Received: 13 October 2020 | Accepted: 19 November 2020

DOI: 10.1111/gcbb.12787

GCB-BIOENERGY BIOPRODUCTS FOR A SUSTAINABLE BIOECONOMY Open Access WILEY

ORIGINAL RESEARCH

Improved productivity, water yield, and water use efficiency by incorporating switchgrass cultivation and native ecosystems in an integrated biofuel feedstock system

Kathryn N. Schmidt | **Chris B. Zou** | **Vijaya Gopal Kakani** | **Yu Zhong** | **Rodney E. Will**

Oklahoma State University, Stillwater, OK, USA

Correspondence
Rodney E. Will, Department of Natural Resource Ecology and Management, 008C Agricultural Dr., Oklahoma State University, Stillwater, OK 74078, USA.
Email: rodney.will@okstate.edu

Present address
Kathryn N. Schmidt, Pennsylvania State University, State College, PA, USA

Funding information
National Science Foundation, Grant/Award Number: OIA-1946093; National Institute of Food and Agriculture, Grant/Award Number: 2014-67010-21653; McIntire-Stennis, Grant/Award Number: OKL0 2931 and OKL0 2929; Oklahoma Agricultural Experiment Station

Abstract

The southern Great Plains of the USA has great potential to produce biofuel feedstock while minimizing the dual stresses of woody plant encroachment and climate change. Switchgrass (*Panicum virgatum*) cultivation, woody biomass captured during removal of the encroaching eastern redcedar (*Juniperus virginiana*) to restore grasslands and thinning of the native oak forest can provide an integrated source of feedstock and improve ecosystem services. In north-central Oklahoma, we quantified productivity and ecosystem water use of switchgrass stands and degraded ecosystems encroached by eastern redcedar and compared these to native oak forest and tallgrass prairie ecosystems. We measured aboveground net primary productivity (ANPP) using allometric equations (trees) and clip plots (herbaceous), and evapotranspiration (ET) using a water balance approach from gauged watersheds, and calculated water use efficiency (WUE = ANPP/ET) from 2016 to 2019. Among vegetation cover types, ANPP averaged 5.1, 5.4, 6.0, and 7.8 Mg ha^{-1} year^{-1} for the prairie, oak, eastern redcedar, and switchgrass watersheds and was significantly greater for switchgrass in 2018 and 2019 (2 and 3 years post establishment) when it reached 8.6 Mg ha^{-1} year^{-1}. Averaged across 2017–2019, ET was significantly greater in the forested watersheds than the grassland watersheds (1022 mm year^{-1} for eastern redcedar, 1025 mm year^{-1} for oak, 874 mm year^{-1} for prairie, and 828 mm year^{-1} for switchgrass). The mean WUE was significantly greater (9.47 kg ha^{-1} mm^{-1}) for switchgrass than for the prairie, eastern redcedar, and oak cover types (6.03, 6.02, and 5.31 kg ha^{-1} mm^{-1}). Switchgrass offered benefits of greater ANPP, less ET, and greater WUE. Our findings indicate that an integrated biofuel feedstock system that includes converting eastern redcedar encroached areas to switchgrass and thinning the oak forest can increase productivity, increase runoff to streams, and improve ecosystem services.

KEYWORDS

aboveground net primary production, biofuel feedstock, cross timbers, *Juniperus virginiana*, *Panicum virgatum*, *Quercus* spp., tallgrass prairie, water use efficiency

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2020 The Authors. *GCB Bioenergy* Published by John Wiley & Sons Ltd

1 | INTRODUCTION

The southern Great Plains of the USA faces the dual stresses of woody plant encroachment and climate change. This region is the transition between the humid east and the arid west (Seager, Lis, et al., 2018), and eastern forests and many eastern tree species reach their western limit. Changes in management, primarily fire exclusion, have caused extensive woody plant encroachment into native grasslands and prairies (e.g., Bragg & Hulbert, 1976; Briggs et al., 2005; Engle et al., 1996). At the same time, climate change is leading to decreasing precipitation and increasing temperatures (causing greater evaporative demand), which is pushing the demarcation between the humid/arid boundary eastward (Seager, Feldman, et al., 2018). In general, areas encroached by woody plants in the region have greater evapotranspiration (ET) than native grasslands (e.g., Zou et al., 2014). Given annual precipitation ranging from 600 to 1200 mm throughout much of this region, this is critical because water is generally limiting, and higher ET causes proportional reductions in runoff. Greater ET associated with woody plant encroachment combined with more arid conditions will greatly reduce or eliminate water availability to streamflow and groundwater recharge which is essential for flows needed for aquatic organisms and ecosystem function as well as human needs related to agricultural, industrial, and municipal use.

