (39.1 N and 96.9 W), co-owned by Kansas State

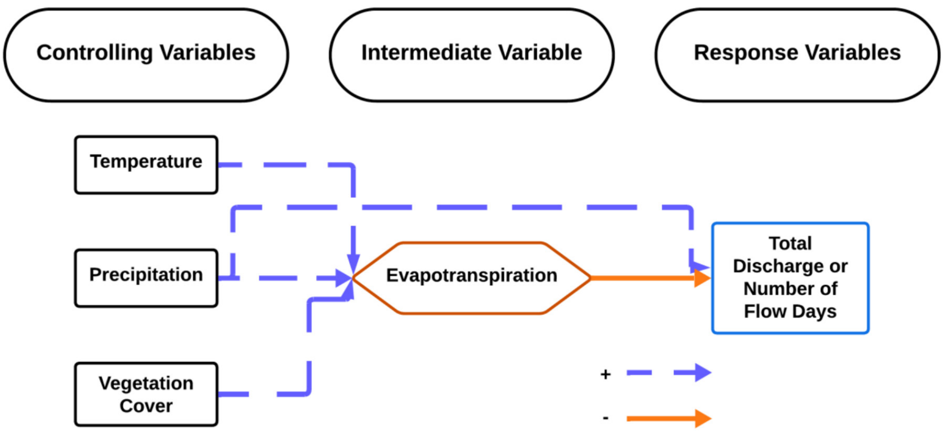


**FIGURE 1** | Conceptual model of our study. The purple dashed arrows represent the hypothesized positive influences, and the orange solid lines represent the hypothesized negative influences of the controlling and intermediate variables on discharge and number of flow days.

University and The Nature Conservancy (Figure 2). The site experiences a mid-continental climate, receiving roughly 800 mm of PPT annually as averaged from 1982 to 2020 (Table 2). Most PPT falls from April to September. Silty-clay loam soils are over two meters deep in lowland areas and at the bottoms of stream valleys (Vinton 1999). Apart from riparian corridors on larger streams and rivers, this area of the Flint Hills historically consisted mostly of native tallgrass prairie and little woody vegetation. Although woody plant expansion is ongoing, the dominating perennial $C_4$ grasses (*Schizachyrium scoparium*, *Sorghastrum nutans*, *Andropogon gerardii* and *Panicum virgatum*) as well as sub-dominant grass, forb and woody species are the primary vegetation of KPBS's regularly burned uplands (Abrams 1986; Collins and Calabrese 2012). The dominant woody species in upland areas consist primarily of rough-leaf dogwood (*Cornus drummondii*), smooth sumac (*Rhus glabra*) and eastern redcedar (*Juniperus virginiana*), while riparian corridors are characterized by a more diverse woody community including American elm (*Ulmus americana*), hackberry (*Celtis occidentalis*), bur oak (*Quercus macrocarpa*) and green ash (*Fraxinus pennsylvanica*). For this study, riparian areas were delineated based on topographic position within 30 m of stream channels, where greater soil moisture and protection from fire historically allowed for the establishment of woody vegetation even in otherwise grass-dominated landscapes.

KPBS features a merokarst geology where the weathering of limestone bedrock layers has produced a complex network of fractures, joints and perched aquifers. Mudstone layers separate these weathered limestone bedrocks, creating a shallow groundwater table (typically 1–5 m below the surface in valleys, and 5–15 m in upland areas) that is well-connected to the Kings Creek stream network. Groundwater residence times vary from days to months in shallow flow paths to several years in deeper aquifers (Sullivan et al. 2019, 2020; Vero et al. 2018). However, connections between the groundwater system and stream network are highly localized (Gambill et al. 2024) typically occurring at scales of tens to hundreds of meters where permeable limestone layers intersect the surface. Recent modelling demonstrated that these localized connections create discrete zones of groundwater discharge supporting baseflow in specific reaches while nearby stream segments remain dry (Swenson et al. 2024; Zipper et al. 2025) Smaller upstream watersheds typically experience more zero flow days, except for short spring-fed reaches (Costigan et al. 2015).

## 2.2 | Watersheds Analysed and Data Sources

Kings Creek is monitored by a USGS stream gauge (06879650 KINGS C NR MANHATTAN, KS) and has been serving as a hydrological benchmark since 1979. The watershed drains native

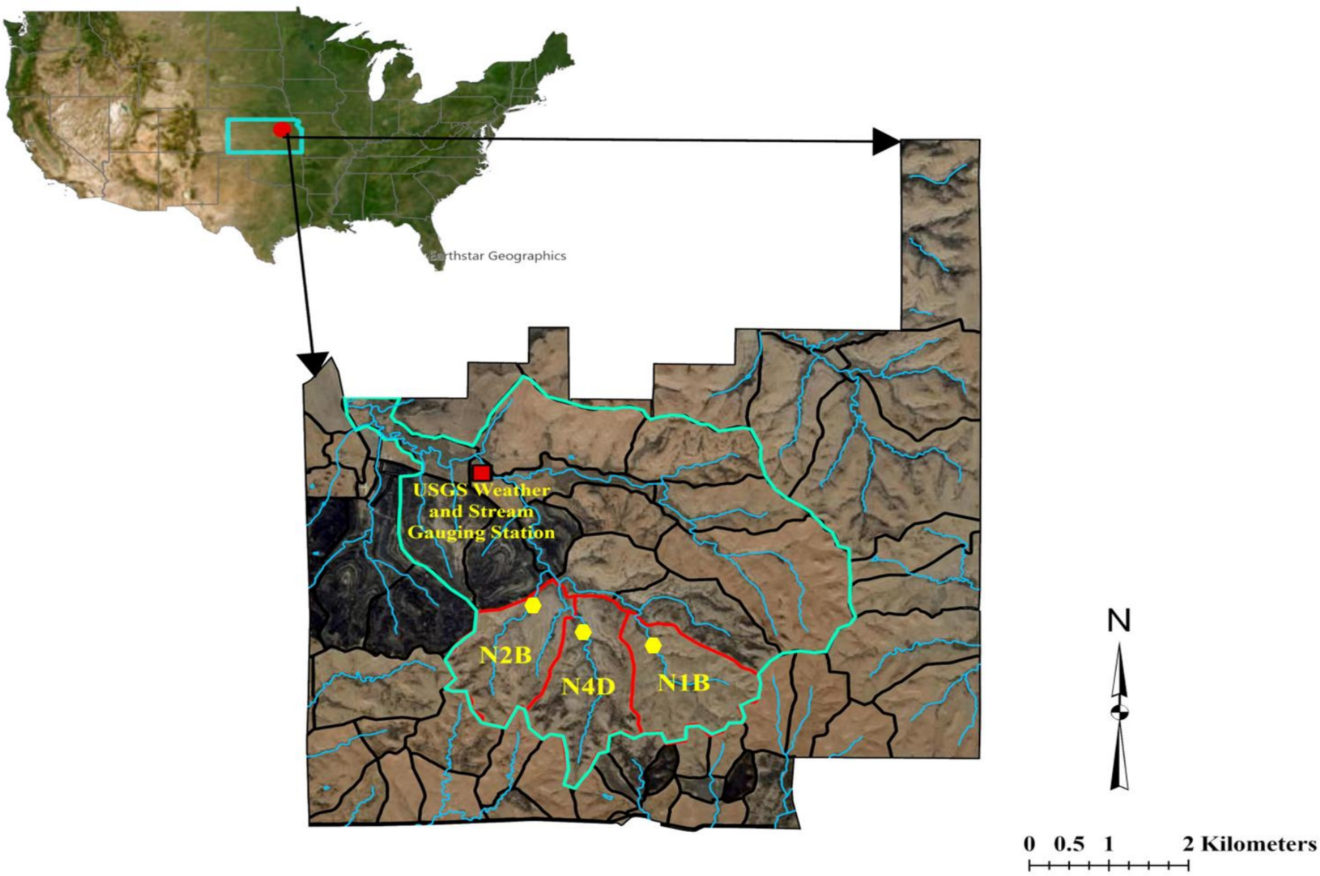


**FIGURE 2** | USGS Kings Creek watershed within the Konza Prairie Biological Station, located in Kansas, USA, including the Long-Term Ecological Research (LTER) watersheds N1B, N2B and N4D. The US Geological Survey has consistently monitored the USGS weather and stream gauging station at this site since 1979 (Gauge 06879650, red square). The yellow dots denote sub-watershed weirs, serving to measure discharge levels since 1987.

tallgrass prairie and has extensive oak riparian forest in its lower reaches. Approximately half of the watershed upstream of the gauging station is under bison grazing and the rest is ungrazed. We compiled discharge data published on the USGS website for the period from 1982 to 2020, consistent with the available meteorological data from the nearby (< 1 km) Konza LTER weather station.

We also have three upstream sub-watersheds in which we have measured discharge using weirs since 1987. These weirs are in intermittent, third-order headwater streams (N1B, N2B and N4D) and were used to characterize discharge variation in sub-basins relative to the downstream USGS station (Table 1). These three small watersheds have been bison-grazed since 1992 and burned every 1, 2 or 4 years (N1B, N2B and N4D, respectively). Data for these three weirs are publicly available (see Table 1). Discharge at these weirs is estimated by water height in v-notched weirs using Druck pressure transducers from 1987 to 2013 and from 2013 to the present using a YSI WaterLOG Bubbler/Pressure Sensor H-3553. During flow periods, discharge is monitored at each site every 5 min, and the sensors are calibrated against manual height readings roughly three times a week during flow. We experienced a few occasions when our depth equipment malfunctioned. For example, about 1.2% of the 95,300 days of data were missing from watershed N4D; however, since we used annual or three-month averages of daily values (see results) this minimizes the influence of missing data.

We also calculated the proportion of riparian woody cover over time in watersheds N1B, N2B and N4D based on data for woody expansion from Dodds et al. (2023) and Keen et al. (2023). These data were created from a time series of remotely sensed images ground-truthed to plant surveys for three watersheds which bracket the burn frequencies of most watersheds in Kings Creek (1-, 2- and 4-year burn frequencies). The aerial imagery was consistently collected at 1-m spatial resolution across all time periods (1982–2020), with images standardized for seasonal timing (predominantly late spring/early summer acquisitions) to minimize phenological differences in vegetation appearance. The classification of woody vegetation was verified through extensive field validation points (> 200 points per watershed) to ensure accuracy across the time series.

To extrapolate these measurements to the entire Kings Creek watershed, we applied a burn frequency-based approach. For sub-watersheds within Kings Creek that were burned annually, biennially or quadrennially, we directly applied the woody cover values from N1B, N2B and N4D, respectively. For sub-watersheds with intermediate burn frequencies (e.g., 3-year burns), we used linear interpolation between the nearest burn frequency categories. For approximately 15% of the Kings Creek watershed with irregular fire histories or burn frequencies outside the 1- to 4-year range, we used the values from the 4-year burn treatment (N4D) as a conservative estimate, as these areas typically experience greater woody encroachment. We then calculated a weighted average based on the proportional area of each burn frequency within the entire Kings Creek watershed to estimate overall woody cover. This approach accounts for the varying management histories across the watershed while being constrained by our detailed measurements from the representative sub-watersheds.

While our gauged sub-watersheds only covered 35.5% of the USGS watershed, the woody vegetation results are similar to an earlier study that assessed riparian woody expansion with aerial imagery of all watersheds feeding the USGS station over a shorter period (Veach et al. 2014, 2015). The data we used covered a longer timespan than the earlier study and allowed the use of our full record of discharge data. The N2B watershed was selected for a riparian woody vegetation removal experiment beginning in 2010. Vegetation within 30 m of the Kings Creek streambed and 10 m within the side channels of the creek was removed mechanically (Dodds et al. 2023; Larson et al. 2019). Vegetation was cut along 4.8 km of stream channel, roughly 21% of the total watershed area, and cutting was repeated every 2 years. The cutting was not effective in decreasing woody vegetation cover, as the shrubs sprouted rapidly and had no observable effect on stream hydrology (Dodds et al. 2023).

