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Research papers

Drier streams despite a wetter climate in woody-encroached grasslands

Kayalvizhi Sadayappan [a], Rachel Keen [b], Karla M. Jarecke [c], Victoria Moreno [c], Jesse B. Nippert [b], Matthew F. Kirk [d], Pamela L. Sullivan [c], Li Li [a,*]

[a] Department of Civil and Environmental Engineering, The Pennsylvania State University, University Park, PA, USA
[b] Division of Biology, Kansas State University, Manhattan, KS, USA
[c] College of Earth, Ocean, and Atmospheric Sciences, Oregon State University, Corvallis, OR, USA
[d] Department of Geology, Kansas State University, Manhattan, KS, USA

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ABSTRACT

Grasslands, covering 40% of ice-free Earth surface, are experiencing woody encroachment globally. The hydrological impacts of woody encroachment are highly uncertain because they are compounded by the concurrent influence of climate change. Here we ask the questions 1) *How water balance (evapotranspiration* versus *streamflow) and streamflow partitioning (into surface runoff and subsurface flows) evolve over time in woody-encroached grasslands?* 2) *What is the relative influence of climate change and woody encroachment?* We used the hydrology model HBV-light and decades of hydrometeorological and streamflow data from two intermittent streams draining catchments with different degrees of woody encroachment at the Konza Prairie, Kansas, US. Results indicate that both streams have become drier and have experienced more hydrological droughts over time, more so in the substantially encroached site, with increasing evapotranspiration despite a wetter climate. In contrast, a modelled hypothetical "Climate Only" scenario without woody encroachment suggests streamflow would have increased under climate change alone. Moreover, results suggest that flow paths have deepened with increasing fractions of deeper groundwater flow in the substantially encroached site. These findings raise questions about mechanisms of these changes and commonality of drier streams in a wetter climate in woody-encroached areas and beyond. Answers to these questions can have far-reaching implications for the occurrence of droughts, water availability, water quality, and ecosystem health.

1. Introduction

Grasslands cover 30 % of the Earth's surface (40 % of ice-free land) and are responsible for ~ 20 % of global runoff (Dodds, 1997). The hydrology of grasslands is heavily influenced by vegetation cover and climate. Woody encroachment, or the expansion of woody cover, is taking place in grasslands worldwide (Ratajczak et al., 2012; Stevens et al., 2017; Van Auken, 2009). North American grasslands, for example, are experiencing an annual increase in woody cover ranging from 0.1 % to 2.3 %, with the highest rates in the Central Great Plains (Barger et al., 2011). At the same time, temperatures and precipitation patterns in these grasslands have also been changing in a warming climate. The extent to which woody encroachment versus climate change is affecting water balance and flow paths in these grasslands however is highly uncertain.

Different vegetation species vary in their water uptake strategies and rooting characteristics (Jackson et al., 1996; Vico et al., 2015), and therefore can alter water balance (evapotranspiration and streamflow) and flow paths differently. Woody species, for instance, tend to use more water than grasses and can access deeper water by growing deeper roots (Caterina et al., 2014; Jackson et al., 1996; Nippert and Knapp, 2007). Roots create 70 % of macropores (0.3 mm or greater in diameter) that are responsible for substantial soil water flow (Beven and Germann, 2013; Wilson and Luxmoore, 1988). Most lateral flow from soil occurs at the depth of greatest root channel abundance (Whipkey, 1965). Grasses with more lateral roots in shallow soils than woody species can promote more shallow lateral flow (Jackson et al., 1996; Nippert et al., 2012). In contrast, deeper and coarser woody roots can create continuous macropore networks that extend deeper (Gaiser, 1952; Hu et al., 2020; Li et al., 2013), possibly penetrating bedrock (Ghestem et al., 2011; Roering et al., 2010), thereby enhancing recharge (Wilcox and Huang, 2010) and contributing to deeper lateral groundwater flow (Laine-Kaulio et al., 2015).

At the catchment scale, woody encroachment has been observed to

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* Corresponding author.
E-mail address: lili@engr.psu.edu (L. Li).

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either increase or decrease streamflow (Hao et al., 2019; Kishawi et al., 2023; Schreiner-McGraw et al., 2020; Wilcox and Huang, 2010; Wine and Zou, 2012). These different responses possibly depend on the spatial arrangement of vegetation patches and bare soil patches above ground and the characteristics of subsurface flow paths (Huxman et al., 2005; Wilcox et al., 2022). In semi-arid or arid areas such as the Sonoran Desert, increased woody cover along with the development of bare soil patches (xerification) have been observed to reduce soil moisture and hydraulic conductivity, reduce streamflow during small rainfall events but increase streamflow during large events (Pierini et al., 2014). In the Great Plains, eastern redcedar (*Juniperus virginiana*) encroachment has been associated with elevated evapotranspiration and reduced streamflow from catchment to basin scales (Kishawi et al., 2022; Qiao et al., 2015; Starks and Moriasi, 2017). In addition, woody encroachment has been found to change streamflow generation mechanisms. Woody encroachment can change main overland flow generation mechanism from saturation excess to infiltration excess, thereby decreasing overland flow except during intense storms (Qiao et al., 2017). In South Concho catchments in Texas, base flow was observed to increase with woody encroachment, indicating enhanced groundwater recharge despite decreasing streamflow (Wilcox et al., 2008a).

Concurrent to woody encroachment, a changing climate presents another disturbance that can alter hydrology. Increasing precipitation has elevated streamflow in the Missouri river basin (Ahiablame et al., 2017), Midwest, and high plains of the USA (Xu et al., 2013). Higher evapotranspiration due to warmer climate can reduce streamflow especially in summer (Das et al., 2011), exacerbate the severity of hydrological droughts (Overpeck and Udall, 2020), reduce groundwater recharge (Ayers et al., 2022; Meixner et al., 2016) and possibly decouple groundwater-surface water interactions. Climate change can additionally affect the relative importance of water flow paths contributing to streamflow (Niraula et al., 2017; Nyenje and Batelaan, 2009). For instance, overland flow has been projected to increase under more frequent extreme rainfall events expected in the future (Choi, 2008; Napoli et al., 2017; Price, 2011). Drier climate can promote macropore formation, magnifying saturated soil hydraulic conductivity (Hirmas et al., 2018) and promoting deeper flow paths (Sullivan et al., 2022).

Most grasslands experience the convoluted impacts of woody encroachment and climate change, challenging the differentiation of their relative influence on hydrology. In an Oklahoma grassland, for example, woody encroachment in riparian area together with increasing precipitation challenge the detection of the cause of streamflow trend even with a 50-year long record (Wine and Zou, 2012). Vegetation-climate feedbacks further complicate our ability to disentangle the relative effects of land cover and climate change, as increasing atmospheric carbon dioxide (CO_2) and temperatures can reduce plant transpiration, thereby increasing streamflow despite woody encroachment (Kishawi et al., 2022; Novick et al., 2016).

Here we ask the questions: *How water balance (evapotranspiration* versus *streamflow) and streamflow partitioning (into surface runoff, shallow soil water flow, and deeper groundwater flow) evolve in woody-encroached grasslands?* and *what is the relative influence of climate change and woody encroachment on streamflow generation?* We hypothesize that 1) woody encroachment outweighs climate change in influencing catchment hydrology by reducing streamflow and increasing evapotranspiration; 2) woody encroachment promotes deeper groundwater flow.

We test these hypotheses using 35 years of hydrometeorology and streamflow data from two intermittent, woody-encroached streams (N01B and N04D) in a mesic tallgrass prairie in Konza Prairie Biological Station (KPBS, 35 km^2, hereafter Konza Prairie), a Long-Term Ecological Research (LTER) site in Kansas, USA. We also leverage a data-informed hydrology model that can be run under various scenarios to differentiate the impacts of climate change versus woody encroachment. These streams have been subject to both woody encroachment and a changing climate in the Central Great Plains. Total annual precipitation in this area has been projected to have no change or slight increases but precipitation is expected to become more variable with larger rain events shifting toward winter and / or spring (IPCC et al., 2021; USGCRP et al., 2018). Intermittent streams are vulnerable but important ecosystems, and are highly sensitive to environmental disturbances (Jaeger et al., 2014). They are estimated to comprise more than 50 % of global stream length (Datry et al., 2014; Shanafield et al., 2021), and have exhibited longer no-flow periods since 1980 (Zipper et al., 2021).