The southern Great Plains has great potential to produce biofuel feedstock, with most efforts focusing on switchgrass (*Panicum virgatum*) cultivation. Switchgrass is an important component of the native tallgrass prairie ecosystem and can be cultivated on marginal lands without irrigation (Wagle et al., 2016) to produce yields in excess of 13 Mg ha^{-1} $year^{-1}$ under moderate drought (Yimam et al., 2015) and 20 Mg ha^{-1} $year^{-1}$ with fertilization (Thomason et al., 2005). In addition to switchgrass, the region contains existing sources of biofuel feedstock such as native tallgrass prairie, encroaching woody plants, and native oak-dominated forest. Understanding the trade-offs between productivity and ET of different vegetation cover types is essential to understand the impact of management decisions related to ecosystem restoration and biofuel feedstock production. This understanding may lead to benefits of using biofuel feedstock systems that integrate switchgrass, encroaching woody plants, native prairie, and oak forest to increase productivity and restore ecosystems while sustaining water resources under future climate conditions.

The tallgrass prairie of North America originally occupied a swath of land between the eastern deciduous forest and the shortgrass prairie stretching from Texas, USA to Saskatchewan, Canada. Originally the biome was approximately 70 million ha, but up to 95% has been converted to agriculture. However, there are still large areas in the southern Great Plains that have either been maintained or have returned to tallgrass prairie following agricultural abandonment. The ecosystem is dominated by warm season grasses and contains rich biodiversity of forbs. Given the relatively high precipitation, this region is susceptible to woody plant encroachment if fire is excluded (e.g., Knight et al., 1994). Management of tallgrass prairie by mowing maintains productivity and diversity (Collins et al., 1998), can prevent encroachment of woody plants, and provide a potential source of biofuel.

Of the woody species encroaching the southern Great Plains, eastern redcedar (*Juniperus virginiana*) is of particular concern in Oklahoma, Texas, Nebraska, and Kansas. Eastern redcedar is a shade-intolerant, drought-resistant, evergreen species with a long growing season (Lawson, 1990). Even in winter, eastern redcedar is physiologically active if temperatures are above freezing (Caterina et al., 2014). It is estimated that 7 million hectares of grassland have been encroached by eastern redcedar in the Great Plains (McKinley et al., 2008). Wang et al. (2017) estimated that eastern redcedar encroachment in Oklahoma has expanded by 8% per year since 1984. Once the encroachment process begins, native tallgrass prairie can convert to a closed-canopy eastern redcedar forest in as few as 40 years (Briggs et al., 2002). Encroachment by eastern redcedar is not irreversible, and redcedar woodland can be converted back to prairie through mechanical treatment and reinstitution of prescribed fire. An alternative is to convert encroached areas into switchgrass stands for biofuel feedstock production, which restores a grassland ecosystem and possibly increases water yield.

The Cross Timbers forest, which was historically dominated by post oak (*Quercus stellata*) and blackjack oak (*Q. marilandica*), occurs at the western edge of the eastern deciduous forest and is interwoven with tallgrass prairie ecosystems in eastern Kansas, central Oklahoma, and central Texas, USA. The Cross Timbers oak forest also has changed in response to fire exclusion, converting from open-canopy woodland to closed-canopy forest (DeSantis et al., 2010, 2011). Additionally, fire exclusion has allowed the infiltration of fire-sensitive species such as eastern redcedar, *Ulmus* spp., and *Celtis* spp. (Hoff, Will, Zou & Lillie, 2018) into the oak forest. These changes have degraded wildlife habitat, increased fuels for wildfire, reduced the quality of recreational activities (Joshi et al., 2019) and reduced biodiversity (van Els et al., 2010). Thinning operations to reduce stand density or harvests to regenerate the oak forest could improve and restore ecosystem services (Joshi et al., 2019). Given the lack of forest product markets in the region, use of Cross Timbers forests as a biofuel feedstock would not compete with traditional markets for pulpwood or fiber.

The purpose of this study was to better quantify the productivity and ecosystem water use of cultivated switchgrass stands and degraded ecosystems encroached by eastern redcedar as compared to native Cross Timbers oak forest and

tallgrass prairie ecosystems. Water use efficiency (WUE), i.e., carbon gain per water loss, is critical to assess the trade-off between carbon uptake and water use. WUE is essential for optimizing biomass production and water yield under water-limited situations. WUE can be estimated from instantaneous to annual time steps and from the leaf- to the regional-scales using techniques measuring leaf-level gas exchange, direct ecosystem fluxes, and satellite-based estimates (see review by Kang & Kang, 2019). We focus on robust, empirical measurements of ET and aboveground net primary production (ANPP) at the watershed scale, which is most appropriate for direct estimation of biofuel feedstock production and water consumption at an annual time step.