We also collected meteorological data from the KPBS headquarters dataset AWE012, which monitors daily mean, maximum and minimum air temperature, relative humidity, total PPT and total solar radiation; mean, maximum and minimum soil temperature and mean wind speed. These data are mostly complete with very few days missing. When equipment malfunctions, it is repaired or replaced rapidly as

**TABLE 1** | Summary of gauged watersheds. Data range represents the first year and the last year of data analysis for each site. Burn frequency at USGS gauge is listed as 'mixed' because various upstream watersheds in this grassland area feed the USGS gauge. These sub-watersheds are grazed and ungrazed, and some have variable burn frequencies (data available at 10.6073/pasta/c7bc668437d3bd7035cff8aa85b567a8).

| Site | Lat. and long. | Data range | Data set name | Watershed area (Ha) | Target burn frequency | Grazers |
|---|---|---|---|---|---|---|
| USGS Gauge | N 39.060747, W 96.354088 | 1982–2020 | 06879650 | 1060 | Mixed | Bison and ungrazed |
| N1B Weir | N 39.08656, W 96.57703 | 1987–2020 | DOI: 10.6073/pasta/7b75a0efa4617f7d34dd9f2f583b686a | 121 | Every year | Bison |
| N2B Weir | N 39.08995, W 96.58900 | 1987–2020 | DOI: 10.6073/pasta/cff758a0736702b20d9b6338e9bbbc25 | 119 | Every 2 years | Bison |
| N4D Weir | N 39.08735, W 96.5844 | 1985–2020 | DOI: 10.6073/pasta/c01278aaaac74572ee53a4a6ba3017d3 | 135 | Every 4 years | Bison |

**TABLE 2** | Summary of data sources on factors that potentially influence discharge. Data range represents each site's first year and last year of data analysis.

| Sample type | Data set name | Locations | Data range | Data citation |
|---|---|---|---|---|
| Meteorological data | AWE012 | Konza Prairie headquarters weather station | 1982–2020 | https://doi.org/10.6073/pasta/743c6b205e38a087bc54925ed258f549 |
| Riparian tree and shrub cover | RIV06 | Watershed N1B, N2B, and N4D | 1982–2020 | 10.6073/pasta/682b8d7a78aa814e96dba672cdabd34c |
| KPBS daily ET | AET011 | Konza Prairie headquarters weather station | 2000–2020 | https://doi.org/10.6073/pasta/b5a57131dc37d035b7c14ec7a8a49604 |

many researchers rely on these data. We also used the Konza dataset AET01, which reports modelled daily grass-based reference ET using meteorological data from AWE012, including wind speed, temperature, PPT and solar radiation under non-limiting water conditions for a hypothetical short grass (height of 0.12 m, a surface resistance of $70\,\mathrm{s\,m^{-1}}$, and an albedo of 0.23) based on meteorological conditions at KPBS from AWE012 (see Table 2).

### 2.3 | Calculation of ET, Excess Water and Excess Energy

We calculated ET for every season for statistical analyses of effects of grass and wood ET. Grass ET was calculated by multiplying daily reference ET obtained from the AET01 dataset by a crop coefficient ($K_c$). Daily $K_c$ values representing tallgrass prairie water use across the growing season used in this study were developed by Hutchinson et al. (2008) at KPBS and vary as a function of day of year. These values follow a seasonal pattern, ranging from 0.2 during the non-growing season (November–March) to 1.1 during peak water use (day of year 189–206, mid-July), with gradual increases during spring green-up and decreases during fall senescence. We applied these day-specific $K_c$ values to the corresponding reference ET value rather than using a single coefficient for the entire growing season. We note that calculated grass ET represents water use under non-limiting water conditions, since Hutchinson et al. (2008) model was used to calculate the expected water use when soil water is not limited (Hervé-Fernández et al. 2023).

Woody vegetation has greater rates of ET than grasses at this site based on work by O'Keefe et al. (2020), who identified roughleaf dogwood (*C. drummondii*) as the primary woody encroacher in upland areas of this grassland and a common species in early woody riparian encroachment. Under field conditions at our site, rough-leaf dogwood demonstrates a notably higher canopy transpiration rate of 2.01 mm/day in contrast to the dominant grass species, big bluestem, which transpires at a rate of 0.91 mm/day during the growing season (O'Keefe et al. 2020). Based on these data, we assumed woody vegetation has two times greater rates of ET than grass modelled in the ET dataset (AET01). This is a conservative estimate because the grasses go dormant earlier than the woody vegetation. We acknowledge this simplification introduces uncertainty, as actual ET ratios likely vary with vegetation age, density, topographic position and seasonal conditions.

We employed exponential equation regression models to analyse the temporal changes in riparian and whole watershed vegetative cover based on remote-sensed, ground-truthed image analyses (Dodds et al. 2023; Keen et al. 2023). The independent variable was year, and the dependent variable was the proportion of vegetation cover. When we averaged the values across all three watersheds, an exponential model exhibited an excellent fit to the change in vegetative cover data over time ($R^2=0.97$) We then calculated three distinct ET values: one for grass ET, a second for grass + riparian woody cover ET, and a third for ET accounting for all woody cover in the entire watershed. We separated out woody riparian cover because riparian vegetation may be able to access stream water as well as groundwater before it enters the streams (Keen et al. 2022).

We also determined excess PPT and energy according to Tomer and Schilling (2009). We note that this is a separate ET calculation from the data used for the statistical analyses. The calculation required estimating reference evapotranspiration ($ET_O$) with the Hargreaves method (Hargreaves and Allen 2003; Hargreaves et al. 1985) for the Kings Creek watersheds using temperature data collected by the KPBS weather station. We used this method to remain consistent with the original Tomer and Schilling (2009) methodology to assess temporal trends in excess energy and PPT with the expansion of woody vegetation.

$$PET = 0.0023R_a\left(\frac{T_{max}-T_{min}}{2}+17.8\right)\sqrt{T_{max}-T_{min}} \tag{1}$$

where PET is in mm $\mathrm{day^{-1}}$, $R_a$ is the extraterrestrial radiation ($\mathrm{MJ\,m^{-2}\,day^{-1}}$), $T_{max}$ is the daily maximum air temperature (°C) and $T_{min}$ is the daily minimum air temperature (°C). $ET_O$ was calculated on a daily time step and then aggregated to seasonal and annual values for analysis.

The availability of unused water and energy are a function of PPT and ET and can fluctuate based on vegetation conditions (Tomer and Schilling 2009). Following Tomer and Schilling (2009), we normalized this unutilized portion on a scale from −1 to 1 where 1 is complete excess, 0 is balanced, and −1 is the complete deficit of PPT ($P_{ex}$) or excess evaporative demand ($E_{ex}$) according to the equations:

$$P_{ex} = \frac{(PPT - ET)}{PPT} \tag{2}$$

$$E_{ex} = \left(\frac{PET - ET}{PET}\right) \tag{3}$$

To ensure valid water balance calculations, we focused on wetter years (those exceeding the 60th percentile of annual PPT, $n = 12$ years between 2001 and 2020). We excluded specific drought years (2002, 2003, 2006, 2011, 2012, 2013 and 2018), which showed consistent patterns of low PPT coinciding with decreased discharge and flow days. This selection was necessary because the Tomer and Schilling (2009) method assumes that soil water storage remains relatively constant between years. During dry years, a significant portion of subsequent PPT replenishes soil moisture deficits and recharges shallow aquifers rather than contributing to streamflow or ET, which would confound the water balance calculations. By focusing on consistently wet years, we minimized the effects of year-to-year variations in soil and groundwater storage, allowing us to more directly analyse changes in PPT-ET partitioning.

## 2.4 | Statistical Data Analysis

We transformed non-normal data when necessary. Log10 transformation of discharge and riparian cover normalized the data for all statistical analyses, including regression, correlation, ANCOVA, and structural equation modelling. This transformation addressed non-normal distributions and unequal variances, meeting critical assumptions for our entire analytical framework. To minimize issues with zero-inflated data, we added 0.0001 cms (one unit less than our minimum detection limit) to each daily discharge value to retain information on daily mean discharge days with zero flow when using the log transformation.

We controlled for temporal autocorrelation in discharge data using an analysis of mean daily discharge from the USGS gauging station over the entire period of record. We offset the temporal series of data against itself starting at 10 days and increasing the sliding window offset by 10-day increments up to 90 days. We used this approach to find the time lag where temporal autocorrelation was no longer statistically significant ($p > 0.05$). This threshold indicates the point at which past daily discharge no longer significantly influenced current daily discharge, meaning observations separated by this time lag could be considered statistically independent of each other.

Once we determined the length of time lag for autocorrelation, we used this window length for subsequent analyses. We moved the window by month through the year to see if varying the window start date influenced the relationship of change in discharge over time to assess if there were natural breaks or seasons with differences in discharge patterns. We then used the results from the USGS Kings Creek site to divide the data to account for seasonal factors for this and the upstream LTER sub-watersheds.

We focused on discharge and the number of flow days as our two key response (dependent) variables and their relationships with potential drivers (PPT, temperature, riparian cover and ET) over time for both USGS Kings Creek and LTER sub-watersheds for each period determined based on the autocorrelation analysis. We first explored the dataset with Pearson correlation for both USGS Kings Creek and individual LTER sub-watersheds to establish correlations among discharge and flow days with year, PPT, temperature and riparian cover by seasons. As the solar radiation and humidity are directly proportional to the temperature, we removed solar radiation and humidity from our further analysis. PPT and temperature were most strongly correlated with discharge, so we used analysis of covariance (ANCOVA) with year, PPT and temperature as the continuous variables, and season as an independent categorical variable to assess if the season interacted with the continuous variables to predict discharge or the number of flow days (i.e., if overall trends were strongly influenced by specific seasons). We also analysed temperature and PPT as separate dependent variables to establish temporal trends in these variables with time.

We assessed the independent variables discharge and seasonal number of flow days against year, PPT, temperature and riparian cover with regression. Then we used ANCOVA to explore discharge and the number of flow days at LTER sub-watersheds as a function of season (categorical) with continuous variables of year, temperature and PPT and interactions of all variables. We analysed the proportion of woody riparian vegetation in each LTER sub-watershed to see how this impacted the discharge. Finally, we performed ANCOVA for discharge and flow days as a function of the sub-watersheds (N4D, N2B and N1B) with continuous variables of year, temperature and PPT.

We also employed ANCOVA to assess the influence of vegetation on the USGS Kings Creek gauge. Initially, we analysed the ET rates for the entire watershed, specifically focusing on grass ET measured in mm/3 months ($ET_{grass}$) with season as a categorical variable and year as a continuous variable. Subsequently, we expanded the analysis to include both grass ET and riparian area woody cover ($ET_{grass+wood}$), examining their combined effects with the same categorical and continuous variables. Finally, we conducted an ANCOVA to explore the influence of grass ET while incorporating the total proportion of woody cover across the entire watershed ($ET_{total\ proportion\ wood}$). For this analysis, we employed temporal interpolation using exponential regression modelling ($R^2 = 0.9691$) fitted to six measured time points of watershed-wide woody cover from 1980 to 2020. This highly significant model ($R^2 > 0.96$) allowed us to interpolate annual woody cover values for years between measurements. We then calculated ($ET_{total\ proportion\ wood}$) by applying the 2× woody ET multiplier to these annual woody cover estimates, weighted by the proportional area of woody vegetation versus grassland across the entire watershed for each year.

We tested the model in Figure 1 with a structural equation model (SEM) to elucidate the interrelationships among key environmental variables. The SEM focused on two response variables: discharge and the number of flow days. ET was modelled as being influenced by three directly measured variables (PPT, temperature and riparian woody encroachment). Discharge and the number of flow days were both modelled as being influenced by ET (grass with riparian wood cover) and PPT, since PPT can directly run off into the streams or be intercepted and lost through ET. All statistics were done with IBM SPSS Statistics 27, except structural equation modelling, which was done in R Studio version 2023.12.1 + 402.

## 3 | Results

### 3.1 | Temporal Trends of Hydrology and Climate at USGS Kings Creek Gauge

Kings Creek at Konza Prairie is an intermittent stream that can flow or dry any month of the year. We found modest evidence for decreases in mean annual discharge, likely related to the high interannual variance; long-term data indicated a decrease in yearly mean discharge over time ($F=2.289$, $p=0.139$). However, using daily data resulted in a clearer decline in discharge; log10 (daily mean discharge + 0.0001 cms) decreased 84% from 1982 to 2020 ($F=413.761$, $p<0.001$) (Figure S1). The annual number of flow days at the USGS Kings Creek gauge showed a downward trend ($F=8.973$, $p<0.005$) with a moderate correlation ($R^2=0.20$), with predicted values from the regression model roughly halving from 240 to 120 days annually between 1982 and 2020 (Figure 3B). Temperature demonstrates a warming trend, increasing by approximately 1.2°C over the 39-year period ($F=19.27$, $p<0.001$) (Figure 3C). Yearly PPT shows a slight visual increase but with high variability and low confidence ($R^2=0.03$, $F=1.21$, $p=0.278$) (Figure 3D and Tables S1–S3). We found no individually significant contributions of season, year, and season*year interaction with PPT patterns, but temperature dynamics are notably influenced by time (years) (Tables S5 and S6).