2. Methods

2.1. Study site

Konza Prairie, located in the Flint Hills region of Kansas (39°05′N, 96°35′W), has a midwestern continental climate with warm, wet summers and cold, dry winters (Fig. 1). The mean annual precipitation is 811 mm (1983–2020), and the mean annual temperature is 11.7 °C (1983–2020). The precipitation is highly variable, with 75 % occurring during the growing season from April to October (Hayden, 1998). Konza Prairie is situated on a highly complex mero-karst bedrock with repeating layers of limestone (1–2 m) and mudstone (2–4 m) (Macpherson, 1996), highly heterogeneous as indicated by geophysical investigations (Sullivan et al., 2020). The soil is silty clay loam with traces of calcite. The soil is thin and rocky in uplands but can be as thick as 1–2 m near streams (Ransom et al., 1998). Tracer tests have indicated that Konza Prairie has deep groundwater flow and inter-basin flow, but their magnitudes have not been quantified (Barry, 2018).

The vegetation is primarily warm-season grasses, including big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*), Indian grass (*Sorghastrum nutans*), and switchgrass (*Panicum virgatum*). The riparian corridor has woody species such as American elm (*Ulmus americana*), honey locust (*Gleditsia triacanthos*), bur oak (*Quercus macrocarpa*), chinquapin oak (*Quercus muehlenbergii*), hackberry (*Celtis occidentalis*) and redbud (*Cercis canadensis*) (Keen et al., 2022; Reisinger et al., 2013). The native woody vegetation historically confined to riparian corridors have been expanding in Konza Prairie. Clonal shrub species, including roughleaf dogwood (*Cornus drummondii*), smooth sumac (*Rhus glabra*), and American plum (*Prunus americana*), occurring in riparian zone as well as interspersed across the grassland as shrub islands, have also been spreading rapidly.

Since 1977, Konza Prairie has been divided into sub-catchments and subjected to different management regimes in terms of fire frequency, fire season, and grazing. Konza Prairie has been experiencing woody encroachment, especially in sub-catchments with infrequent fires (Briggs et al., 2005; Ratajczak et al., 2014; Veach et al., 2014). The shrub cover has increased by up to 60 % in sub-catchments with 4-year and 20-year fire intervals (Ratajczak et al., 2014). While riparian zones are more resistant to fires than upland due to their wetter condition, an aerial study still showed that catchments with more frequent fires have experienced less riparian woody expansion. For example, percent woody cover in riparian zone (30 m around streams) increased from 40 % in 1985 to 57 % in 2010 in a catchment burnt annually but from 52 % to 90 % in a catchment burnt once every 20 years (Veach et al., 2014). While frequent fires control expansion of both upland and riparian woody cover, even annual burning does not stop or reverse woody encroachment (Heisler et al., 2003; Veach et al., 2014).

This study focuses on two adjoining headwater sub-catchments, N01B (1-year burn frequency) and N04D (4-year burn frequency), with an area of 120.9 ha and 135.7 ha respectively. Stream gauges established on headwater streams in N01B and N04D drain 120.9 ha and 120.4 ha respectively. These streams flow into Kings Creek. As of 2020, N01B and N04D had approximately 20 % and 40 % woody species cover respectively. These estimates may slightly underestimate the actual extent of woody encroachment, as the experimental plots monitored for woody cover lie only on uplands and lowlands but not in riparian zones (Keen et al., 2022). Aerial photographs however did show woody expansion in riparian zones (Dodds et al., 2023; Veach et al., 2014). We

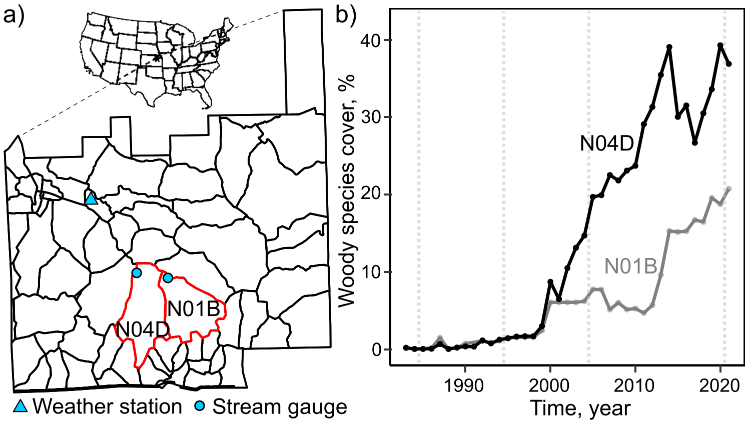

Fig. 1. A) n01b and n04d in Konza Prairie; b) Evolving woody cover percentages in N01B (burned annually) and N04D (burned every four years), where woody encroachment was roughly 20% and 40% of the land cover in 2020, respectively (adapted from Ratajczak et al. (2014). Woody cover in N01B did not accelerate until the drought of 2012. The dotted lines show periods representing different stages of woody encroachment: 1985 – 1994, 1995 – 2004, and 2005 – 2020, which we modelled separately to accommodate evolving catchment characteristics.

call these two catchments mildly and substantially encroached as they represent 1/3 and 2/3 of the maximum degree of encroachment observed at the Konza Prairie thus far. Catchment with 20-year burn frequency was not selected as it flows rarely and has a median of 15 flow days per year (calculated over 1987–2020). N01B and N04D are situated within similar limestone and shale units and have similar soil thickness. Subsurface geophysical investigations in N04D have revealed high vertical connectivity between limestone layers and locally permeable shale units (Sullivan et al., 2020). The catchments have never been cultivated but have been grazed by native American bison (*Bison bison*) since 1992.

2.2. Data

Daily meteorological data are available from April 1982 to December 2020, which include daily precipitation and air temperature (daily mean, maximum and minimum) from the weather station at the Konza Prairie headquarters (Nippert, 2021). This open access data is available at Konza LTER website (http://lter.konza.ksu.edu). In cases where daily data was missing, climate data from the Automated Surface Observing System network at the nearby Manhattan Regional Airport was used to fill the data gap (https://mesonet.agron.iastate.edu). Potential evapotranspiration was calculated using the Hargreaves and Samani equation as implemented in the “Evapotranspiration” R package (Guo et al., 2016; Hargreaves and Samani, 1985). Stream levels have been measured at the triangular throated flumes located at the outlets of the N01B and N04D from 1987 and 1985 onwards respectively (Dodds, 2021a, b). Daily streamflow, calculated using stream water level and rating curves, were downloaded from the Konza LTER website.

2.3. Model

The extensively-used model HBV-light (Hydrologiska Bryåns Vattenbalansavdelning) was utilized to simulate the hydrological processes at N01B and N04D (Bergstrom, 1992; Seibert and Vis, 2012). The model has been used to study land use and land cover changes including woodland to grassland conversion (Niemeyer et al., 2017), forest clear cutting (Seibert and McDonnell, 2010), afforestation (Cabrera-Balarezo et al., 2022), forest regeneration (Beck et al., 2013), and conversion of natural landcover to cultivated fields (Birhanu et al., 2019). However, the model has not been used to study impact of woody encroachment on streamflow previously to our knowledge.

HBV-light partitions incoming precipitation (snow and rainfall) into evapotranspiration and streamflow (Q) based on temperature, precipitation, and vegetation cover. Streamflow occurs from two zones: the upper zone and lower zone that conceptually represent the shallow soil zone and deeper groundwater zone (Fig. 2). These zones are loosely defined and can be differentiated based on water transit times. The upper zone or shallow soil zone typically contains highly weathered materials rich in organic matter and contributes relatively fast-flowing water with short water transit time to stream at high flows (Li et al., 2021). The lower zone often represents deeper unweathered bedrock and contributes older water to stream consistently throughout a year as baseflow (Sullivan et al., 2016). The model simulates three water fluxes that contribute to streamflow Q via three flow paths. The quick flow Q_0 conceptually represents overland or surface runoff that occurs when the water content of the shallow soil zone (upper zone) exceeds a threshold; Q_1 represents shallow lateral flow from the shallow soil zone (upper zone); and Q_2 represents deeper groundwater flow from the deeper groundwater zone (lower zone). The water flow from the upper to the lower zone represents groundwater recharge (or percolation in HBV language). HBV-light does not represent inter-basin water exchanges or loss to deeper regional aquifer. The geology of Konza Prairies contains repeating layers of shale/mudstone and limestone. Though traditionally considered as primarily horizontal flow systems, geophysical investigations showed presence of strong vertical connectivity across shale and limestone layers (Sullivan et al., 2020). The deep zone therefore can be considered as representing the bedrock (including both shale and limestone) units contributing groundwater to stream.