Specifically, the objectives of our study were to (1) compare the ANPP of watersheds composed of eastern redcedar woodland, native tallgrass prairie, cultivated switchgrass, and native Cross Timbers oak forest for years ranging from above to below average precipitation and (2) compare the WUE and ET of these same ecosystems. Based on previous studies, our first hypothesis was that ANPP would be greatest in the switchgrass and oak-dominated forest followed by eastern redcedar encroached areas, and then native prairie. For instance, productivities as high as 14.9 Mg ha^{-1} $year^{-1}$ were calculated for a Cross Timbers oak forest (Johnson & Risser, 1974), productivities between 7.3 and 10.4 Mg ha^{-1} $year^{-1}$ were calculated for eastern redcedar woodland (Norris et al., 2001), and productivity of approximately 4.0 Mg ha^{-1} $year^{-1}$ was measured for upland areas of tallgrass prairie (Nelson et al., 2006). While the ANPPs of the vegetation cover types we studied were previously measured elsewhere, ours is the first effort to measure them all in one location over the same time intervals to eliminate confounding influences. Our second hypothesis was the forested ecosystems would have higher watershed-level WUE than switchgrass and native prairie. We expected that the productivity of the forests would be proportionately greater per unit increase in ET compared to grasslands (Webb et al., 1978). Comparing switchgrass to tallgrass prairie, we expected switchgrass to have greater WUE due to both greater productivity and lower ET (Wagle & Kakani, 2014; Zeri et al., 2013).

2 | MATERIALS AND METHODS

2.1 | Site description

This study was conducted at the Oklahoma State University Cross Timbers Experimental Range (CTER) which is on 710 hectares located 15 km southwest of Stillwater, Payne County, Oklahoma, USA (36°03′46.73″N, 97°11′03.33″W, and elevation approximately 330 m.a.s.l.). Average annual temperature is 15°C with an average monthly minimum of −3.2°C in January and an average monthly maximum of 33.3°C in July. The long-term annual average precipitation was 880 mm (Yimam et al., 2015). The Cross Timbers Experimental Range sits along the ecotone between the eastern deciduous forest and the southern Great Plains. This region was a mix of tallgrass prairie and relatively short-statured (~15 m tall) Cross Timbers forest. Following the Land Run in 1889, most of the prairie at this location was plowed to grow cotton (*Gossypium* spp.) and later abandoned in the 1950s and the fields naturally reseeded as native prairie. Eastern redcedar began to appear on the landscape by the 1970s and as of 2011, it had an estimated cover of 75% in areas where it had encroached.

There were nine experimental watersheds, i.e., catchments, ranging in size from 1.3 to 4.6 ha: two originally tallgrass prairie watersheds (G1, G2) composed of approximately 85% graminoid:15% forb as estimated from biomass sampling, four watersheds originally encroached by eastern redcedar (F1–F4), and three oak watersheds (D1–D3; Figure 1). In July 2015, eastern redcedar was cut on two of the four encroached watersheds (F3, F4), allowed to dry for 6 months, and then removed. One of the two cut watersheds revegetated naturally (F4).