### 3.2 | Temporal Autocorrelation in Discharge

We offset the USGS discharge using a sliding window of 10 days up to 90 days (increasing the window size by 10 days for each correlation) to estimate the temporal autocorrelation period and explore the times of the year that were most influential in the observed decrease in discharge and the number of flow days. By the time we reached the 90-day sliding window, temporal autocorrelation of discharge became non-significant. We then used a 5-day window between 80 and 90 days, and the temporal autocorrelation abruptly became non-significant with an 85-day time lag. Based on this, we divided the data into four 3-month seasonal periods in each year (Figure 4; see Table S4). We also tested if it mattered if we started the three-month periods in January, February, March or April using temporal autocorrelation. It made little difference ($p>0.05$) which of the months we started our 3-month periods, so we analysed seasonal effects with January to March as season one (Julian Days 1–90), April–June as season two (Julian Days 91–181), July–September (Julian Days 182–273) as season three and

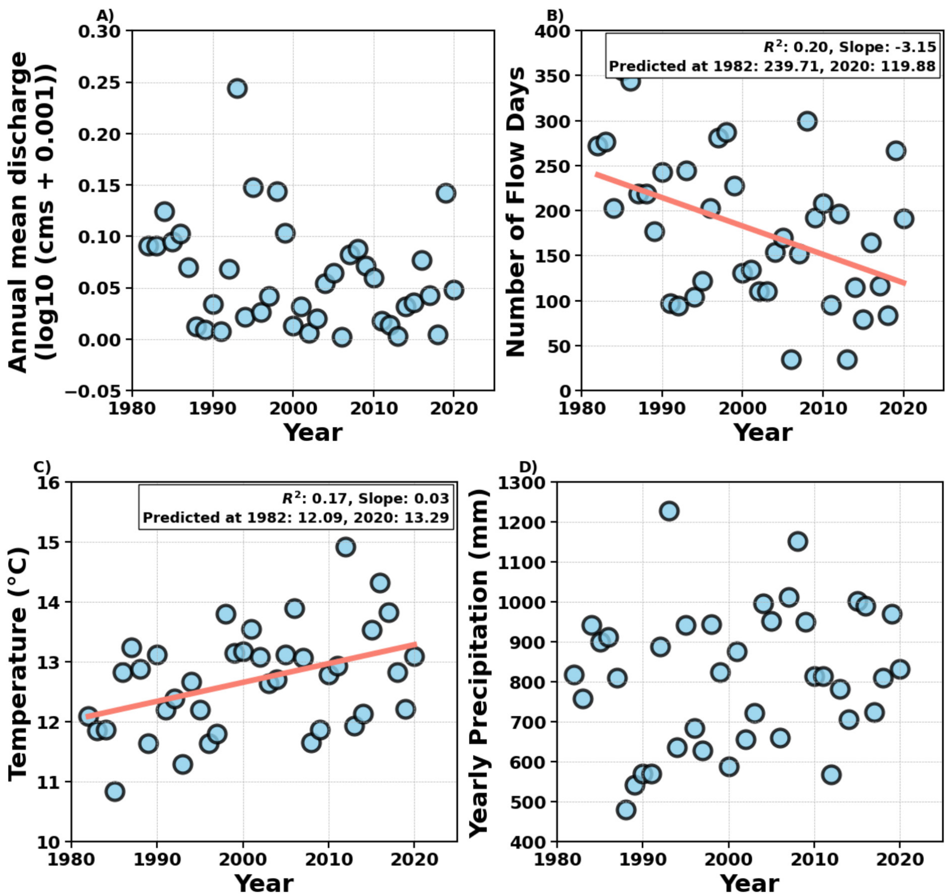


**FIGURE 3** | Annual mean daily discharge by year (A) and number of annual flow days by year (B), annual mean daily temperature (C) and annual total precipitation (D) at the USGS gauge in the Kings Creek watershed. The solid salmon-red line illustrates a regression fit for each graph where $p<0.05$.

October–December (Julian Days 274 to 365 or 366 depending upon leap-year) as season four (Figure 4).

### 3.3 | Factors Influencing Discharge and Total Flow Days Per Season in the Three Sub-Watersheds

Watershed N4D (burned every 4 years) had an approximately sevenfold increase in the proportion of riparian woody cover between 1980 and 2020 ($F = 8921$, $p < 0.001$; Figure 5C). At the N2B watershed, which burns every 2 years and excluding the years of manual removal, total riparian cover increased almost 200% over the same period (Figure 5B). The manual vegetation removal carried out in the N2B watershed during 2011–2013 had minimal impact on the long-term trend, causing a short-term decrease during the removal experiment but a rapid return to the trajectory of exponential increase. Annually burned N1B had a riparian cover increase of about twofold from 1982 to 2020 (Figure 5A). The riparian zones cover approximately 20% of each watershed.

The ANCOVA for the sub-watersheds revealed that season, sites, PPT and riparian cover all influenced discharge ($p < 0.01$). PPT emerges as the dominant factor, with the highest *F* value (72.410). Temperature, however, does not impact discharge ($p = 0.285$). The interaction between sites and riparian cover ($p < 0.001$) suggests that riparian cover's influence on discharge varies across locations (Table S7). In contrast, for flow days, season and PPT remain highly influential ($p < 0.001$), but watershed less so ($p = 0.309$). Temperature and riparian cover also show no significant main effects. Notably, interaction terms indicate that temperature, PPT and riparian cover affect flow days consistently across sites and seasons (Table S8).

### 3.4 | Correlations With Discharge and the Number of Flow Days and How They Are Changing Over the Years for USGS Gauge and Upstream Sub-Basins

At the USGS Kings Creek gauge, discharge showed strong positive correlations with both annual PPT and the number of flow days. The number of flow days exhibited negative relationships with both year (Figure 3B) and temperature (not shown). Temperature displayed a positive relationship with year (Figure 3C and Table S9).

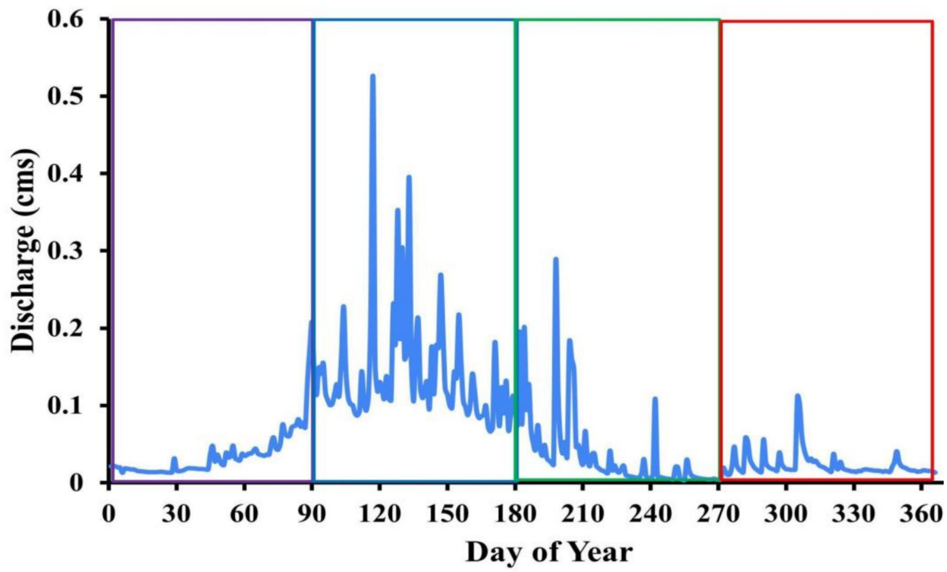


**FIGURE 4** | Discharge averaged for each day from 1982–2020 at the USGS Kings Creek gauge. Boxes indicate the 'seasons' we used for subsequent analyses, which were defined based on periods where temporal autocorrelation was not significant.

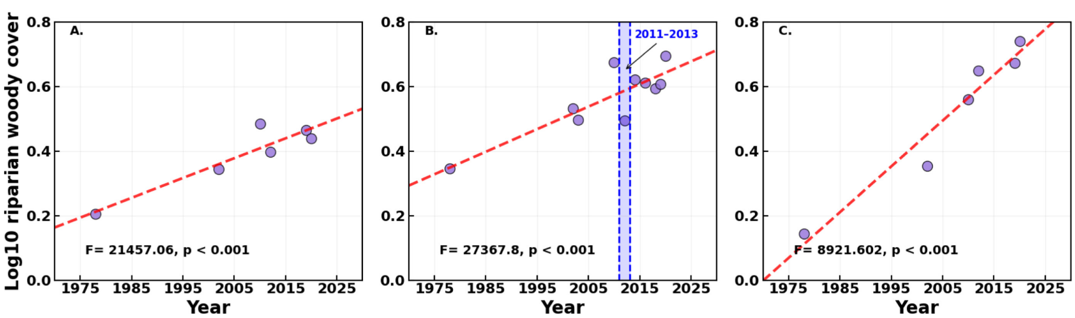


**FIGURE 5** | $\text{Log}_{10}$ scaled proportion of shrub and tree cover in riparian zones over time at the Kings Creek sub-basin watersheds with different burning frequencies. (A) N1B burns every year, (B) N2B burns every 2 years and (C) N4D burns every 4 years. All watersheds showed a significant increase in the total riparian cover. Note the vertical dashed line in Panel (B) indicates when riparian removal temporarily decreased woody cover following the whole watershed riparian removal experiment.

The flow characteristics (mean discharge and number of flow days) were very variable in the sub-watersheds, generally with fewer flow days than at the USGS gauge. The LTER N4D watershed displayed strong positive correlations of both discharge (annual) and the number of flow days with PPT. Unlike the USGS site, no significant correlation was found between discharge and temperature in this watershed. Over the study period, riparian cover steadily increased; yet, this increase did not correlate strongly with discharge or the number of flow days (Table S10).

The N2B watershed demonstrated similar patterns to those observed in N4D, with discharge and the number of flow days positively correlated with PPT amounts. Temperature had a weak relationship with discharge and flow days (Table S11). In contrast, the N1B watershed exhibited different patterns compared to N4D and N2B. Discharge did not significantly relate to PPT, and there was a positive relationship between the number of flow days and PPT (Table S12).

### 3.5 | What Might Influence Discharge and the Number of Flow Days at the USGS Station Over the Years by Season?

The ANCOVA for discharge at USGS Kings Creek gauge reveals PPT is a key driver affecting discharge ($p=0.002$, $F=10.264$). Season had weak relationships with discharge ($p=0.623$) as did temperature and riparian cover. The absence of strong interaction terms (all $p>0.05$) suggests consistent effects of temperature, PPT and riparian cover across seasons. At this site, PPT drove discharge variation (see Table S13). Analysis of flow days presents a contrasting result to the discharge model. Increases in riparian cover were associated with a decrease in flow days ($F=4.074$, $p=0.048$), unlike in the discharge model. Surprisingly, neither season nor PPT showed significant main effects at the USGS gauge, diverging from sub-watershed results. Temperature remained weakly related. Again, interaction terms all had $p>0.12$, indicating consistent variable effects across factor combinations (Table S14). In sum, these analyses suggest riparian cover is a key control in determining the number of flow days at USGS Kings Creek, outweighing PPT and season.

### 3.6 | Assessing ET Dynamics With Wood Across Seasons

Our ANCOVA analyses revealed that woody vegetation substantially amplifies both seasonal ET patterns and long-term ET increases. For the grassland-only ET scenario, we found modest seasonal variation ($F_{3,72}=2.562$, $p=0.061$) and a weak constant yearly increase ($F_{1,72}=4.245$, $p=0.043$), with a marginal season-by-year interaction ($F_{3,72}=2.696$, $p=0.052$). When woody vegetation was included, these patterns became much more pronounced. For the ET with riparian woody vegetation scenario, both season ($F_{3,72}=6.616$, $p=0.001$) and year ($F_{1,72}=26.801$, $p<0.001$) had strong effects, with a powerful season-by-year interaction ($F_{3,72}=7.096$, $p<0.001$). Similar strong effects were observed for the ET with total watershed woody vegetation scenario, with notable effects of season ($F_{3,72}=6.440$, $p=0.001$), year ($F_{1,72}=25.937$, $p<0.001$) and their interaction ($F_{3,72}=6.908$, $p<0.001$). See Tables S15–17 for full ANCOVA results.