2.4. Model calibration and validation in three stages of woody encroachment

The catchment characteristics change as woody encroachment progresses. The model was calibrated and validated separately in three periods (Fig. 1b) to represent different stages of woody encroachment in early (1985–94), transition (1995–04), and recent periods (2005–20). Parameter sets calibrated for each of the three periods reflect the average catchment characteristics, for example, average rooting depth and vegetation characteristics during that period, although it does not simulate these processes explicitly. The model does not explicitly differentiate the transpiration rates of woody plants versus grasses either.

To calibrate the model in each period, we used roughly 80 % of the streamflow data in the earlier years in each period, and the remaining 20 % data for validation. The parameter ranges used for model calibration are in Table S-1. Monte Carlo simulation was carried out with 500,000 cases, among which 25 best-performing cases with the highest daily Nash Sutcliffe Efficiency (NSE) and Kling Gupta Efficiency (KGE)

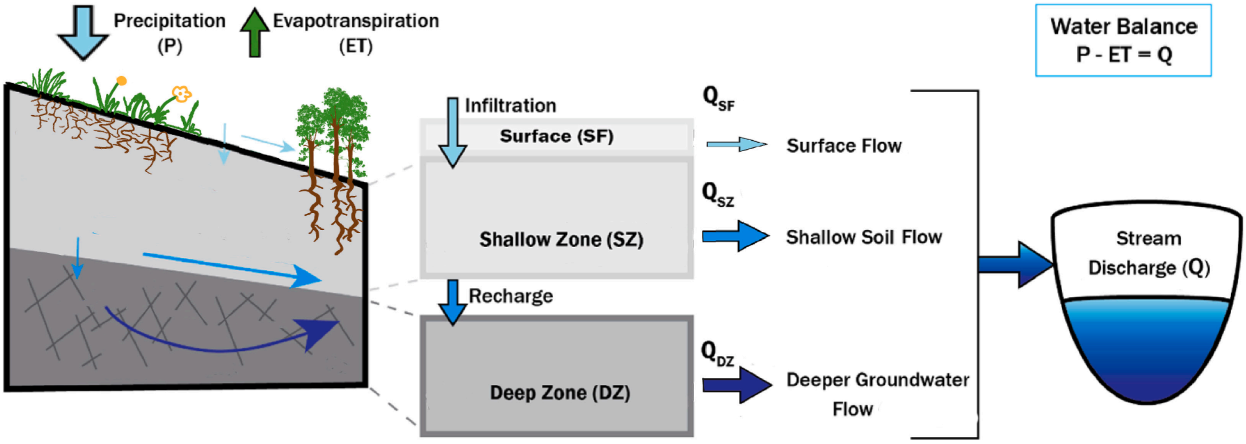

Fig. 2. Streamflow generation in HBV-light, a widely used hydrological model. The model calculates water balance by partitioning precipitation into evapotranspiration (ET) and streamflow (Q). It includes upper and lower zones (representing shallow soil zone and deeper groundwater zone respectively). It simulates three streamflow components, including surface runoff $Q_{SF,}$ shallow soil water flow $Q_{SW,}$ and deeper groundwater flow $Q_{GW,}$ corresponding to Q_0, Q_1, and $Q_{2\ in}$ in HBV, respectively. All three flow components eventually enter the stream.

values were selected for each period and catchment combination. These parameter sets were then tested for model performance during the validation period. Cases with daily NSE and KGE values of over 0.5 for both training and testing period data were selected to avoid overfitting. For N01B, few simulation cases met these criteria in 1995–04 and 2005–20, so a threshold of 0.45 (instead of 0.5) was used for both metrics for those two periods.

2.5. Temporal trend analysis

High inter-annual variations in meteorological and hydrological variables can mask long-term trends. To circumvent this, we used moving average of a 5-year window following the methods in Keen et al. (2022). We calculated the 5-year moving average of total streamflow, different flow components, and their relative contribution to streamflow for temporal trend analysis. The fraction of daily flow component was calculated as the ratio of daily flow component to daily streamflow, both in 5-year moving averages. We also similarly quantified seasonal flow component fractions (Winter — January-February and December, Spring — March-May, Summer — June-August, and Fall — September-November). For temporal trend analysis, we used the “modifiedmk” R package (Patakamuri et al., 2020) that implements the Mann-Kendall test with trend-free pre-whitening (Kendall, 1948; Mann, 1945; Von Storch, 1999).

2.6. Drought analysis

The Standardized Precipitation Index (SPI), a widely used meteorological drought index, was calculated based on precipitation data (Zargar et al., 2011). SPI can be calculated for different accumulation periods, ranging from 1 to 48 months, reflecting SPI patterns at different time scales. SPI-n represents SPI for “n” months accumulation period. To fit SPI-n, the accumulated precipitation series (total precipitation over n months) was fit to a statistical probability distribution, which was then transformed to a normal distribution with the mean centered at zero. SPI-n for any month is the number of standard deviations by which that month’s accumulated precipitation differs from the mean accumulated precipitation (McKee et al., 1993). The SPI value is 0 for mean accumulated precipitation. Positive SPI values indicate wet conditions (i.e., accumulated precipitation higher than mean accumulated precipitation), and negative values indicate dry conditions.

The Standardized Streamflow Index (SSI) was used to quantify hydrological droughts (Nalbantis and Tsakiris, 2009; Vicente-Serrano et al., 2012). SSI was calculated in the same way as SPI, except using streamflow instead of precipitation. A zero value represents mean streamflow, while non-zero values represent the number of standard deviations by which the accumulated streamflow in that month differs from the mean. We tried six candidate distributions and chose the one that best fit the data based on L-moment ratio (Svensson et al., 2017; Vicente-Serrano et al., 2012). Both SPI and SSI were calculated using the “SCI” R package at 1-month and 12-month scales or accumulation periods (Gudmundsson and Stagge, 2016).

2.7. The hypothetical “Climate Only” scenario

The historical streamflow data in N01B and N04D reflect the compounded effects of climate change and woody encroachment since 1985. The model parameter sets that best reproduce streamflow at each of the three stages therefore represent catchment properties with different extent of woody cover during the early, transition, and recent stages of woody encroachment. To differentiate the impacts of woody encroachment and climate change, we additionally simulated a hypothetical case using the parameter sets calibrated for 1985–94 when the woody encroachment was minimal (<1.5 % woody encroached area, Fig. 1b). Assuming that these parameters reflect catchment properties at that time and remain constant, the hypothetical climate scenario represents the water balance and flow partitioning that would have been observed if these catchments had been subjected to climate change (increasing precipitation and temperature) alone. This scenario however does not explicitly account for the physiological response of vegetation to increasing atmospheric CO_2 levels as the model does not simulate plant processes. The average vegetation characteristics represented by the parameter sets used for hypothetical scenario therefore correspond to plant transpiration rates at lower CO_2 levels of 1985–94. By comparing the hypothetical case (Climate Only) with the calibrated case under the convoluted influence of climate change and woody encroachment (Climate + WE), we attempted to differentiate the effect of woody encroachment.