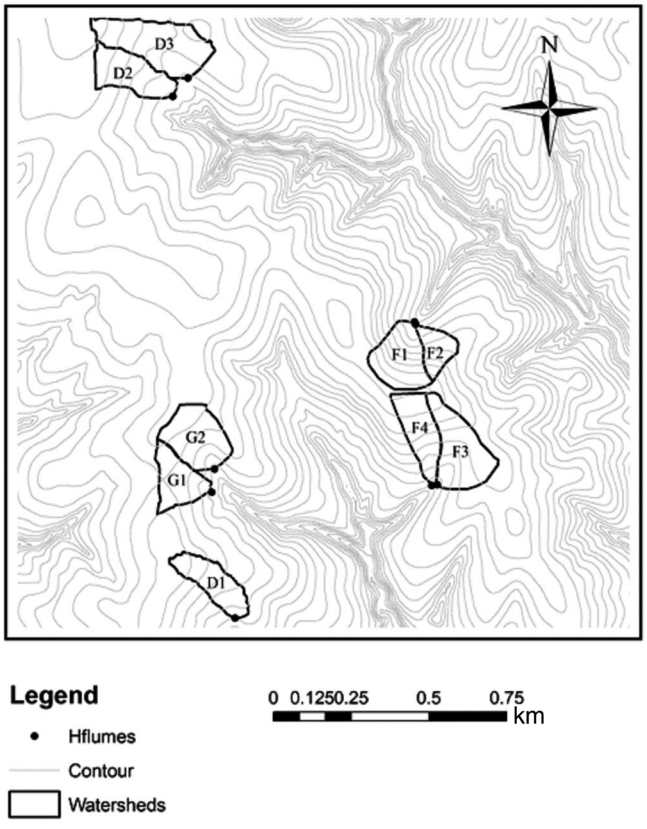


FIGURE 1 Topographic imagery of the ten experimental watersheds at the Oklahoma State University Cross Timbers Experimental Range (CTER) near Stillwater, Oklahoma, USA. Refer to Table 1 for description of each watershed. Created on June 21, 2019. At the time of study, D1–D3 were oak watersheds, F1 and F2 were eastern redcedar woodland, F3 and G2 were switchgrass, and F4 and G1 were native prairie. Contour lines indicate 2 m intervals

The other cut watershed (F3) and one of the grassland watersheds (G2) were treated with herbicide in spring and summer of 2016 and again in spring of 2017 to eliminate herbaceous vegetation. In April 2017, switchgrass was planted on these two watersheds using the lowland cultivar "Alamo". No fertilizer was applied. The aboveground biomass of the switchgrass was cut at ~10 cm in height annually after first frost and removed from the treatment areas. Soils at the study site were mainly of loamy texture with the most common soil series being Stephenville-Darnell complex which comprised 38% of the total land area at CTER and covered over 50% of five of the watersheds (Tables 1 and 2).

2.2 | Aboveground net primary production

Twenty 0.04 ha plots were located within each of the oak and eastern redcedar encroached watershed and trees within plots were permanently tagged to allow for annual diameter measurements. Initial measurements were taken in early

TABLE 1 Watershed name, vegetation, area, and soil series[a] of nine watersheds located at Oklahoma State University Cross Timbers Experimental Range near Stillwater, Oklahoma, USA

Watershed	Vegetation	Area (m^2)	Soil series	Watershed percentage (%)
D1	Oak 1	23,853	Stephenville-Darnell complex, 3–8 percent slopes, rocky	100
D2	Oak 2	28,297	Doolin silt loam, 1–3 percent slopes	4
			Coyle loam, 3–5 percent slopes, eroded	47
			Coyle and Zaneis soils, 3–5 percent slopes, severely eroded	12
			Stephenville fine sandy loam, 3–5 percent slopes	35
			Renfrow loam, 3–5 percent slopes, eroded	2
D3	Oak 3	46,528	Renfrow loam, 3–5 percent slopes, eroded	8
			Coyle and Zaneis soils, 3–5 percent slopes, severely eroded	1
			Coyle loam, 3–5 percent slopes, eroded	23
			Stephenville fine sandy loam, 3–5 percent slopes	68
G1	Prairie	22,872	Coyle Loam, 1–3 percent slopes	20
			Harrah-Pulaski complex, 0–12 percent slopes, very rocky	15
			Stephenville-Darnell complex, 3–8 percent slopes, rocky	64
			Zaneis-Huska complex, 1–5 percent slopes	1
G2	Prairie→Switchgrass	33,211	Coyle Loam, 3–5 percent slopes	18
			Coyle Loam, 1–3 percent slopes	15
			Stephenville-Darnell complex, 3–8 percent slopes, rocky	67
F1	Cedar 1	29,866	Coyle and Zaneis soils, 3–5 percent slopes, severely eroded	2
			Grainola-Lucien complex, 5–12 percent slopes	7
			Stephenville-Darnell complex, 3–8 percent slopes, rocky	91
F2	Cedar 2	13,449	Coyle and Zaneis soils, 3–5 percent slopes, severely eroded	56
			Grainola-Lucien complex, 5–12 percent slopes	22
			Stephenville-Darnell complex, 3–8 percent slopes, rocky	22
F3	Cedar→Switchgrass	37,899	Renfrow and Grainola, 3–8 percent slopes, severely eroded	29
			Stephenville fine sandy loam, 3–5 percent slopes, eroded	9
			Coyle-Lucien complex, 1–5 percent slopes	20
			Grainola-Lucien complex, 5–12 percent slopes, rocky	13
			Stephenville-Darnell complex, 3–8 percent slopes, rocky	29
F4	Cedar→Prairie	25,737	Renfrow and Grainola soils, 3–8 percent slopes, eroded	11
			Stephenville fine sandy loam, 3–5 percent slopes, eroded	8
			Grainola-Lucien complex, 5–12 percent slopes, rocky	3
			Stephenville-Darnell complex, 3–8 percent slopes, rocky	78

[a]Soil series were obtained from the NRCS Web Soil Survey.