Our most striking finding is the significant increase in ET with time due to woody encroachment, with this effect most pronounced during late summer months. Specifically, the July–September trendline for $ET_{grass+wood}$ and $ET_{total\ proportion\ wood}$ exhibited the steepest positive slopes, approximately 9.94 and 7.39 mm per decade, respectively, while $ET_{grass}$ showed a more moderate slope of 6.36 mm per decade (Figure 6). This indicates that woody vegetation amplified the increasing trend in summer ET over the study period. Over the entire 2001–2020 period, summer (July–September) ET increased dramatically by 56 mm (2.78 mm/year) in areas with riparian woody vegetation compared to just 28 mm (1.42 mm/year) in grass-only areas. Total ET during this critical period reached approximately 400 mm per three-month season in woody-influenced watersheds by 2020, representing an ~15% increase from the 350-mm seasonal totals observed in 2000. The spring (April–June) period also showed notable increases in ET with woody vegetation present, with positive slopes of 1.42 mm/decade for $ET_{grass}$, 3.44 mm/decade for $ET_{total\ proportion\ wood}$ and 1.42 mm/decade for $ET_{grass+wood}$ suggesting an upward trend, although not as steep as the July–September period (Figure 6). Winter and fall periods showed minimal change over time, regardless of vegetation type. The predominant summer ET increase is particularly important

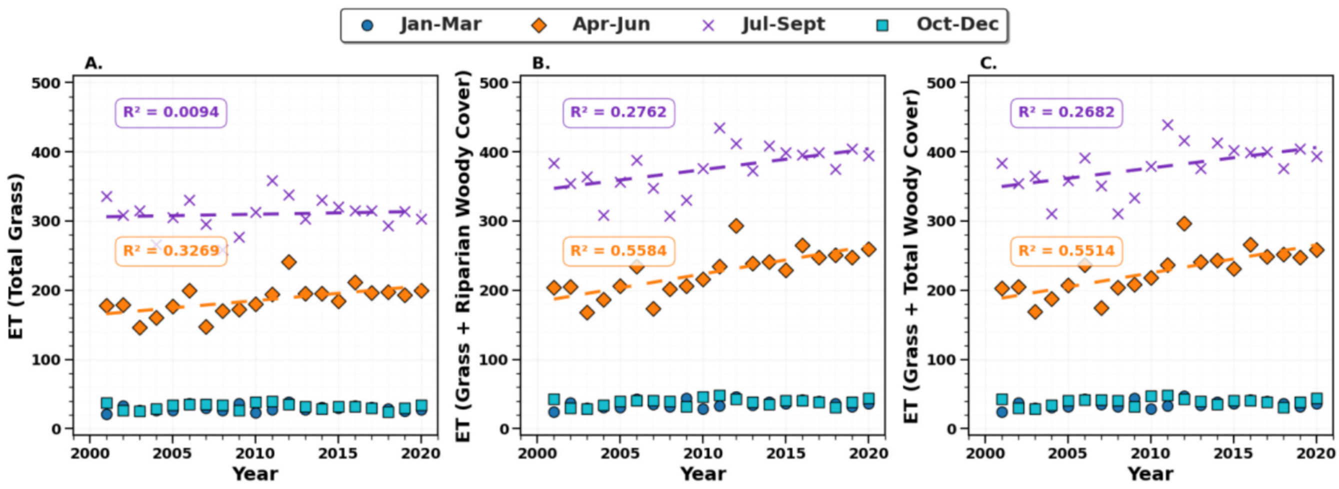


**FIGURE 6** | Seasonal variation in evapotranspiration (mm/3 months (cumulative seasonal total)) dynamics for total watershed grass ET (A), total watershed grass + riparian woody cover ET (B) and total watershed grass + total woody cover ET (C) in the USGS Kings Creek watershed.

for streamflow as it occurs during the period when water availability is limited and demand is high, creating a seasonal water deficit that contributes directly to fall stream drying.

We analysed the relationship between PPT excess ($P_{ex}$) and energy excess ($E_{ex}$) for the USGS Kings Creek watershed (Figure 7) to understand the temporal dynamics of these drivers. During these wet years, both $E_{ex}$ and $P_{ex}$ were generally positive (Figure 7). During the spring (April–June) and fall (October–December) seasons, $P_{ex}$ was generally high and there was variability primarily along the $E_{ex}$ dimension among years (Figure 8), indicating that during these seasons, the availability of energy is the primary factor varying among years. In winter (January–March) and summer (July–September), the points generally shift downward and to the left through time, indicating both $P_{ex}$ and $E_{ex}$ are decreasing, which is a pattern that would be expected under woody vegetation encroachment (Tomer and Schilling 2009).

The path coefficient of the structural equation modelling (Figure 9) indicates strong effects of PPT on both discharge and the number of flow days and a very strong influence of ET on discharge, but not flow days. This modelling also shows that ET has a modest negative relationship with streamflow discharge (coefficient $= -0.002$, $p = 0.002$). While the p value is small, the magnitude is relatively small in standardized terms. Temperature (16.58) and riparian cover (219.29) show much larger direct effects on ET than ET shows on discharge. This explains the apparent contradiction in our earlier analyses: the relationship is statistically strong (highly significant) but modest in effect size. PPT maintains the dominant direct effect on discharge (0.006, $p < 0.001$), while ET's influence operates both directly and through complex indirect pathways. The relationship between ET and flow days is even weaker ($-0.041$, $p = 0.178$), suggesting different mechanisms control flow persistence. The large coefficients highlight the strong impacts of temperature and riparian areas, while the small coefficients suggest weaker effects for the other relationships in this watershed hydrological network, where ET serves as a key mediating process.

## 4 | Discussion

### 4.1 | Expanded Woody Vegetation Plays a Role in Declines in Stream Discharge and Flow Days

Our results highlight a decline in daily discharge by 84% and flow days by 55% at the USGS Kings Creek gauge from 1982 to 2020. The USGS Kings Creek watershed basin is on a trajectory of change with riparian woody expansion occurring that could eventually spread to all streams in all watersheds at the site and replace all grass-dominated riparian areas (Dodds et al. 2023). This expansion was dramatic: near doubling of riparian cover in watersheds N1B and N2B, and a sevenfold increase in watershed N4D. This progressive increase in woody vegetation substantially expanded the total leaf area available for transpiration, particularly in watersheds with less frequent burning.

The negative association of riparian cover with discharge, as mediated by ET in our study, indicates that increased woody vegetation is associated with reduced discharge, as has been shown

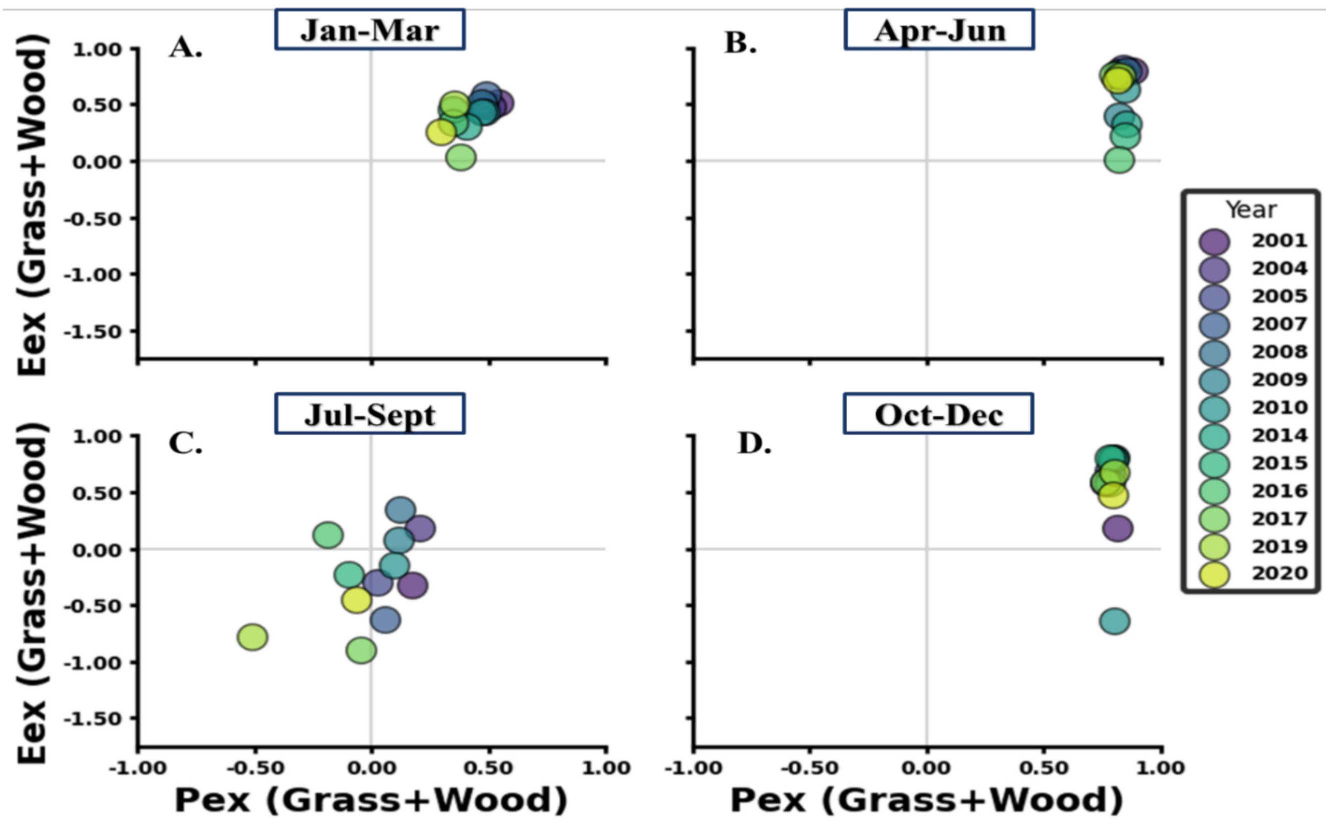


**FIGURE 7** | (A–D) Comparative plots of excess precipitation ($P_{ex}$) versus excess evaporative demand ($E_{ex}$) for grass with wood in the USGS Kings Creek watershed for wet years from 2001 to 2020.

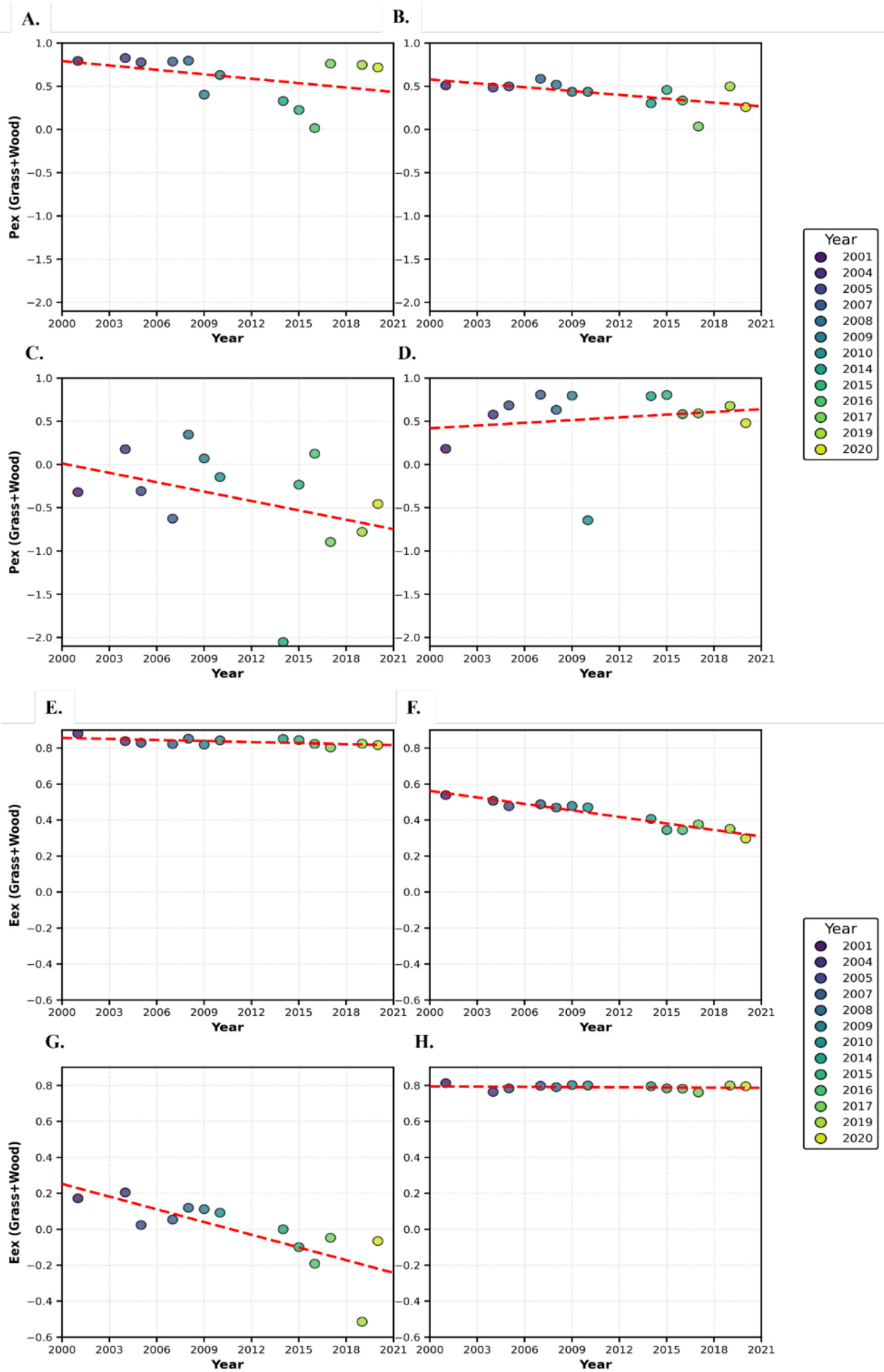


**FIGURE 8** | Legend on next page.

FIGURE 8 | Seasonal breakdown of excess precipitation ($P_{ex}$) versus excess evaporative demand ($E_{ex}$) for the USGS Kings Creek watershed from 2001–2020 (wet years only). Panels show (A–D) $P_{ex}$ patterns and (E–H) $E_{ex}$ patterns for winter (January–March), spring (April–June), summer (July–September) and fall (October–December), respectively. Colour gradient represents the year progression from 2001 (cool colours) to 2020 (warm colours). Red dashed lines indicate linear trends.