3. Results

3.1. Changing climate and streamflow

The long-term data (Fig. 3**,** red dots) in the Konza Prairies indicate that the streamflow is intermittent, characterized by long no-flow periods interspersed by large precipitation events with substantial

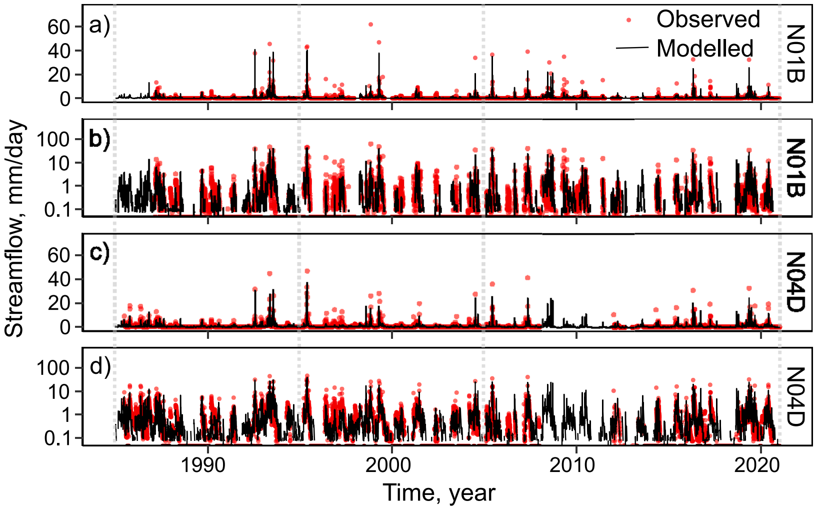

Fig. 3. Comparison between observed (red dots) and modeled (black line) streamflow for N01B (mildly encroached, a and b) and N04D (substantially encroached, c and d) in arithmetic (a and c) and log scales (b and d). The modeled line is the arithmetic mean of all 25 cases. The lower limit of streamflow was set at 0.07 mm/day, corresponding to the detection limit of streamflow. The streams are intermittent and have long periods with no flow (below detection limit). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

interannual variability. The modeled line is the arithmetic mean of daily streamflow calculated from the 25 best-performing cases. The range of NSE and KGE values are 0.46 – 0.81, and 0.49 – 0.90, respectively (details in Table S-2). Note that as encroachment increases, streamflow decreases and the system becomes drier. The model validation performance values are lower in transition and recent time periods compared to early period. This echoes literature that low streamflow is challenging to reproduce in hydrology models, whether physics-based (Seibert et al., 2018) or machine learning (Feng et al., 2020). Comparison between the observed and modelled streamflow shows that the model generally captured the temporal dynamics of the streamflow but also missed some peaks (Fig. 3a and c). The model output shows low values of streamflow at dry times that are below the detection limit (0.07 mm/day) (Fig. 3b and d in log scale). The logarithmic figures (Fig. 3b and d) allow viewing of more low flow dynamics.

The temporal dynamics of the observed and modeled streamflow in the two catchments are similar (Fig. 4), as they are subject to very similar weather and climate. In this karst landscape, the deeper groundwater flow Q_2 predominates and overlaps with the total streamflow Q most of the time. The exception is during very wet periods or during large events such as the event in June 2005 with the largest streamflow peaks. During precipitation events, Q_2 responds rapidly and increases considerably. Shallow lateral flow Q_1 occurs during precipitation events as transient, short pulses. The overland flow Q_0 occurs rarely, usually following a large precipitation event or consecutive events. The streams are intermittent, with dry periods in the late summer and winter. These dynamics are similar to what was observed based on mixing calculations in Hatley et al. (2023).

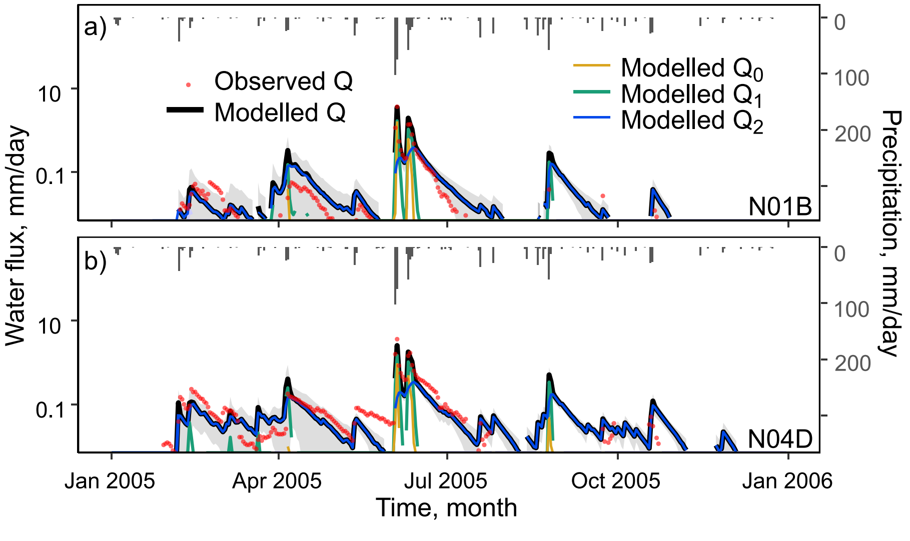

Fig. 4. Temporal dynamics of observed (red dots) and modeled (black line) streamflow, as well as modeled flow components in a) N01B and b) N04D catchments in a typical year 2005. The flow components in Q (total streamflow) are Q_0 (overland flow), Q_1 (shallow lateral flow), and Q_2 (deep groundwater flow). The modeled Q is the arithmetic mean of the 25 best performing cases. Grey shade is one standard deviation above and below the mean. Q_0 occurs only during largest rainfall events or in already wet conditions; Q_1 occurs in most rainfall events; Q_2 is the dominant flow and overlaps with Q most of the time except during large rainfall events when Q_1 also contributes substantially to the streamflow such as in June and in August 2005. The streams are dry in late summer and winter and thus data is limited in that period. Most streamflow occurred in relatively wet spring and summer. The lower limit of streamflow was set as 0.07 mm/day, corresponding to detection limit of streamflow. (For interpretation of the references to colour in this figure legend, readers are referred to the web version of this article.)

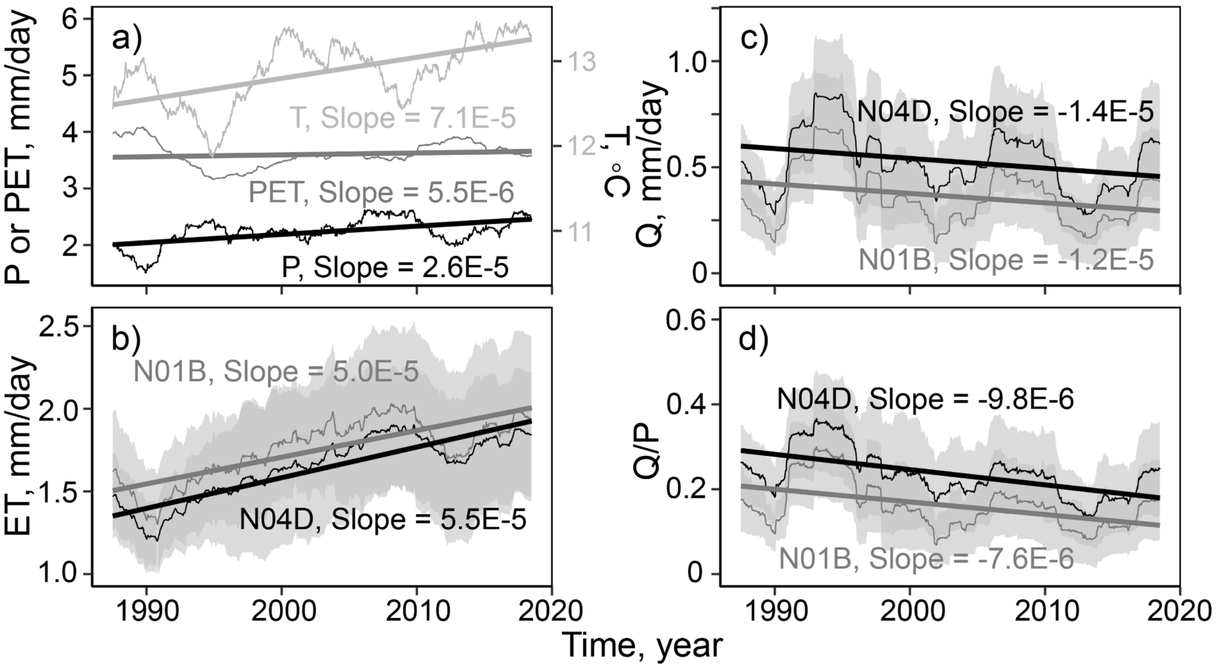

Fig. 5. Temporal trends based on the five-year moving average of a) observed daily precipitation (P), temperature (T), and daily potential evapotranspiration (PET), b) modeled daily evapotranspiration (ET), c) modeled daily streamflow (Q), d) modeled daily streamflow to precipitation ratio (Q/P, or runoff ratio) in N01B (mildly encroached) and N04D (substantially encroached). Grey shade indicates one standard deviation about moving average. Sen's Slopes ($p < 0.001$) represent the rates of change in fluxes (mm/day/day) and runoff ratio Q/P (day^{-1}). Slopes are based on data record over 1982–2021 for P, T and PET and 1985–2020 for ET, Q and Q/P. Precipitation, temperature and evapotranspiration have increased whereas streamflow has decreased from 1985 to 2020.