TABLE 2 Taxonomic classification of the soils series[a] found at Oklahoma State University Cross Timbers Experimental Range near Stillwater, Oklahoma, USA

Soil series	Taxonomic classification
Coyle	Fine-loamy, siliceous, active, thermic Udic Argiustolls
Darnell	Loamy, siliceous, active, thermic, shallow Udic Argiustolls
Doolin	Fine, smectitic, thermic Typic Natrustolls
Grainola	Fine, mixed, active, thermic Udertic Haplustalfs
Harrah	Fine-loamy, siliceous, active, thermic Ultic Paleustalfs
Huska	Fine, mixed, superactive, thermic Mollic Natrustastalfs
Lucien	Loamy, mixed, superactive, thermic, shallow Udic Haplustolls
Pulaski	Coarse-loamy, mixed, superactive, nonacid, thermic Udic Ustifluvents
Renfrow	Fine, mixed, superactive, thermic Udertic Paleustolls
Stephenville	Fine-loamy, siliceous, active, thermic Ultic Haplustalfs
Zaneis	Fine-loamy, siliceous, active, thermic Udic Argiustolls

[a]Soil series were obtained from the NRCS Web Soil Survey.

TABLE 3 Allometric equations for standing dry biomass of eastern redcedar predicted from tree DBH (diameter at breast height; 1.37 m)[a]

	Open grown[b,c]				
Component	y^0	a	x^0	b	R^2
Total tree	−91.3	1190	28.1	10.3	0.987
Bole	−11.9	384	35.0	9.81	0.993
Live branch	−40.7	585	31.9	11.1	0.956
Foliage	0	209	18.9	4.64	0.973
	Closed grown[d]				
Component	y^0	a		b	R^2
Total tree	1.10	0.0774		2.46	0.989
Bole	1.72	0.0228		2.68	0.985
Live branch	−0.538	0.0204		2.32	0.996
Foliage	0	0.0612		1.89	0.987
Dead branch	−0.134	0.0274		2.12	0.832

[a]From Lykins (1995) and our destructive sampling.

[b]$Y = y^0 + a/(1 + \exp(-(\text{DBH} - x^0)/b))$. Y is predicted biomass in kilograms and diameter is in centimeters.

[c]Equation for open grown dead branches not shown in table: $Y = -3.2526 + 0.5668*\text{DBH} + (-0.0302)*\text{DBH}^2 + 0.0006*\text{DBH}^3$. $R^2 = 0.90$. Y is predicted biomass in kilograms and diameter in centimeters.

[d]$Y = y^0 + a*\text{DBH}^b$. Y is predicted biomass in kilograms and diameter in centimeters.

2016 and trees were identified by species. All tree measurements were taken between growing seasons, i.e., November to February, through 2019. Diameter was measured at breast height (DBH; 1.4 m) using a diameter tape to the nearest mm. Erroneous measurements, of which there were approximately 40, were resolved by averaging the previous and next diameter measurements.

Aboveground eastern redcedar dry biomass was calculated using locally derived allometric equations. Data for the allometric equations were acquired from Lykins (1995) for trees with DBH ranging from 13 to 50 cm. To extend the equations to smaller trees, we destructively sampled eight trees ranging in DBH from 1.1 to 7.2 cm. These data were combined with those from Lykins (Supplemental S1) and equations were fit. Eastern redcedar trees measured on the watersheds were classified based on growing conditions: open-grown trees and closed-grown trees. Open-grown trees were growing without aboveground competition and had live branches along the entire stem. Closed-grown trees were growing with canopy competition and often had branches only on the upper half or less of the stem. Different allometric equations were used to calculate biomass for the two contrasting growth forms. Equations of eastern redcedar biomass were fit for bole, live branch, foliage, dead branch, and total tree independently ($R^2 > 0.95$; Table 3). Aboveground dry biomass for oak and remaining species was calculated using equations from Clark et al. (1986) which used different equations for trees smaller and larger than 30 cm DBH.

Each of the twenty plots in the eastern redcedar watersheds also contained a 0.5 m^2 litter trap to collect litter and estimate annual foliage production. Litter was collected every 6 weeks and dried at 60°C and then weighed to the nearest 0.01 g. The fraction of total redcedar foliage shed each year was estimated as 14% by comparing the biomass of collected litter to the total standing foliage biomass. Therefore, annual foliage production of eastern redcedar was calculated by multiplying standing foliage by 0.14.

For all trees, ANPP for the growing seasons 2016–2019 was determined by the difference in aboveground biomass between successive years. Eastern redcedar biomass was calculated in kilograms and all other species including oak were calculated in pounds (original equations) and converted to kilograms. Per hectare ANPP for the woody component was calculated by summing trees within plots, averaging the 20 plots within a watershed, and scaling to the hectare basis.