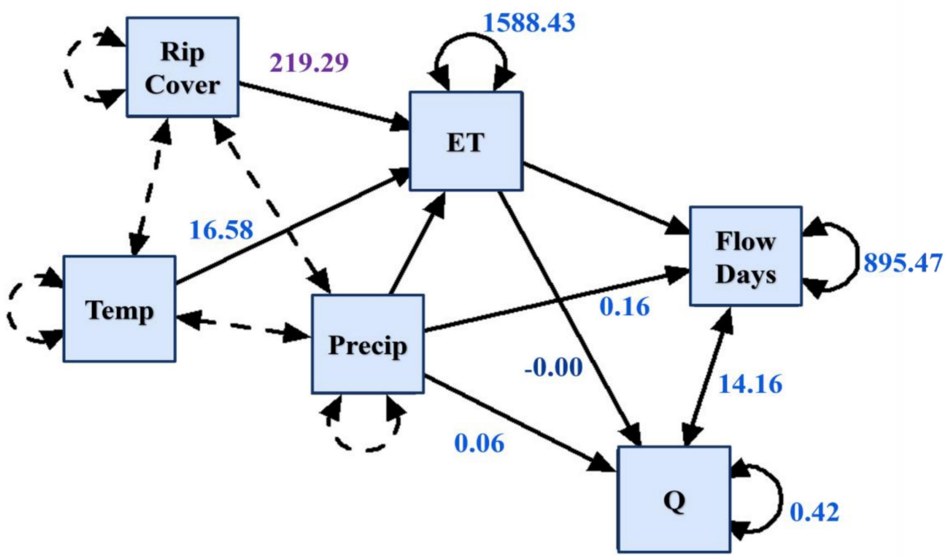


FIGURE 9 | Structural equation model illustrating significant relationships according to the conceptual model. Blue estimates are significant at $p < 0.002$, while the purple estimate indicates significance at $p = 0.032$. (Here, 'Q' = log discharge, 'ET' = actual evapotranspiration, 'Precip' = precipitation, 'Temp' = temperature and 'Rip Cover' = log riparian cover.) Solid arrows represent direct causal relationships, while dashed arrows represent covariances without assumed direct causality. Straight arrows indicate hypothesized directional effects, and curved arrows represent residual variances (self-loops) or correlations between variables. Numbers on paths are standardized path coefficients.

by others in catchment-scale hydrological systems (Bosch and Hewlett 1982; Zhang et al. 2001). Our data suggest a nonlinear response where impacts intensify once woody cover exceeds critical thresholds (approximately 30% in watershed N4D). This supports recent work suggesting that stream intermittency can be characterized by tipping point behaviour between wet and dry states (Zipper et al. 2022).

Encroachment of woody species in mesic grasslands is associated with increased ET due to the generally higher transpiration rates exhibited by woody plants compared to grasses (Huxman et al. 2005; Keen et al. 2022; O'Keefe et al. 2020; Wilcox et al. 2022). In the KPBS riparian area, about 75% of the total PPT is lost to ET (Steward et al. 2011). This proportion is well supported by our $P_{ex}$ analysis, which shows winter (January–March) and fall (October–December) seasons with positive $P_{ex}$ values around 0.2–0.5, indicating 50%–80% of PPT consumed by ET. Spring (April–June) shows similar patterns, while summer (July–September) shows $P_{ex}$ values approaching or below zero, particularly in recent years, indicating nearly 100% of PPT consumed by ET. The significant increase in ET we documented during July–September, particularly in models incorporating woody vegetation, reflects the capture of subsurface water by woody species. This is further supported by observed correlations between the spatial distribution of stream drying and seasonal to annual ET rates in the watershed (Zipper et al. 2025).

The well-distributed and deeper root systems of woody vegetation compared to grasses enable them to access deeper soil water or groundwater, altering infiltration rates and flow paths (Nippert and Knapp 2007). While grasses are predominantly dependent upon water within the top 30 cm of the soil, with a majority of grass root biomass in the upper soil profile (Dahlman and Kucera 1968; Hintz 1999), woody $C_3$ species access deeper soil water through extensive taproot systems. The use of stream water by shrubs along riparian areas, as indicated by water stable isotopes, shows substantial shrub consumption of stream water during portions of the growing season (Keen et al. 2022). When comparing our ET models, we found that riparian woody vegetation had a stronger per-area impact on streamflow than upland woody vegetation, likely due to riparian trees' direct access to stream water and shallow groundwater. While both riparian-only and total watershed woody vegetation models predicted significant increases in ET, the riparian model explained a slightly higher proportion of discharge variance.

Our findings on decreasing streamflow align with changing vegetation-water dynamics in this watershed. Even during wet periods, over 95% of PPT travels through the subsurface rather than as direct runoff (Hatley et al. 2023), with increasingly long flow paths as the stream network dries (Swenson et al. 2024). Our discharge and ET results suggest this subsurface flow path is increasingly exploited by woody vegetation. The differential response we observed in watersheds with varying woody encroachment levels (N1B vs. N4D) further supports this mechanism.

Rising atmospheric $CO_2$ and temperature will complicate vegetation–water relationships. Current $CO_2$ levels of 420 ppm are projected to reach 550–900 ppm by 2100 (Change 2007), which will enhance woody $C_3$ species' dominance by increasing their water-use efficiency, allowing them to keep stomata closed more often without becoming carbon-limited (Anadón et al. 2014; Volder et al. 2013; Wang et al. 2018). Warming of 2.5°C–5.5°C by 2100 (RCP4.5-8.5) will increase ET by 3%–5% per°C (Acharya et al. 2017), potentially raising annual ET demand by 10%–25%. Our data show a shift towards more intense, less frequent PPT events—a trend projected to continue (Davenport and Diffenbaugh 2021). These larger storms would likely lead to greater proportions of runoff and less infiltration, favouring woody vegetation with deeper roots that can tap into stored subsurface water.

Our results indicate that yearly burning in this grassland ecosystem could somewhat slow the expansion of woody vegetation, as the increase of woody riparian cover was slower in watershed N1B (burned annually) compared to N2B and N4D. However, even the annually burned watershed with slower encroachment still experienced discharge declines once sufficient woody cover was established. This threshold effect highlights important implications for targeted management interventions, suggesting that prevention of initial establishment may be more effective than managing established woody vegetation. Due to the complexity of stream intermittency, there might be many physical factors involved, each of which has a moderate effect (Snelder et al. 2013). However, our results and those of Keen et al. (2023) suggest that the increase in gross water use associated with woody encroachment both inside and outside the riparian area leads to an increase in overall water use, making it more likely that woody cover decreases the amount of water that reaches streams and groundwater, regardless of the specific water source used by trees and shrubs.

## 4.2 | Temporal Dynamics of ET Driven by the Interplay of Water and Energy

PPT and discharge usually display weak correlations due to interception by plants (Costigan et al. 2015; Wine and Zou 2012). Our system is hyper-variable because average potential ET over all of the years is roughly equal to annual PPT (Acharya et al. 2017; Sadayappan et al. 2023). Thus, slightly wetter seasons or years can lead to streamflow, and modestly drier years or seasons lead to dry streams. The effect of woody ET is most strongly illustrated by our results from late summer when vegetation demand for water is high, the temperature is high, and even with periodic large storms, the streams often stop flowing.

The analysis of the excess PPT ($P_{ex}$) versus excess evaporative demand ($E_{ex}$) from 2001 to 2020 reveals additional evidence for vegetation-induced changes in the local hydrology as streamflow requires positive $P_{ex}$. The July–September period reveals the gradual transition towards increased woody vegetation within the watershed that creates more evaporative demand as indicated by a shift downward and to the left on Figure 7C. The seasonal breakdown (Figure 8) shows this pattern is most pronounced during summer (July–September) and winter (January–March) months with $E_{ex}$ decreasing most strongly during July–September over time, while spring and fall seasons exhibit more variable patterns with less clear temporal trajectories. This pattern aligns with the watershed afforestation effects on the water and energy balance following woody vegetation expansion in other watersheds (Bosch and Hewlett 1982; Zhang et al. 2001). We note this trend was evident even though we restricted the analysis to wetter years, which was necessary to avoid the problem of PPT renewing groundwater or soil moisture. The trend would be stronger if we included drier years. This trend is particularly significant given that July to September typically represents the warmest and driest part of the year.

The temporal shift of the energy and PPT balance provides substantial evidence of potential consequences of an ecosystem transition from grassland to a more woody-dominated landscape, a change that can have profound implications for biodiversity, carbon storage, and local climate regulation (Banerjee et al. 2023; Dodds et al. 2023; Ekberzade et al. 2023; Feurdean et al. 2021; Keen et al. 2024; Liu et al. 2023). The trend could be part of a positive feedback loop, where initial increases in woody vegetation alter local surface water availability, further favouring woody encroachment (Wilcox et al. 2006, 2022). This self-reinforcing process aligns with documented threshold dynamics in grassland ecosystems (Ratajczak et al. 2012; Scheffer et al. 2015), where transitions accelerate once woody cover exceeds critical thresholds. D'Odorico et al. (2012) specifically identified hydrological feedbacks as key drivers of irreversible state changes in grasslands, where woody plants modify soil moisture regimes to their advantage, further suppressing grasses. It is important to consider these vegetation-induced changes in the context of broader climate change patterns, as rising temperatures and altered PPT regimes could amplify the hydrologic effects of vegetation change.

Specific drought years (2002, 2003, 2006, 2011, 2012, 2013 and 2018) revealed a consistent pattern where low PPT coincided with decreased discharge and reduced flow days. These drought years exhibited discharge and flow day values 35%–50% lower than wet years, demonstrating how climate variability amplifies vegetation-driven hydrological changes. With projected PPT changes bringing more intense but infrequent storms that favour woody vegetation, our models suggest riparian woody cover may reach 70%–90% by 2050, potentially reducing annual discharge by 30%–50% and increasing zero-flow days by 20–40 days. Even with intensive management (annual burning and woody removal), discharge may still drop 15%–25%. Only aggressive vegetation control combined with climate mitigation could maintain near-current streamflow patterns.

While our analysis focused on flow at watershed outlets, cumulative PPT and ET can also have significant impacts on the spatial distribution of flow within watersheds (Zipper et al. 2025), indicating potential widespread ecological impacts. The compound effects of below-average PPT and increased ET demands from woody vegetation were particularly evident during these drought periods, resulting in more extensive stream drying than would be expected from PPT deficits alone in a grass-dominated system.

The structural equation model in our study showed a high degree of unexplained variance in flow days, as evidenced by the substantial flow days-flow days coefficient. This finding underscores the complex nature of flow persistence in the USGS Kings Creek watershed system and suggests that factors beyond PPT and ET play crucial roles in determining the number of flow days. For example, the karstic landscape leads to complex hydrology as various geological layers connected by intricate flow paths respond to a variable climate (Costigan et al. 2015; Gambill et al. 2024; Zipper et al. 2025).

The largely unexplained decreases in flow days highlight a key distinction in hydrological drivers. While both our ANCOVA and structural equation modelling captured PPT's positive and ET's negative effects on discharge, flow persistence remained poorly explained. This suggests that unmeasured factors such as groundwater dynamics and subsurface characteristics play crucial roles in determining flow days, representing an important area for future research (Huxman et al. 2005; Wilcox et al. 2022). Additionally, the high unexplained variance may indicate the presence of non-linear relationships or time-lagged effects that our linear model does not account for (although accounting for temporal autocorrelation could obviate this problem).

### 4.3 | How Might This Apply to Other Grasslands?

While a decrease in streamflow with increased woodiness is common, diverse responses have been observed, indicating context dependence. Alterations in streamflow patterns resulting from either woody encroachment or shifts in climate occur in diverse geographical contexts. For example, declines in streamflow occurred in encroached prairie regions, notably in Canada and the Great Plains of the United States (Starks and Moriasi 2017; Zou et al. 2018). In the North Concho catchments of Texas, an up to 70% reduction in streamflow coincided with an increase in woody cover as degraded grassland recovered to savannah grassland, and was probably related to decreased stormflows (Wilcox et al. 2008). In the karst regions of the Matese and Picentini massifs in Southern Italy, spring discharge showed a significant declining trend despite a slightly positive (though not statistically significant) trend in annual PPT, with temperature increases playing an important role in this decline. This was especially evident in the Caposele spring catchment, which is notably undisturbed by groundwater abstraction or land-use changes (Fiorillo et al. 2021).