The climate at Konza Prairie has become progressively wetter and warmer, as shown in the precipitation and temperature trends (Fig. 5a). However, both the streamflow Q and runoff ratio (Q/P) has declined in the two catchments, with a more rapidly declining trend in the substantially encroached N04D as indicated by its slightly greater rate compared to the mildly encroached N01B (1.4E-5 versus 1.2E-5 mm/day/day for Q, Fig. 5c and d). Evapotranspiration in both catchments has been increasing (Fig. 5b), with a more rapid increase in N04D, which is consistent with a greater streamflow decline in N04D than N01B. Evapotranspiration in N04D is however smaller than N01B despite experiencing higher woody encroachment rates, consistent with N04D's higher runoff ratio. This difference is apparent even during early period when both catchments had relatively low woody cover. A potential reason could be the presence of inter-basin water transfers or groundwater loss to regional aquifers, which has been discussed in previous work (Sullivan et al., 2020) but not simulated in the model. The model assumes closed water balance such that ET = P – Q. If there is additional groundwater loss, the model could potentially be adding the groundwater losses to evapotranspiration losses. If this is the case, it would indicate that N04D loses less groundwater than N01B, which leads to higher "apparent" ET in N01B. However, lack of monitoring data makes it hard to test this hypothesis.

3.2. Changing flow paths

Streamflow Q in both catchments is predominantly deeper groundwater flow Q_2, followed by shallow lateral flow Q_1, whereas surface overland flow Q_0 is negligible (Fig. 6). In early years, the mildly encroached N01B had a greater groundwater fraction (Q_2/Q) compared to the substantially encroached N04D. Over time, deep groundwater flow has increased more rapidly in N04D, leading to similar Q_2/Q ratios in the two catchments (Fig. 6f). In N01B, rates of all flow components have decreased (Fig. 6a–c), similar to total streamflow; the groundwater flow fraction (Q_2/Q) however still increased, although not as rapidly in N04D. Considering deep groundwater fraction as proxy for recharge, this indicates recharge has increased more in N04D than N01B.

Although the groundwater fraction (Q_2/Q) decreased during the transition period (1995–2004), it has been increasing overall, especially in the most recent period (2005–2020). The increasing trend is significant across all seasons for substantially encroached N04D (Fig. 7). Across different seasons, the groundwater fraction has increased faster in the summer and fall in N04D. In N01B, the groundwater fraction has not increased as much and fall season does not exhibit a significant trend.

3.3. Increasing occurrence of hydrological droughts

The standardized precipitation index SPI has increased, indicating a wetter climate over time (Fig. 8). However, the standardized streamflow index SSI, an indicator for hydrological droughts, has decreased in both catchments, indicating more droughts over time. Distributions selected to fit these indices are summarized in Table S-3. The steepest increase in the SPI occurred at the 12-month timescale, indicating increasing precipitation at the annual scale. SSI in the substantially encroached N04D has declined at over twice the rate of the mildly encroached N01B. SSI-12 indicates sustained low stream flows over extended periods. SSI-12 at N01B has decreased at a faster rate than SSI-1, indicating more common, elongated periods of low stream flows instead of short periods of low flow. The substantially encroached site, on the other hand, has experienced almost similar rates of increase in drought severity across all timescales.

3.4. Woody encroachment is more influential than climate

The modeled streamflow and groundwater flow are compared under climate influence only with observed climate change (Climate Only) and under combined influence of climate change and differing degrees of woody encroachment (Climate + WE) (Fig. 9). In the "Climate Only"

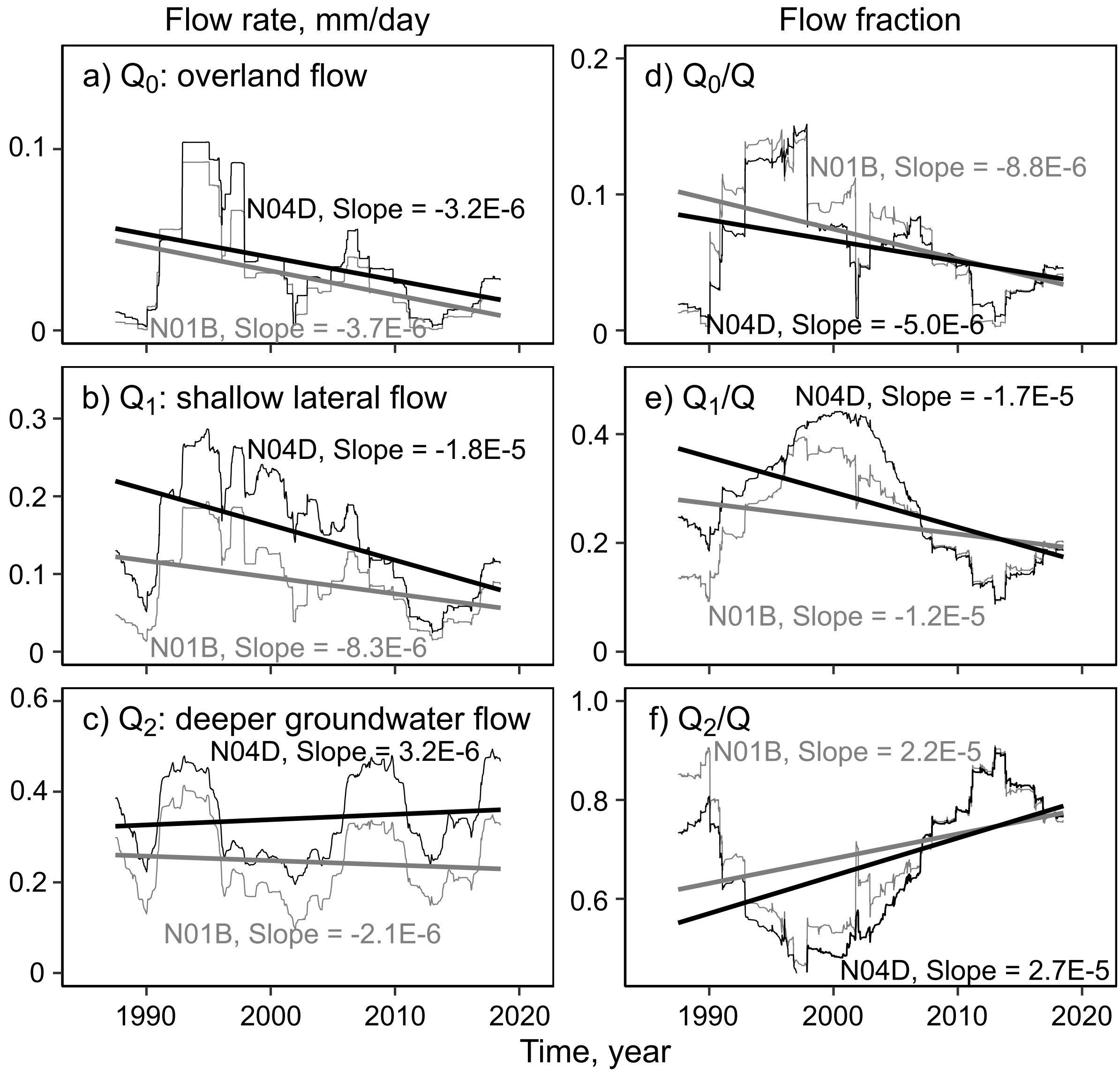

Fig. 6. Temporal trends of a-c) flow rates and d-f) fractions of different flow components in N01B (mildly encroached) and N04D (substantially encroached). The thin lines are five year moving average of each variable. The trend slopes (thick straight lines) are the Sen's Slope ($p < 0.001$) in units of mm/day/day for flow rates and day^{-1} for flow fractions. Q_0 – overland flow, Q_1 – shallow lateral soil flow, Q_2 – deep groundwater flow. The deeper groundwater fraction (Q_2/Q) has increased in N01B and N04D, whereas flow fractions of other components have decreased.

scenario, streamflow in both catchments increased over time while the runoff ratio Q/P decreased by 0.01 and 0.03 in the mildly and substantially encroached watersheds, respectively. This result indicates that higher ET in a warmer climate will inevitably change the water balance and reduce the proportion of streamflow. In addition, Q_2 itself also increased over time, indicating more precipitation would lead to more recharge into the deeper groundwater. In the "Climate + WE" case, streamflow decreased in both catchments. The deeper flow Q_2 increased slightly in N04D and decreased slightly in N01B, but the groundwater flow to total streamflow fraction Q_2/Q increased in both catchments.