Herbaceous biomass produced during the current year was measured using twenty 0.25 m^2 quadrats in each watershed. Plots were located randomly in the grassland watersheds and were measured near the litter traps in each forested watershed plot. All biomass within each quadrat was clipped and placed into paper bags. Samples were placed in a drying oven at 60°C until constant weight

and then weighed to the nearest 0.01 g. Plots were sampled each year after the growing season in October or November. Herbaceous biomass was measured in g m^{-2} and converted to kg ha^{-1}. The total ANPP was calculated as the sum of tree ANPP and herbaceous ANPP for growing seasons 2016–2019 and converted to Mg ha^{-1}. No measure of ANPP was available for the switchgrass watersheds for the 2016 growing season because the watersheds were mostly kept clear of living vegetation in preparation for the planting in spring 2017. Herbaceous ANPP was not measured in 2016 for the D1 and in 2017 for the D2 and D3 watersheds. To estimate the missing values, we calculated and applied the average percentage of total ANPP that herbaceous growth composed in these watersheds for the other 3 years. The percentages used were 7.1, 8.4, and 11.3 for the D1, D2, and D3 watersheds, respectively.

2.3 | Precipitation, runoff, and evapotranspiration

Precipitation was measured using automatic tipping bucket rain gauges (model TAB3, Hydrological Services America). Gauges were located at four locations across CTER: one in a native grassland watershed, one in a cut eastern redcedar watershed, one in an opening near a redcedar watershed, and one in an opening near an oak watershed. Total precipitation was calculated as the average of the four locations.

Water yield was continuously measured from all nine watersheds. H-flumes were installed at the outlet of each watershed which measured event-based runoff volume by gauging water level using stilling wells equipped with floats and optical shaft encoders (0.25 mm resolution, 50386SE-105 HydroLynx). Water level in the flumes was recorded every 5 min using CR200 or CR1000 dataloggers (Campbell Scientific). Annual runoff depth was calculated by dividing the total runoff volume by the area of the watershed.

For 2016–2019, precipitation and runoff events were grouped by the United States Geological Survey water year which runs from October 1st of the previous year to September 30th of the current year. This matched the growing season effects better than calendar year because precipitation after October did not influence the current growing season but helped recharge soil moisture for the coming growing season. For instance, the 2016 water year included rainfall and runoff collected from October 2015 until September 2016 and corresponded to biomass data for the 2016 growing season.

For an upland watershed without surface water inflow, for any given period, the total precipitation input is balanced by output (ET, runoff, deep recharge), and the change in soil water storage in the rooting zone. As a result, ET = precipitation – runoff – deep recharge – change in soil water storage. The deep recharge for these upland watersheds is very low and negligible for water balance calculation (Acharya et al., 2017) as is the change in soil water storage at the end of each water year. For a given water year, therefore, the annual ET for these upland watersheds was estimated as the difference between water year precipitation and runoff. WUE was evaluated at the watershed level as the ratio between ANPP (kg ha^{-1} y^{-1}) and ET (mm y^{-1}).

2.4 | Data analysis

Data were analyzed using mixed effects models (SAS ver 9.4) with year as a repeated measures factor (2017–2019 growing seasons). We did not include the 2016 growing season in these analyses because switchgrass stands had not yet been established. Watersheds served as replicates of the four treatments: eastern redcedar ($n = 2$), oak ($n = 3$), switchgrass ($n = 2$), and prairie ($n = 2$). The 'pdiff' statement was used within 'proc mixed' to conduct mean separation as needed. Statistical significance was assumed $p < 0.05$.

3 | RESULTS

In total, 3571 trees were initially measured for DBH across the five forested watersheds. From 2015 to 2019, 28 trees died. Mean tree DBH among the watersheds in 2019 ranged from 11.5 cm in the Oak 1 watershed to 15.3 cm in the Oak 3 watershed. The average DBH of all trees increased from 12.5 cm in 2015 to 13.8 cm in 2019. Basal area (BA) was greatest in the Cedar 1 watershed for all 4 years, and in 2019 was 27.8 m^2 ha^{-1}. The smallest was 9.4 m^2 ha^{-1} in the Oak 1 watershed. Average BA grew from 14.1 to 16.7 m^2 ha^{-1} between the end of 2015 and the end of the 2019 growing seasons.