At KPBS, groundwater storage is one of the most important sources of stream water. In a recent investigation within the N4D watershed, Hatley et al. (2023) elucidated that groundwater discharge played a predominant role, contributing over 95% to streamflow during their sampling period from April to July 2021. The study found minimal contributions from soil water (below 1%) and direct surface runoff (below 4%) to the overall streamflow dynamics. These findings are consistent with the substantive influence of groundwater in sustaining flow across various aquatic ecosystems, encompassing both small headwater non-perennial streams (Costigan et al. 2014; Hatley et al. 2023; Warix et al. 2021) and larger intermittent rivers (Vu et al. 2018; Zipper et al. 2022). The observed cyclical patterns of ET, both seasonally and annually, enhance our understanding of water and energy balance in grassland ecosystems and relate to stream drying at differing timescales (Zipper et al. 2025). This may contribute to the phenomenon observed by Swenson et al. (2024), wherein a transition to slower and deeper flow paths occurred as the USGS Kings Creek stream network dried out over the summer.

Our Kings Creek studies offer a key comparison for global grassland studies. In the Edwards Plateau's karst catchments, streamflow increased from 1925 to 2010 alongside rising woody cover, while an Oklahoma catchment (1938–1992) saw stable streamflow and increased baseflow due to riparian woody expansion and slight PPT increases ( 2015; Wine and Zou 2012). Studies from Australian grasslands found that shrub encroachment altered soil infiltration patterns, with infiltration rates varying spatially between shrub canopies and interspaces (Eldridge et al. 2015). Archer et al. (2017) observed increased dry season flow in South American grasslands following woody encroachment, attributed to reduced fire and enhanced hillslope infiltration. These global contrasts highlight how climate, hydrogeology and management shape hydrological responses, with USGS Kings Creek providing critical insights into temperate grassland stream dynamics. Researchers and land managers in various grassland territories may consider adopting similar methodologies to scrutinize the ecological repercussions of evolving ET patterns and integrate these insights into the broader context of ecosystem dynamics (Cook et al. 2020; Ryu and Hayhoe 2017).

These substantial increases in woody cover reflect broader regional trends in the Great Plains. Assessments of land cover change across Kansas show dramatic increases of 40%–60% in riparian corridors (Briggs et al. 2005). Similar patterns have been observed throughout the central Great Plains, where woody plant cover has increased by approximately 8%–15% per decade in areas without active management (Symstad and Leis 2017). The rates of woody encroachment in our more study watersheds exceed these regional averages, particularly in the 4-year burn watershed (N4D), suggesting that local factors such as topography, hydrology and specific management histories may not have been taken into account previously.

### 4.4 | Ecological and Water Yield Implications

Low and zero flow can impact various physical characteristics of stream habitats, including wetted area, maximum depth, and dissolved oxygen concentrations (Leopold and Maddock 1953). The ecological consequences are multifaceted, affecting the availability and suitability of habitats for organisms reliant on streamflow. Macroinvertebrate density and diversity, critical components of aquatic ecosystems, may experience significant reductions in diverted reaches (McKay and King 2006), posing challenges for species adapted to historical flow regimes (Maskey et al. 2022). Changes in discharge patterns also influence nutrient transport and cycling, with potential repercussions for both terrestrial and aquatic nutrient dynamics (Dodds et al. 2004; Von Schiller et al. 2011; von Schiller et al. 2017). The role of hydrology in shaping water quality is pivotal (Li 2019), with studies establishing a correlation between low streamflow and elevated concentrations of solutes in rivers and streams on a continental scale (Li et al. 2022).

While heightened riparian cover corresponds to decreased discharge, ecological processes are also influenced by riparian vegetation, including nutrient retention, sediment filtration, habitat complexity, autotrophic/heterotrophic balance in grassland streams (Stagliano and Whiles 2002) and stream biology (Vandermyde and Whiles 2015). While woody vegetation might be more efficient at sediment and nutrient removal, the tradeoff between these vegetation benefits and reduced streamflow raises crucial questions about the overall ecological balance and sustainability of the watershed.

Cascading effects of decreased discharge may extend to downstream areas, where vegetation relying on streamflow may undergo water stress, impacting growth, reproduction, and community composition (Stromberg et al. 2010). In agricultural and human contexts, the decrease in mean discharge and flow days holds significant water yield implications, potentially affecting downstream uses such as agricultural irrigation and municipal water supply. Long-term hydrological analyses of the Kansas River (which USGS Kings Creek drains to), indicate that drought-like flows are becoming more common even with relatively constant annual PPT (Putnam et al. 2008). Woody expansion in the region, combined with widespread agricultural water use, could partially explain this phenomenon. The characterization of seasonal influences on ET dynamics provides insights into the water use patterns of different vegetation types. Our assessment of hydrological effects of woody expansion suggests that woody encroachment will continue shaping water availability and demand in the watershed. Although our analysis focused on surface hydrology, groundwater dynamics play a crucial role in stream intermittency within the USGS Kings Creek watershed's merokarst geology (Sullivan et al. 2020), and will be influenced by woody encroachment as well.

Woody encroachment likely affects groundwater-surface water dynamics in Kings Creek in three key ways: (1) deep-rooted woody species, as opposed to grasses, tap groundwater, lowering water tables and reducing streamflow (Keen et al. 2022); (2) encroachment alters infiltration and subsurface flow, redistributing recharge patterns (Gambill et al. 2024); and (3) as the stream network dries, baseflow becomes critical, but increased ET from woody plants accelerates depletion, extending zero-flow periods (Swenson et al. 2024). The uncorrelated discharge-PPT pattern in the annually burned N1B watershed suggests that hydrogeological buffering, rather than immediate PPT, governs streamflow. Future studies should integrate groundwater monitoring, seasonal water table dynamics, and isotopic analyses to refine our understanding of woody encroachment's impact on intermittent streams.

## 5 | Conclusions

Our study demonstrates that the USGS Kings Creek watershed has experienced significant hydrological changes from 1982 to 2020, with an 84% decrease in daily discharge and a 55% reduction in annual flow days. These changes coincided with substantial increases in woody vegetation cover across all watersheds, ranging from a two-fold increase in annually burned areas to a sevenfold increase in areas burned every 4 years. Through structural equation modelling and seasonal analysis, we found that expanded riparian woody vegetation significantly influences stream discharge through increased ET, particularly during summer months. While our SEM showed a weaker direct relationship between ET and flow days than between ET and discharge, our results indicated that riparian woody cover was significantly associated with decreased flow days. This suggests that woody vegetation affects flow persistence through complex pathways that may not be fully captured in our structural models. Notably, this impact showed pronounced seasonal variation, with the strongest effects during summer months (July–September) when increased ET from woody vegetation combined with higher temperatures created conditions where water demand frequently exceeded availability, leading to more extensive stream drying.

This effect is amplified by rising temperatures, which showed a 1.2°C increase over the study period, and increased rates of ET. This warming rate of approximately 0.31°C per decade is consistent with broader regional warming trends across the Great Plains, where average temperatures have increased by 0.25°C–0.35°C per decade since the 1970s (Shafer et al. 2014; Tebaldi et al. 2021). However, the warming at Kings Creek is almost twice as high as the global average of approximately 0.18°C per decade over the same period (Change 2007), indicating that this grassland ecosystem may be experiencing accelerated warming compared to global means. Yearly PPT shows a slight increase but with high variability and low confidence, which also aligns with regional climate assessments showing increased PPT variability rather than consistent directional changes for the central Great Plains.

In the USGS Kings Creek watershed and similar regions, our findings indicate an increased need for adaptive management strategies to counteract ongoing vegetation changes and their hydrological impacts. These efforts may include intensified actions to maintain the historical grassland ecosystem. The observed trends provide insight into the current state of the watershed and raise critical questions about the ecosystem's future trajectory under continued climate change and vegetation shifts.

Our results emphasize the need for a more comprehensive approach to modelling flow persistence in ecohydrological systems. Future research should focus on incorporating additional variables such as soil moisture dynamics, groundwater table fluctuations, root depth distributions, karst connectivity patterns, and antecedent watershed conditions. Additionally, exploring non-linear modelling techniques and considering various spatial and temporal scales could better capture the intricate dynamics governing flow days. This finding not only highlights the complexity of eco-hydrological systems but also opens new avenues for investigating the factors that control flow persistence in intermittent streams.

While the number of studies of intermittent streams has greatly increased in the last decade, especially focused on its ecology (Allen et al. 2020; DelVecchia et al. 2022), much work is needed to understand the hydrology of intermittent streams.

Our findings could extend beyond just the USGS Kings Creek watershed, forming a foundational basis for identifying potential strategies to enhance resilience in grasslands regionally and potentially globally. Policymakers and managers, guided in part by the techniques used in this study, could potentially evaluate and predict how streams may be vulnerable to climate-induced intermittency, enabling more effective decision-making.


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### Data Availability Statement

The data that support the findings of this study are openly available in Konza Prairie LTER at https://lter.konza.ksu.edu/konza-prairie-long-term-ecological-research-lter.

### References


Abrams, M. D. 1986. "Historical Development of Gallery Forests in Northeast Kansas." *Vegetatio* 65, no. 1: 29–37.

Acharya, B. S., Y. Hao, T. E. Ochsner, and C. B. Zou. 2017. "Woody Plant Encroachment Alters Soil Hydrological Properties and Reduces Downward Flux of Water in Tallgrass Prairie." *Plant and Soil* 414, no. 1–2: 379–391. https://doi.org/10.1007/s11104-016-3138-0.

Allen, D. C., T. Datry, K. S. Boersma, et al. 2020. "River Ecosystem Conceptual Models and Non-Perennial Rivers: A Critical Review." *WIREs Water* 7, no. 5: e1473. https://doi.org/10.1002/wat2.1473.

Anadón, J. D., O. E. Sala, and F. T. Maestre. 2014. "Climate Change Will Increase Savannas at the Expense of Forests and Treeless Vegetation in Tropical and Subtropical a Mericas." *Journal of Ecology* 102, no. 6: 1363–1373. https://doi.org/10.1111/1365-2745.12325.

Archer, S. R., E. M. Andersen, K. I. Predick, S. Schwinning, R. J. Steidl, and S. R. Woods. 2017. "Woody Plant Encroachment: Causes and Consequences." In *Rangeland Systems: Processes, Management and Challenges*, 25–84. Springer International Publishing.

Banerjee, S., D. Das, H. Zhang, and R. John. 2023. "Grassland-Woodland Transitions Over Decadal Timescales in the Terai-Duar Savanna and Grasslands of the Indian Subcontinent." *Forest Ecology and Management* 530: 120764.

Bosch, J. M., and J. D. Hewlett. 1982. "A Review of Catchment Experiments to Determine the Effect of Vegetation Changes on Water Yield and Evapotranspiration." *Journal of Hydrology* 55, no. 1–4: 3–23.

Briggs, J. M., A. K. Knapp, J. M. Blair, et al. 2005. "An Ecosystem in Transition: Causes and Consequences of the Conversion of Mesic Grassland to Shrubland." *Bioscience* 55, no. 3: 243–254.

Change, I. P. O. C. 2007. "Climate Change 2007: The Physical Science Basis." *Agenda* 6, no. 7: 333.

Collins, S. L., and L. B. Calabrese. 2012. "Effects of Fire, Grazing and Topographic Variation on Vegetation Structure in Tallgrass Prairie." *Journal of Vegetation Science* 23, no. 3: 563–575. https://doi.org/10.1111/j.1654-1103.2011.01369.x.

Cook, B. I., J. S. Mankin, K. Marvel, A. P. Williams, J. E. Smerdon, and K. J. Anchukaitis. 2020. "Twenty-First Century Drought Projections in the CMIP6 Forcing Scenarios." *Earth's Future* 8, no. 6: e2019EF001461. https://doi.org/10.1029/2019EF001461.

Costigan, K. H., M. D. Daniels, and W. K. Dodds. 2015. "Fundamental Spatial and Temporal Disconnections in the Hydrology of an Intermittent Prairie Headwater Network." *Journal of Hydrology* 522: 305–316.

Costigan, K. H., M. D. Daniels, J. S. Perkin, and K. B. Gido. 2014. "Longitudinal Variability in Hydraulic Geometry and Substrate Characteristics of a Great Plains Sand-Bed River." *Geomorphology* 210: 48–58.

Dahlman, R. C., and C. L. Kucera. 1968. "Tagging Native Grassland Vegetation With Carbon-14." *Ecology* 49, no. 6: 1199–1203. https://doi.org/10.2307/1934516.

Datry, T., S. T. Larned, and K. Tockner. 2014. "Intermittent Rivers: A Challenge for Freshwater Ecology." *Bioscience* 64, no. 3: 229–235.

Datry, T., A. Truchy, J. D. Olden, et al. 2023. "Causes, Responses, and Implications of Anthropogenic Versus Natural Flow Intermittence in River Networks." *Bioscience* 73, no. 1: 9–22.

Davenport, F. V., and N. S. Diffenbaugh. 2021. "Using Machine Learning to Analyze Physical Causes of Climate Change: A Case Study of U.S. Midwest Extreme Precipitation." *Geophysical Research Letters* 48, no. 15: e2021GL093787. https://doi.org/10.1029/2021GL093787.