4. Discussion

The hydrology effects of climate change and woody encroachment are often intertwined, challenging our understanding of their relative influence on streamflow and flow path partitioning. Here we aim to differentiate their impacts using hydrology modeling and temporal trend analysis in two differentially-encroached catchments in the Konza Prairie. We hypothesize that 1) woody encroachment outweighs climate change in influencing catchment hydrology; 2) woody encroachment promotes deeper groundwater flow. Results confirm the hypotheses, showing that despite a wetter climate, evapotranspiration has increased whereas streamflow has decreased with higher fraction of deeper groundwater flow in woody-encroached grassland (Fig. 10).

4.1. *Drier streams in a wetter climate – The role of woody encroachment*

Woody cover in N01B and N04D has increased by about 20 % and 40 %, respectively, over the past four decades (Fig. 1b). Meanwhile, mean annual precipitation and temperature have increased by ~ 125 mm and by 0.93°C, respectively (Fig. 5a). These changes are expected in the midwestern region of the United States (IPCC et al., 2021; USGCRP et al., 2018). Data and modeling results indicate that, in response to increased woody cover and climate change, mean annual streamflow has declined from 1985 to 2020 by 56.4 mm and 66.6 mm, in the mildly and substantially encroached sites. Correspondingly, the Q/P ratios have

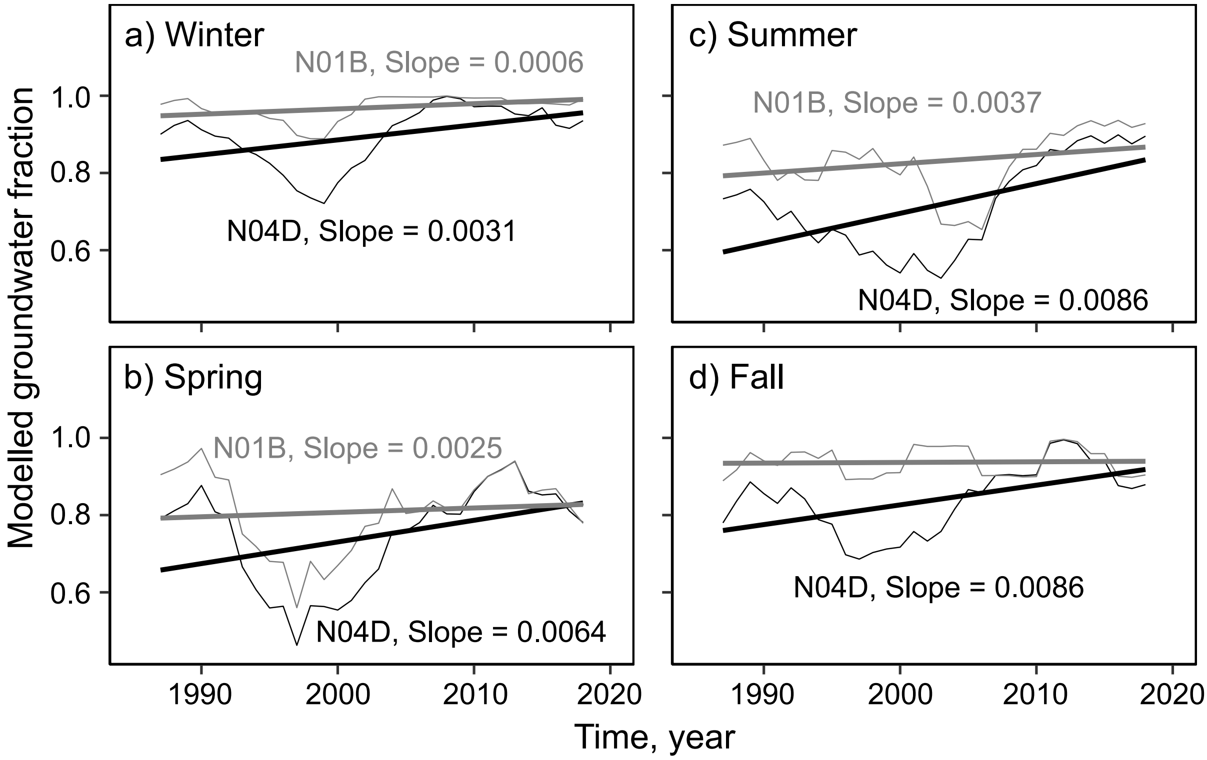

Fig. 7. Temporal trends of groundwater flow component fraction (Q_2/Q) in N01B (mildly encroached) and N04D (substantially encroached) in a) winter b) spring c) summer and d) fall. The thin lines are five year moving average. The trend slopes (thick straight lines) are Sen's Slope (day^{-1}) ($p < 0.001$ for N04D and $p < 0.05$ for N01B). The groundwater fraction has increased across all seasons in both catchments except fall in N01B. The flow fractions increased most in summer and fall in N04D.

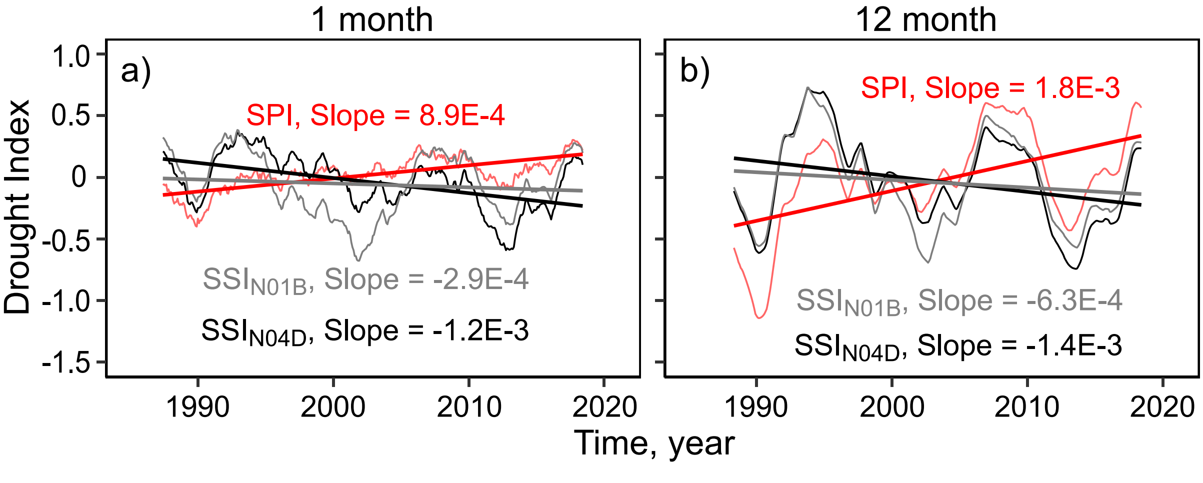

Fig. 8. Temporal trends of meteorological drought index SPI (Standardized Precipitation Index, red line), and hydrological drought index SSI (Standardized Streamflow Index) in N01B (grey line) and N04D (black line) at time scales (accumulation periods) of a) 1 month and b) 12 months. The thin lines are five year moving averages. Their trend slopes (thick straight lines) are Sen's slope ($p < 0.001$, month^{-1}). SPI has been increasing due to increasing precipitation, whereas SSI has been decreasing, indicating more hydrological droughts over time. (For interpretation of the references to colour in this figure legend, readers are referred to the web version of this article.)

decreased by 0.08 and 0.1 respectively (Fig. 5c&d). Similar declines have been noticed in Kings Creek, the bigger stream that N01B and N04D drain to (Dodds et al., 2012).