Tree standing biomass in 2019 ranged from 46.7 Mg ha^{-1} in the Oak 1 watershed to 116.8 Mg ha^{-1} in the Cedar 1 watershed (Figure 2). Total standing biomass of the oak watersheds averaged 67.3 Mg ha^{-1} and the eastern redcedar watersheds averaged 90.3 Mg ha^{-1} in 2019. The biomass of the Cedar 1 watershed was significantly greater than all other forested watersheds ($p < 0.0001$) and the Cedar 2 was significantly greater than Oak 1 watershed ($p < 0.0001$). The Oak 2 and Oak 3 watersheds had significantly greater tree standing biomass than Cedar 2 and Oak 1 watersheds ($p < 0.001$) but were not significantly different from one another. Overall, average standing biomass of the trees increased from 62.8 Mg ha^{-1} after the 2015 growing season to 76.6 Mg ha^{-1} after the 2019 growing season. In the eastern

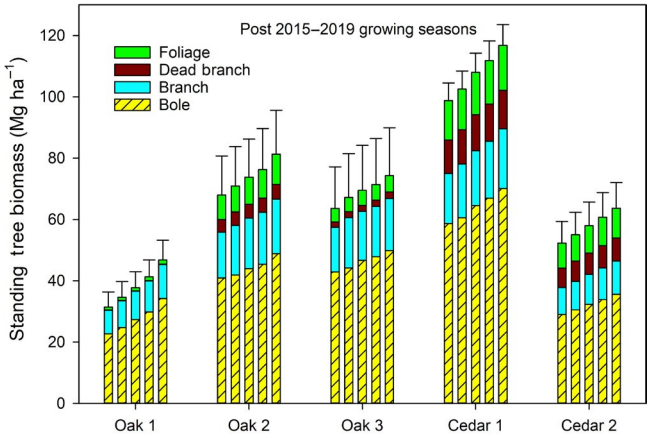


FIGURE 2 Standing biomass (Mg ha^{-1}) of forested watersheds broken into components of bole, branches, dead branches, and foliage. Bars represent the individual years measured after the 2015 to 2019 growing seasons. Dead branch was only calculated for eastern redcedar because they retain dead branches for extended periods of time. Vertical bars represent +SE of total biomass

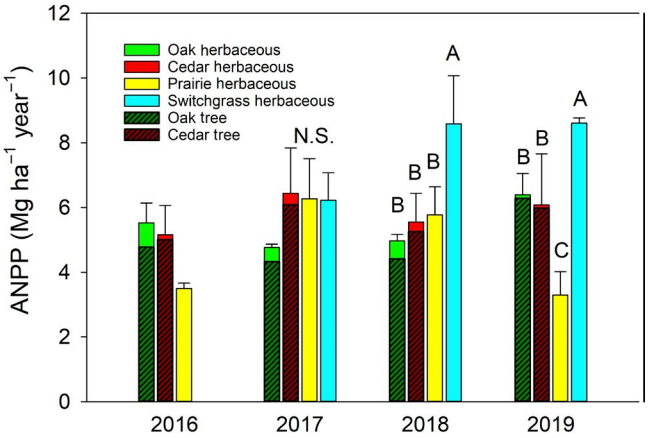


FIGURE 3 Aboveground net primary production (ANPP) for growing seasons 2016–2019 separated into woody and herbaceous components. Vertical bars indicate standard error for total ANPP. No measurements were possible for the switchgrass watersheds in 2016 as they lacked vegetation during the transition. Statistical analysis only for 2017–2019

redcedar watersheds, 58% of the biomass was composed of the bole, 17% by branches, 11% by dead branches, and 14% by foliage. In the oak watersheds, 66% of the biomass was composed of the bole, 23% by branches, 3% by dead branches, and 7% by foliage (Figure 2). In 2019, the percent of total tree biomass made up by eastern redcedar of Cedar 1 and Cedar 2 watersheds was 91% and 99%, respectively. Oak species composed 95% and 66% of the Oak 1 and Oak 3 watersheds, respectively. The Oak 2 watershed had 62% eastern redcedar and 36% oak in 2019. The percentage of biomass composed of other tree species (non-oak and non-redcedar) ranged from 0.1% to 7%.