DelVecchia, A. G., M. Shanafield, M. A. Zimmer, et al. 2022. "Reconceptualizing the Hyporheic Zone for Nonperennial Rivers and Streams." *Freshwater Science* 41, no. 2: 167–182. https://doi.org/10.1086/720071.

Dodds, W. K. 1997. "Distribution of Runoff and Rivers Related to Vegetative Characteristics, Latitude, and Slope: A Global Perspective." *Journal of the North American Benthological Society* 16, no. 1: 162–168. https://doi.org/10.2307/1468248.

Dodds, W. K., K. Gido, M. R. Whiles, K. M. Fritz, and W. J. Matthews. 2004. "Life on the Edge: The Ecology of Great Plains Prairie Streams." *Bioscience* 54, no. 3: 205–216.

Dodds, W. K., Z. Ratajczak, R. M. Keen, et al. 2023. "Trajectories and State Changes of a Grassland Stream and Riparian Zone After a Decade of Woody Vegetation Removal." *Ecological Applications* 33, no. 4: e2830. https://doi.org/10.1002/eap.2830.

Dodds, W. K., C. T. Robinson, E. E. Gaiser, et al. 2012. "Surprises and Insights From Long-Term Aquatic Data Sets and Experiments." *Bioscience* 62, no. 8: 709–721.

D'Odorico, P., G. S. Okin, and B. T. Bestelmeyer. 2012. "A Synthetic Review of Feedbacks and Drivers of Shrub Encroachment in Arid Grasslands." *Ecohydrology* 5, no. 5: 520–530. https://doi.org/10.1002/eco.259.

Ekberzade, B., Yetemen, O., Lutfi Sen, O., & Nuzhet Dalfes, H. (2023). Transitioning: The Role of Disturbances on Instigating Cross-Overs of Vegetation Zones (a Biome Perspective). *EGU General Assembly Conference Abstracts*, EGU-141. https://ui.adsabs.harvard.edu/abs/2023EGUGA..25..141E/abstract.

Eldridge, D. J., L. Wang, and M. Ruiz-Colmenero. 2015. "Shrub Encroachment Alters the Spatial Patterns of Infiltration." *Ecohydrology* 8, no. 1: 83–93. https://doi.org/10.1002/eco.1490.

Eng K. Carlisle D. Grantham T. E. Wolock D. M. Eng R. L. 2019 Severity and Extent of Alterations to Natural Streamflow Regimes Based on Hydrologic Metrics in the Conterminous United States, 1980–2014 US Geological Survey. https://pubs.usgs.gov/publication/sir20195001.

Feurdean, A., R. Grindean, G. Florescu, et al. 2021. "The Transformation of the Forest Steppe in the Lower Danube Plain of Southeastern Europe: 6000 Years of Vegetation and Land Use Dynamics." *Biogeosciences* 18, no. 3: 1081–1103.

Fiorillo, F., G. Leone, M. Pagnozzi, and L. Esposito. 2021. "Long-Term Trends in Karst Spring Discharge and Relation to Climate Factors and Changes." *Hydrogeology Journal* 29, no. 1: 347–377. https://doi.org/10.1007/s10040-020-02265-0.

Gambill I. Zipper S. Kirk M. Seybold E. 2024 Exploring Drivers of Groundwater Recharge at Konza Prairie (Flint Hills Region, Kansas, USA) Using Transfer Function Noise Models. https://www.kgs.ku.edu/Publications/OFR/2024/OFR2024-6.pdf.

Hammond, J. C., M. Zimmer, M. Shanafield, et al. 2021. "Spatial Patterns and Drivers of Nonperennial Flow Regimes in the Contiguous United States." *Geophysical Research Letters* 48, no. 2: e2020GL090794. https://doi.org/10.1029/2020GL090794.

Hargreaves, G. H., and R. G. Allen. 2003. "History and Evaluation of Hargreaves Evapotranspiration Equation." *Journal of Irrigation and Drainage Engineering* 129, no. 1: 53–63. https://doi.org/10.1061/(ASCE)0733-9437(2003)129:1(53).

Hargreaves, G. L., G. H. Hargreaves, and J. P. Riley. 1985. "Irrigation Water Requirements for Senegal River Basin." *Journal of Irrigation and Drainage Engineering* 111, no. 3: 265–275. https://doi.org/10.1061/(ASCE)0733-9437(1985)111:3(265).

Hatley, C. M., B. Armijo, K. Andrews, C. Anhold, J. B. Nippert, and M. F. Kirk. 2023. "Intermittent Streamflow Generation in a Merokarst Headwater Catchment." *Environmental Science: Advances* 2, no. 1: 115–131.

Hervé-Fernández, P., R. Muñoz-Arriagada, C. Glucevic-Almonacid, L. Bahamonde-Vidal, and S. Radic-Schilling. 2023. "Influence of Rangeland Land Cover on Infiltration Rates, Field-Saturated Hydraulic Conductivity, and Soil Water Repellency in Southern Patagonia." *Rangeland Ecology & Management* 90: 92–100.

Hintz, H. W. 1999. "Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie." *Journal of Environmental Quality* 28, no. 5: 1685.

Hutchinson, S. L., J. K. Koelliker, and A. K. Knapp. 2008. "Development of Water Usage Coefficients for A Fully Watered Tallgrass Prairie." *Transactions of the ASABE* 51, no. 1: 153–159.

Huxman, T. E., B. P. Wilcox, D. D. Breshears, et al. 2005. "Ecohydrological Implications of Woody Plant Encroachment." *Ecology* 86, no. 2: 308–319. https://doi.org/10.1890/03-0583.

Jaeger, K. L., J. D. Olden, and N. A. Pelland. 2014. "Climate Change Poised to Threaten Hydrologic Connectivity and Endemic Fishes in Dryland Streams." *Proceedings of the National Academy of Sciences* 111, no. 38: 13894–13899. https://doi.org/10.1073/pnas.1320890111.

Keen, R. M., J. B. Nippert, P. L. Sullivan, et al. 2023. "Impacts of Riparian and Non-Riparian Woody Encroachment on Tallgrass Prairie Ecohydrology." *Ecosystems* 26, no. 2: 290–301. https://doi.org/10.1007/s10021-022-00756-7.

Keen, R. M., K. Sadayappan, K. M. Jarecke, et al. 2024. "Unexpected Hydrologic Response to Ecosystem State Change in Tallgrass Prairie." *Journal of Hydrology* 643: 131937.

Keen, R. M., S. L. Voelker, S.-Y. S. Wang, et al. 2022. "Changes in Tree Drought Sensitivity Provided Early Warning Signals to the California Drought and Forest Mortality Event." *Global Change Biology* 28, no. 3: 1119–1132. https://doi.org/10.1111/gcb.15973.

Krabbenhoft, C. A., G. H. Allen, P. Lin, et al. 2022. "Assessing Placement Bias of the Global River Gauge Network." *Nature Sustainability* 5, no. 7: 586–592.

Larson, D. M., W. K. Dodds, and A. M. Veach. 2019. "Removal of Woody Riparian Vegetation Substantially Altered a Stream Ecosystem in an Otherwise Undisturbed Grassland Watershed." *Ecosystems* 22, no. 1: 64–76. https://doi.org/10.1007/s10021-018-0252-2.

Leigh, C., A. J. Boulton, J. L. Courtwright, et al. 2016. "Ecological Research and Management of Intermittent Rivers: An Historical Review and Future Directions." *Freshwater Biology* 61, no. 8: 1181–1199. https://doi.org/10.1111/fwb.12646.

Leopold, L. B., and T. Maddock. 1953. *The Hydraulic Geometry of Stream Channels and Some Physiographic Implications*. Vol. 252. US Government Printing Office.

Li, L. 2019. "Watershed Reactive Transport." *Reviews in Mineralogy and Geochemistry* 85, no. 1: 381–418.

Li, L., B. Stewart, W. Zhi, et al. 2022. "Climate Controls on River Chemistry." *Earth's Future* 10, no. 6: e2021EF002603. https://doi.org/10.1029/2021EF002603.

Liu, H., C. Banfield, S. I. Gomes, M. Gube, A. Weig, and J. Pausch. 2023. "Vegetation Transition From Meadow to Forest Reduces Priming Effect on SOM Decomposition." *Soil Biology and Biochemistry* 184: 109123.

Maskey, M. L., G. Facincani Dourado, A. M. Rallings, D. E. Rheinheimer, J. Medellín-Azuara, and J. H. Viers. 2022. "Assessing Hydrological Alteration Caused by Climate Change and Reservoir Operations in the San Joaquin River Basin, California." *Frontiers in Environmental Science* 10: 765426.

McCabe, G. J., and D. M. Wolock. 2002. "Trends and Temperature Sensitivity of Moisture Conditions in the Conterminous United States." *Climate Research* 20, no. 1: 19–29.

McKay, S. F., and A. J. King. 2006. "Potential Ecological Effects of Water Extraction in Small, Unregulated Streams." *River Research and Applications* 22, no. 9: 1023–1037. https://doi.org/10.1002/rra.958.

Messager, M. L., B. Lehner, C. Cockburn, et al. 2021. "Global Prevalence of Non-Perennial Rivers and Streams." *Nature* 594, no. 7863: 391–397.

Nippert, J. B., and A. K. Knapp. 2007. "Soil Water Partitioning Contributes to Species Coexistence in Tallgrass Prairie." *Oikos* 116, no. 6: 1017–1029. https://doi.org/10.1111/j.0030-1299.2007.15630.x.

O'Keefe, K., D. M. Bell, K. A. McCulloh, and J. B. Nippert. 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, no. 2: e2019JG005446. https://doi.org/10.1029/2019JG005446.

Perkin, J. S., K. B. Gido, J. A. Falke, et al. 2017. "Groundwater Declines Are Linked to Changes in Great Plains Stream Fish Assemblages." *Proceedings of the National Academy of Sciences* 114, no. 28: 7373–7378. https://doi.org/10.1073/pnas.1618936114.

Price, A. N., M. A. Zimmer, A. Bergstrom, et al. 2024. "Biogeochemical and Community Ecology Responses to the Wetting of Non-Perennial Streams." *Nature Water* 2, no. 9: 815–826.

Putnam, J. E., Perry, C. A., & Wolock, D. M. 2008. Hydrologic Droughts in Kansas: Are They Becoming Worse? US Department of the Interior, US Geological Survey. https://pubs.usgs.gov/fs/2008/3034/pdf/fs2008-3034.pdf.

Ratajczak, Z., J. B. Nippert, and S. L. Collins. 2012. "Woody Encroachment Decreases Diversity Across North American Grasslands and Savannas." *Ecology* 93, no. 4: 697–703. https://doi.org/10.1890/11-1199.1.

Rodgers, K., V. Roland, A. Hoos, E. Crowley-Ornelas, and R. Knight. 2020. "An Analysis of Streamflow Trends in the Southern and Southeastern US From 1950–2015." *Water* 12, no. 12: 3345.

Ryu, J.-H., and K. Hayhoe. 2017. "Observed and CMIP5 Modeled Influence of Large-Scale Circulation on Summer Precipitation and Drought in the South-Central United States." *Climate Dynamics* 49, no. 11–12: 4293–4310. https://doi.org/10.1007/s00382-017-3534-z.

Sadayappan, K., R. Keen, K. M. Jarecke, et al. 2023. "Drier Streams Despite a Wetter Climate in Woody-Encroached Grasslands." *Journal of Hydrology* 627: 130388.

Sauquet, E., M. Shanafield, J. C. Hammond, C. Sefton, C. Leigh, and T. Datry. 2021. "Classification and Trends in Intermittent River Flow Regimes in Australia, Northwestern Europe and USA: A Global Perspective." *Journal of Hydrology* 597: 126170.

Scheffer, M., S. R. Carpenter, V. Dakos, and E. H. Van Nes. 2015. "Generic Indicators of Ecological Resilience: Inferring the Chance of a Critical Transition." *Annual Review of Ecology, Evolution, and Systematics* 46, no. 1: 145–167. https://doi.org/10.1146/annurev-ecolsys-112414-054242.

Shafer, M., D. Ojima, J. M. Antle, et al. 2014. "Ch. 19: Great Plains." In *Climate Change Impacts in the United States: The Third National Climate Assessment*, edited by J. M. Melillo, T. C. Richmond, and G. W. Yohe, 441–461. U.S. Global Change Research Program.

Shanafield, M., S. Godsey, T. Datry, et al. 2020. *Science Gets Up to Speed on Dry Rivers*. Vol. 101. Eos. https://par.nsf.gov/biblio/10252961.

Snelder, T. H., T. Datry, N. Lamouroux, et al. 2013. "Regionalization of Patterns of Flow Intermittence From Gauging Station Records." *Hydrology and Earth System Sciences* 17, no. 7: 2685–2699.

Stagliano, D. M., and M. R. Whiles. 2002. "Macroinvertebrate Production and Trophic Structure in a Tallgrass Prairie Headwater Stream." *Journal of the North American Benthological Society* 21, no. 1: 97–113. https://doi.org/10.2307/1468303.