Both woody encroachment and increasing temperature can explain the declining streamflow as they alter evapotranspiration. Evapotranspiration can increase during woody encroachment in mesic grasslands due to the generally higher transpiration rates of woody species compared to grasses (Huxman et al., 2005; Keen et al., 2022; O'Keefe et al., 2020; Wilcox et al., 2022). As an example, roughleaf dogwood, the dominant encroaching woody species in Konza Prairie, has a relatively high canopy transpiration rate of 2.01 mm/day compared to big bluestem, the dominant grass species, which transpires 0.91 mm/day during the growing season (O'Keefe et al., 2020). At the Konza Prairie, grass species preferentially use water from the shallow soil (top 30 cm), while shrubs often extract water from deeper soil under dry conditions (Keen et al., 2022; Nippert and Knapp, 2007; Ratajczak et al., 2011). Stable

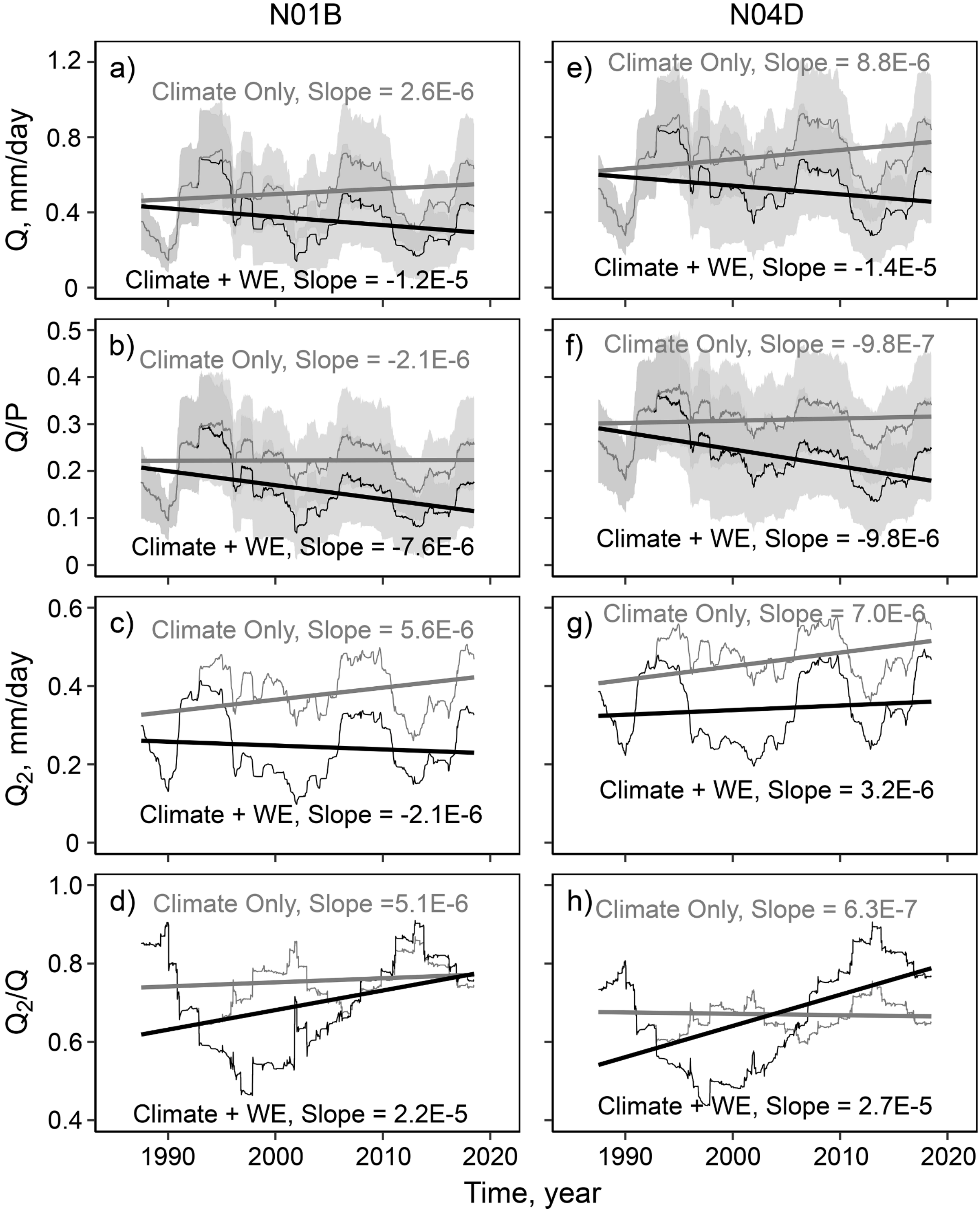

Fig. 9. Comparison of water balance and deeper groundwater flow in a hypothetical scenario under climate change alone (Climate Only) and under both climate and woody encroachment impacts (Climate + WE, the real scenario based on data) in N01B (left; mildly encroached) and N04D (right; substantially encroached). a + e: modeled daily streamflow (Q); b + f: modeled daily streamflow to precipitation ratio (Q/P); c + g: modeled groundwater flow (Q_2); d + h: modeled groundwater flow to total streamflow fraction (Q_2/Q). All thin lines are five year moving averages. Grey shade indicates one standard deviation about moving average. Trends with Sen's slope (straight lines, $p < 0.001$) are in units of mm/day/day for water flow rates (Q, Q_2) and day^{-1} for runoff ratio and flow fraction (Q/P, Q_2/Q). In the "Climate Only" scenario, streamflow would have increased in both catchments in a wetter climate with more precipitation, whereas in reality streamflow has decreased under compounded impacts of climate and woody encroachment (Climate + WE). The fractions of deeper flow (Q_2/Q) show increasing trend in both "Climate Only" and "Climate + WE" scenarios but more so in the substantially encroached N04D.

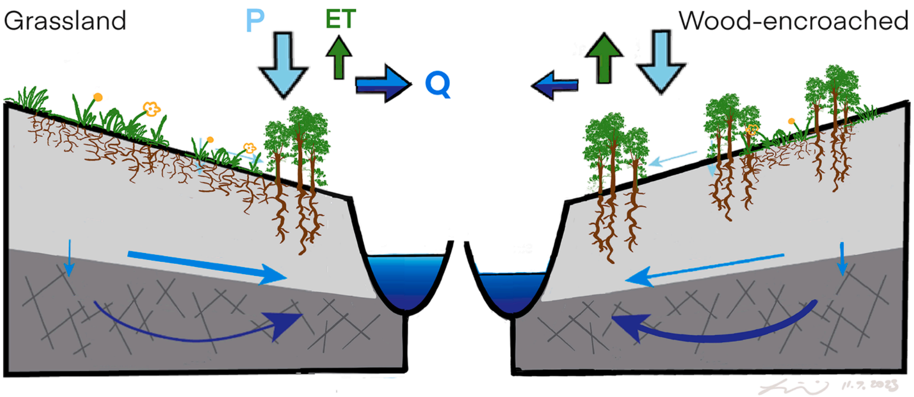

Fig. 10. A conceptual illustration of distinct ecohydrology in mildly encroached (left) and substantially encorached (right) grasslands. In the substantially encroached grassland, ET is higher and streamflow is lower with higher fraction of deepening groundwater flow.

isotope analysis revealed that shallow soil water contributes about 78.3 % of water extracted by big bluestem while roughleaf dogwood utilizes similar amounts of soil water and groundwater, which gives dogwood competitive advantage over grass (Keen et al., 2022). At the catchment scale, evapotranspiration (based on eddy flux measurements) remained high in a more woody-encroached catchment during a drought year as woody species circumvented drought by extracting deeper water (Brunsell et al., 2014; Logan and Brunsell, 2015). Increasing temperatures can also independently increase evapotranspiration rates by escalating soil evaporation and plant transpiration rates, as atmospheric demand for water increases (Allen et al., 1998; Schreiber, 2001).

The comparison between the hypothetical "Climate Only" and the real "Climate + WE" scenarios however indicates that without woody encroachment, annual streamflow would have increased by 12.4 mm and 42.2 mm in mildly and substantially encroached catchments, respectively, from 1985 to 2020 (Fig. 9). The "Climate Only" scenario does not account for possible decrease in evapotranspiration due to plant physiological response to increasing CO_2 levels and therefore may underestimate the modelled streamflow increase. This shows that the wetter and warmer climate would have enhanced streamflow. Streamflow in both catchments however declined under the combined impact of climate change and woody encroachment. In addition, the substantially encroached N04D has experienced greater declines in streamflow (Fig. 4). All these observations indicate that woody encroachment has been a stronger driver (compared to climate change) for declining streamflow in Konza.