Starks, P. J., and D. N. Moriasi. 2017. "Impact of Eastern Redcedar Encroachment on Stream Discharge in the North Canadian River Basin." *Journal of Soil and Water Conservation* 72, no. 1: 12–25.

Steward, D. R., X. Yang, S. Y. Lauwo, S. A. Staggenborg, G. L. Macpherson, and S. M. Welch. 2011. "From Precipitation to Groundwater Baseflow in a Native Prairie Ecosystem: A Regional Study of the Konza LTER in the Flint Hills of Kansas, USA." *Hydrology and Earth System Sciences* 15, no. 10: 3181–3194.

Stromberg, J. C., S. J. Lite, and M. D. Dixon. 2010. "Effects of Stream Flow Patterns on Riparian Vegetation of a Semiarid River: Implications for a Changing Climate." *River Research and Applications* 26, no. 6: 712–729. https://doi.org/10.1002/rra.1272.

Sullivan, P. L., M. W. Stops, G. L. Macpherson, L. Li, D. R. Hirmas, and W. K. Dodds. 2019. "How Landscape Heterogeneity Governs Stream Water Concentration-Discharge Behavior in Carbonate Terrains (Konza Prairie, USA)." *Chemical Geology* 527: 118989.

Sullivan, P. L., C. Zhang, M. Behm, F. Zhang, and G. L. Macpherson. 2020. "Toward a New Conceptual Model for Groundwater Flow in Merokarst Systems: Insights From Multiple Geophysical Approaches." *Hydrological Processes* 34, no. 24: 4697–4711. https://doi.org/10.1002/hyp.13898.

Swenson, L. J., S. Zipper, D. M. Peterson, et al. 2024. "Changes in Water Age During Dry-Down of a Non-Perennial Stream." *Water Resources Research* 60, no. 1: e2023WR034623. https://doi.org/10.1029/2023WR034623.

Symstad, A. J., and S. A. Leis. 2017. "Woody Encroachment in Northern Great Plains Grasslands: Perceptions, Actions, and Needs." *Natural Areas Journal* 37, no. 1: 118–127.

Tebaldi, C., K. Debeire, V. Eyring, et al. 2021. "Climate Model Projections From the Scenario Model Intercomparison Project (ScenarioMIP) of CMIP6." *Earth System Dynamics* 12, no. 1: 253–293.

Tomer, M. D., and K. E. Schilling. 2009. "A Simple Approach to Distinguish Land-Use and Climate-Change Effects on Watershed Hydrology." *Journal of Hydrology* 376, no. 1–2: 24–33.

Tramblay, Y., A. Rutkowska, E. Sauquet, et al. 2021. "Trends in Flow Intermittence for European Rivers." *Hydrological Sciences Journal* 66, no. 1: 37–49. https://doi.org/10.1080/02626667.2020.1849708.

Vandermyde, J. M., and M. R. Whiles. 2015. "Effects of Experimental Forest Removal on Macroinvertebrate Production and Functional Structure in Tallgrass Prairie Streams." *Freshwater Science* 34, no. 2: 519–534. https://doi.org/10.1086/680442.

Veach, A. M., W. K. Dodds, and A. Skibbe. 2014. "Fire and Grazing Influences on Rates of Riparian Woody Plant Expansion Along Grassland Streams." *PLoS ONE* 9, no. 9: e106922.

Veach, A. M., W. K. Dodds, and A. Skibbe. 2015. "Correction: Fire and Grazing Influences on Rates of Riparian Woody Plant Expansion Along Grassland Streams." *PLoS ONE* 10, no. 5: e0129409.

Vero, S. E., G. L. Macpherson, P. L. Sullivan, et al. 2018. "Developing a Conceptual Framework of Landscape and Hydrology on Tallgrass Prairie: A Critical Zone Approach." *Vadose Zone Journal* 17, no. 1: 1–11. https://doi.org/10.2136/vzj2017.03.0069.

Vinton, M. A. 1999. "Review of Grassland Dynamics: Long-Term Ecological Research in Tallgrass Prairie Edited by Knapp, Alan K., Briggs, John M., Hartnett, David C., and Collins, Scott L." *Great Plains Research: A Journal of Natural and Social Sciences* 9: 470.

Volder, A., D. D. Briske, and M. G. Tjoelker. 2013. "Climate Warming and Precipitation Redistribution Modify Tree–Grass Interactions and Tree Species Establishment in a Warm-Temperate Savanna." *Global Change Biology* 19, no. 3: 843–857. https://doi.org/10.1111/gcb.12068.

Von Schiller, D., V. Acuña, D. Graeber, et al. 2011. "Contraction, Fragmentation and Expansion Dynamics Determine Nutrient Availability in a Mediterranean Forest Stream." *Aquatic Sciences* 73, no. 4: 485–497. https://doi.org/10.1007/s00027-011-0195-6.

von Schiller, D., S. Bernal, C. N. Dahm, and E. Martí. 2017. "Nutrient and Organic Matter Dynamics in Intermittent Rivers and Ephemeral Streams." In *Intermittent Rivers and Ephemeral Streams*, edited by C. N. Dahm, 135–160. Elsevier. https://www.sciencedirect.com/science/article/pii/B9780128038352000061.

Vu, H. M., M. Shanafield, and O. Batelaan. 2018. "Flux Dynamics at the Groundwater-Surface Water Interface in a Tropical Catchment." *Limnologica* 68: 36–45.

Wang, J., X. Xiao, Y. Zhang, et al. 2018. "Enhanced Gross Primary Production and Evapotranspiration in Juniper-Encroached Grasslands." *Global Change Biology* 24, no. 12: 5655–5667. https://doi.org/10.1111/gcb.14441.

Warix, S. R., S. E. Godsey, K. A. Lohse, and R. L. Hale. 2021. "Influence of Groundwater and Topography on Stream Drying in Semi-Arid Headwater Streams." *Hydrological Processes* 35, no. 5: e14185. https://doi.org/10.1002/hyp.14185.

Wilcox, B. P., S. Basant, H. Olariu, and P. A. Leite. 2022. "Ecohydrological Connectivity: A Unifying Framework for Understanding How Woody Plant Encroachment Alters the Water Cycle in Drylands." *Frontiers in Environmental Science* 10: 934535.

Wilcox, B. P., Y. Huang, and J. W. Walker. 2008. "Long-Term Trends in Streamflow From Semiarid Rangelands: Uncovering Drivers of Change." *Global Change Biology* 14, no. 7: 1676–1689. https://doi.org/10.1111/j.1365-2486.2008.01578.x.

Wilcox, B. P., M. K. Owens, W. A. Dugas, D. N. Ueckert, and C. R. Hart. 2006. "Shrubs, Streamflow, and the Paradox of Scale." *Hydrological Processes* 20, no. 15: 3245–3259. https://doi.org/10.1002/hyp.6330.

Wine, M. L., and C. B. Zou. 2012. "Long-Term Streamflow Relations With Riparian Gallery Forest Expansion Into Tallgrass Prairie in the Southern Great Plains, USA." *Forest Ecology and Management* 266: 170–179.

Zhang, L., W. R. Dawes, and G. R. Walker. 2001. "Response of Mean Annual Evapotranspiration to Vegetation Changes at Catchment Scale." *Water Resources Research* 37, no. 3: 701–708. https://doi.org/10.1029/2000WR900325.

Zimmer, M. A., K. E. Kaiser, J. R. Blaszczak, et al. 2020. "Zero or Not? Causes and Consequences of Zero-Flow Stream Gage Readings." *WIREs Water* 7, no. 3: e1436. https://doi.org/10.1002/wat2.1436.

Zipper, S., I. Popescu, K. Compare, C. Zhang, and E. C. Seybold. 2022. "Alternative Stable States and Hydrological Regime Shifts in a Large Intermittent River." *Environmental Research Letters* 17, no. 7: 074005.

Zipper, S., C. T. Wheeler, D. M. Peterson, S. C. Cook, S. E. Godsey, and K. Aho. 2025. "STICr: An Open-Source Package and Workflow for Stream Temperature, Intermittency, and Conductivity (STIC) Data." *Environmental Modelling & Software* 106484: 106484.

Zipper, S. C., J. C. Hammond, M. Shanafield, et al. 2021. "Pervasive Changes in Stream Intermittency Across the United States." *Environmental Research Letters* 16, no. 8: 084033.

Zou, C. B., D. J. Turton, R. E. Will, D. M. Engle, and S. D. Fuhlendorf. 2014. "Alteration of Hydrological Processes and Streamflow With Juniper (*Juniperus virginiana*) Encroachment in a Mesic Grassland Catchment: Alteration of Hydrological Processes After Juniper Encroachment." *Hydrological Processes* 28, no. 26: 6173–6182. https://doi.org/10.1002/hyp.10102.

Zou, C. B., D. Twidwell, C. H. Bielski, et al. 2018. "Impact of Eastern Redcedar Proliferation on Water Resources in the Great Plains USA—Current State of Knowledge." *Water* 10, no. 12: 1768.

### Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Table S1:** Regression analysis of USGS stream gage yearly mean discharge as a function of year. **Table S2:** Regression analysis of USGS stream gage daily mean log10 discharge as a function of year **Table S3:** Regression analysis of USGS stream gage number of flow days by year as the independent variables. **Table S4:** Offset the USGS daily log10 discharge data by the periods from 10 days up to 90 days to estimate the autocorrelation period. ** Correlation $p<0.01$ (2-tailed). * Correlation $p<0.05$ level (2-tailed). $n=15{,}349$ **Table S5:** Precipitation at Konza Prairie Biological Station as a function of the season as an independent categorical variable and year as a continuous variable. R Squared = 0.554 (Adjusted R Squared = 0.532) **Table S6:** Temperature at Konza Prairie Biological Station as a function of the season as an independent categorical variable and year as a continuous variable. R Squared = 0.976 (Adjusted R Squared = 0.975) **Table S7:** ANCOVA for log10 discharge at LTER watersheds (N4D, N2B, and N1B) as a function of Season (categorical) and site (N4D, N2B, and N1B) with continuous variables of temperature, precipitation, and riparian cover. R Squared = 0.585 (Adjusted R Squared = 0.567) **Table S8:** eco70108-sup-0001-Supplementary_Material.docx.: ANCOVA for the number of flow days at LTER watersheds (N4D, N2B, and N1B) as a function of Season (categorical) and site (N4D, N2B, and N1B) with continuous variables of temperature, precipitation, and riparian cover. R Squared = 0.486 (Adjusted R Squared = 0.463) **Table S9:** Pearson Correlation for USGS Kings Creek log10 discharge and associated variables. From 1982 to 2020. **. Indicates that correlation is significant at the 0.01 level (2-tailed) where *. Indicates correlation is significant at the 0.05 level (2-tailed). Mean daily temperature (Temp), log10 discharge, Number of flow days (flow days), and total precipitation (Precip) within each season. The riparian cover is the average of the three LTER watersheds. The discharge and riparian cover were log-transformed. $N=39$. **Table S10:** Pearson Correlation for LTER watershed N4D log10 discharge and associated variables. From 1985 to 2020. **. indicates that correlation is significant at the 0.01 level (2-tailed) where *. indicates correlation is significant at the 0.05 level (2-tailed). Variables are similar to Table 2. $N=34$ **Table S11:** Pearson Correlation for LTER watershed N2B log10 discharge and associated variables. From 1987 to 2020. **. indicates that correlation is significant at the 0.01 level (2-tailed) where *. indicates correlation is significant at the 0.05 level (2-tailed). Variables are the same to table 2. $N=34$ **Table S12:** Pearson Correlation for LTER watershed N1B log10 discharge and associated variables. From 1987 to 2020. **. indicates that the correlation is significant at the 0.01 level (2-tailed). Variables are same as table 2. $N=34$ **Table S13:** ANCOVA for discharge at USGS Kings Creek gage as a function of Season (categorical) with continuous variables of temperature, precipitation, and riparian cover. R Squared = 0.586 (Adjusted R Squared = 0.528). **Table S14:** ANCOVA for the number of flow days at USGS Kings Creek gage as a function of Season (categorical) with continuous variables of temperature, precipitation, and riparian cover. R Squared = 0.412 (Adjusted R Squared = 0.330) **Table S15:** ANCOVA for the whole watershed grass ET (mm/season) at USGS Kings Creek gage as a function of Season (categorical) with continuous variables of year. R Squared = 0.961 (Adjusted R Squared = 0.957. **Table S16:** ANCOVA for the whole watershed grass ET and riparian area woody cover (mm/season) at USGS Kings Creek gage as a function of Season (categorical) with continuous variables of year. R Squared = 0.962 (Adjusted R Squared = 0.958). **Table S17:** ANCOVA for whole watershed grass ET including whole watershed total prop wood (mm/season) at USGS Kings Creek gage as a function of Season (categorical) with continuous variables of year. R Squared = 0.962 (Adjusted R Squared = 0.958). **Figure S1:** Long-Term Decline in Kings Creek Discharge (1987–2020) via 5-Year Moving Average