Streamflow changes due to woody encroachment and / or changing climate have been observed in other places. Decreasing streamflow has been well documented in encroached prairies of Canada and Great Plains of USA (Starks and Moriasi, 2017; Zou et al., 2018). In North Concho catchments in Texas, streamflow declined as much as 70 % as woody cover increased following land degradation (Wilcox et al., 2008a). In minimally disturbed karst areas of Southern Italy, groundwater flow contribution to streams has declined despite increasing precipitation (Fiorillo et al., 2021). While declining streamflow has been more commonly reported, other responses have been observed as well. For instance, streamflow in karst catchments in Edwards Plateau increased with increasing woody cover from 1925 – 2010. Streamflow remained relatively constant but baseflow increased in an Oklahoma catchment from 1938 – 1992 under the influence of both riparian woody expansion and slightly increasing precipitation (Wine and Zou, 2012).

Similar to the Konza Prairie, many places experience both woody encroachment and climate change. Although it remains challenging to differentiate the relative importance of woody encroachment and a changing climate, woody encroachment has been highlighted to influence hydrology more than projected climate change scenarios in drylands such as the Chihuahuan desert (Schreiner-McGraw et al., 2020). Streamflow in the Konza Prairie has declined in the Central Great Plains where annual precipitation has been projected to slightly increase or have little to no change (IPCC et al., 2021; USGCRP et al., 2018). This raises the question: how commonly do streams dry up even as climate becomes wetter? Is this phenomenon unique to the Konza Prairie, or is it occurring in other areas with woody-encroachment, both within and beyond the Central Great Plains?

4.2. *Deepening flow paths*

Ample evidence has shown that the hydrology at Konza Prairie is groundwater dominated. Hatley et al. (2023) and Keen et al. (2022) have identified groundwater as the dominant source for the intermittent stream draining N04D. Shallow lateral flow through soils is negligible most of the time except during storm events, a common observation in karstic terrain (Wilcox and Huang, 2010; Wilcox et al., 2008b). Groundwater flow contribution to streamflow initially decreased at both catchments but rebounded later (Fig. 6) and became even higher in recent years than earlier periods. This increase is evident across almost all seasons (Fig. 7). Groundwater contribution to total streamflow (Q_2/Q) similarly increased in the "Climate Only" scenario (Fig. 9). However, the "Climate + WE" scenario shows a much higher increasing rate (42.9 times, slope in Fig. 9) compared to Climate scenario in the substantially encroached site, and 3.6 times that of the "Climate Only" scenario in the mildly encroached site. This suggests that woody encroachment has contributed substantially to the deepening of flow paths, although it is not clear if this arises from deepening roots or more macropores. Similar observations have been reported in South Concho catchments with karst bedrock in Texas, where baseflow increased with woody encroachment despite decreasing annual streamflow (Wilcox et al., 2008a). Similarly, baseflow was observed to increase in karst catchments of Edwards Plateau with woody encroachment due to rapid groundwater recharge (Wilcox and Huang, 2010).

One hypothesis is that such deepening flow paths may be driven by the unique rooting characteristics of encroaching shrubs. Shrub roots can form deep and connected macropores, channeling water through soil quickly (Laine-Kaulio et al., 2015; Wang et al., 2020). Macropores often contribute to up to 70 % of water flow despite only making up 1–2 % of soil volume (Beven and Germann, 2013). Soils beneath shrubs in woody-encroached grasslands have shown well-developed, convoluted and deeper macropores, leading to higher hydraulic conductivity (Hu et al., 2019; Hu et al., 2020; Li et al., 2013) and higher infiltration rates (Eldridge et al., 2015; Leite et al., 2020). Deepening woody roots could have easily reached the underlying bedrock, thereby enabling water flowing through macropore to recharge groundwater (Ghestem et al., 2011), promoting groundwater flow as observed at the Konza Prairie. The increased groundwater flow also suggests that the vertical conductivity between mudstone and limestone layers in localized areas is high enough to support the higher groundwater recharge facilitated by woody encroachment (Sullivan et al., 2020). More research however is warranted to fully test this hypothesis.

An alternative hypothesis is that the decreasing streamflow but increasing groundwater flow may arise because some of the water that would have reached stream as shallow soil water has potentially shifted to deeper groundwater that enters regional groundwater table and bypasses the stream outlets. Shallow soil water flow mostly tends to contribute to streams and, therefore, is detected at the flume. For deeper groundwater, it is possible only a portion of the recharged groundwater is delivered to the stream, with the rest recharging deeper regional groundwater. In other words, it is possible some water is “lost” to deeper stratigraphical units below the flume, and may emerge in some other streams (i.e., inter-basin groundwater flow). Therefore, by shifting some of the runoff to deeper groundwater, a greater portion of the precipitation may be “lost” such that streamflow declines. Testing these hypotheses require consistent and comprehensive sets of data that document changes in streamflow, conductivity, ET, and recharge in woody-encroached grasslands, which are mostly lacking in literature.

4.3. Implications

The decreasing flow in intermittent Konza Prairie streams means more zero-flow days and a loss in stream connectivity (Dodds et al., 2012; Lapides et al., 2021). In addition to affecting aquatic life, this can have implications on water quality as intermittency affects various processes within and beyond streams (Dodds et al., 2004; von Schiller et al., 2011; von Schiller et al., 2017). Hydrology plays a significant role in determining water quality (Li, 2019). Low streamflow has been linked to high concentrations of solutes in rivers and streams at the continental scale (Li et al., 2022). This indicates that mean solute concentrations in Konza Prairie can increase in the future. Increasing solute concentrations in fact have already been observed in N04D (Macpherson and Sullivan, 2019).

Increasing connectivity and higher fractions of deeper groundwater can possibly accelerate carbonate dissolution and inorganic carbon export, especially if the percolating water transports more acidic, CO_2-rich soil water to the depth (Stewart et al., 2022; Wen et al., 2022). Concentration of dissolved inorganic carbon in groundwater of N04D has been observed to be increasing faster than atmospheric CO_2 (Macpherson et al., 2008). Enhanced carbonate dissolution can mobilize solutes including calcium, magnesium, and heavy metals. Moreover, it can further enhance deeper flow paths and form positive feedbacks. Deepening roots and flow paths in fact have been shown to double carbonate weathering rates compared to a subsurface with shallow roots (Wen et al., 2021). Given the different rates of soil respiration (including both root and microbial respiration) in woody plants and grasses (McKinley and Blair, 2008; Smith and Johnson, 2004), it raises the question of how much changing water fluxes and flow paths versus soil CO_2 levels have been contributing towards these observed increases in geochemical solute concentrations at the Konza Prairie, and in woody-encroached grasslands in general.

5. Conclusion

Woody plant expansion in grasslands can affect hydrology, but its impacts vary by location and time and are convoluted with the influence of climate change. We analyzed over three decades of data from two catchments with different degrees of woody encroachment at the Konza Prairie to understand the relative impacts of climate change and woody encroachment on streamflow. Our findings show that despite a wetter climate with increasing precipitation, streams draining both encroached catchments have become drier over time, especially in the substantially encroached site. Woody encroachment plays a crucial role in reducing streamflow, as demonstrated by increasing streamflow in the hypothetical “Climate Only” scenario without encroachment. Furthermore, flow pathways have deepened, with increasing fraction of deeper groundwater flow despite declining streamflow, particularly in the more encroached catchment. These findings raise the question about how common do streams become drier even as climate becomes wetter, and whether it occurs only in Konza, or it is a common phenomenon in woody-encroached grasslands in the Great Plains and beyond. These questions are important as drier streams not only reduce water availability and threaten aquatic ecosystems and biodiversity, but also affect water quality and carbon cycling in grasslands that cover 40 % of the ice-free Earth surface.

CRediT authorship contribution statement

Kayalvizhi Sadayappan: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Writing – review & editing, Visualization. **Rachel Keen:** Data curation, Writing – review & editing. **Karla M. Jarecke:** Writing – review & editing. **Victoria Moreno:** Writing – review & editing. **Jesse B. Nippert:** Writing – review & editing, Funding acquisition. **Matthew F. Kirk:** Writing – review & editing. **Pamela L. Sullivan:** Writing – review & editing, Project administration, Funding acquisition. **Li Li:** Conceptualization, Resources, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

Authors declare no competing interest.

Data availability

Data and model are already publicly available and has been cited in methods

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jhydrol.2023.130388.

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