For all growing seasons, the measured ANPP of the prairie and switchgrass watersheds was composed entirely of herbaceous plants. For the eastern redcedar and oak watersheds, the percent of herbaceous ANPP ranged from 0.6% to 16.4% (Figure 3). Overall, the effect of treatment ($p = 0.042$) and the treatment × year interaction ($p = 0.048$) for ANPP were significant. The overall average ANPP ranged from 5.9 Mg ha^{-1} year^{-1} in 2017 to 6.2 Mg ha^{-1} year^{-1} in 2018. Among vegetation cover types, ANPP averaged across the 2017–2019 growing seasons was 5.1, 5.4, 6.0, and 7.8 Mg ha^{-1} year^{-1} for the prairie, oak, eastern redcedar, and switchgrass watersheds. However, the interaction between vegetation cover type and year occurred because the ANPP of the switchgrass watersheds was similar to other vegetation cover types in the first year of establishment (2017; n.s.) and significantly increased relative to the others in the second (2018) and third (2019) year after establishment (Figure 3). The ANPP of switchgrass watersheds in 2019 was 8.6 Mg ha^{-1} year^{-1}, while the maximum ANPP for the other vegetation cover types ranged from 6.2 to 6.4 Mg ha^{-1} year^{-1}. In 2019, the ANPP of the prairie watersheds was significantly lower than the forested watersheds.

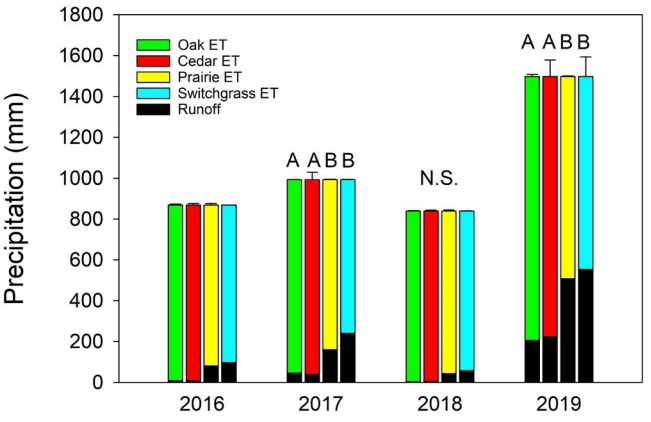


FIGURE 4 Total precipitation (mm) for the years 2016–2019 separated into runoff and evapotranspiration (ET). Total precipitation was calculated based on water year (October to September). Vertical bars indicate SE of ET. Statistical analysis only for 2017–2019

Between 2016 and 2018, precipitation ranged between 868 and 992 mm year^{-1} and averaged 900 mm year^{-1} (Figure 4). The 2019 water year was exceptionally wet with 1498 mm, which increased the average of the 4 years to 1049 mm year^{-1}. Additional details of intra-annual precipitation were provided by Zhong et al. (2020). Not surprisingly, runoff followed similar trends as annual precipitation and was 48, 120, 26, and 371 mm year^{-1} in 2016–2019, respectively. During the period after switchgrass establishment (2017–2019), runoff was greater ($p < 0.008$) in the grassland watersheds than in the forested watersheds, i.e., 235 and 281 mm year^{-1} in the prairie and switchgrass watersheds and 87 and 84 mm year^{-1} in the eastern redcedar and oak watersheds.

The lower volumes of runoff for the eastern redcedar and oak watersheds were presumably due to greater

ET (Figure 4). For the statistical analysis that included years after switchgrass establishment (2017–2019), the effects of year ($p < 0.0001$), vegetation cover type ($p < 0.0001$), and year × cover type interaction ($p = 0.002$) were all highly significant. For the 2019 water year which had almost 1500 mm of precipitation, ET averaged 1126 mm year^{-1} across treatments which was higher than the 872 and 913 mm year^{-1} in 2017 and 2018. Averaged across 2017–2019, ET was greater in the forested watersheds than the grassland watersheds (1022 mm year^{-1} for cedar, 1025 mm year^{-1} for oak, 874 mm year^{-1} for prairie, and 828 mm year^{-1} for switchgrass). However, the differences between forested and grassland watersheds were only statistically significant in 2017 and 2019 (Figure 4). The water year 2018 had the lowest precipitation (813 mm) which resulted in almost all precipitation partitioned to ET regardless of vegetation cover type.

When analyzed for the period after switchgrass establishment (2017–2019), WUE significantly varied with year ($p = 0.01$) and vegetation cover type ($p = 0.0007$), and the effects of vegetation cover type were consistent among years (year × cover type $p = 0.20$). Overall, WUE was inversely related to annual precipitation and was 6.88, 7.69, and 5.54 kg ha^{-1} mm^{-1} for 2017, 2018, and 2019, respectively (Figure 5). WUE in 2019 was significantly lower than in 2017 ($p = 0.057$) or 2018 ($p = 0.003$). Averaged across 2017–2019, WUE was significantly greater for the switchgrass cover type ($p < 0.001$) than the other cover types, which were not statistically different from one another. The mean WUE was 9.47 kg ha^{-1} mm^{-1} for switchgrass and 6.03, 6.02, and 5.31 kg ha^{-1} mm^{-1} for the prairie, eastern redcedar, and oak cover types (Figure 5).

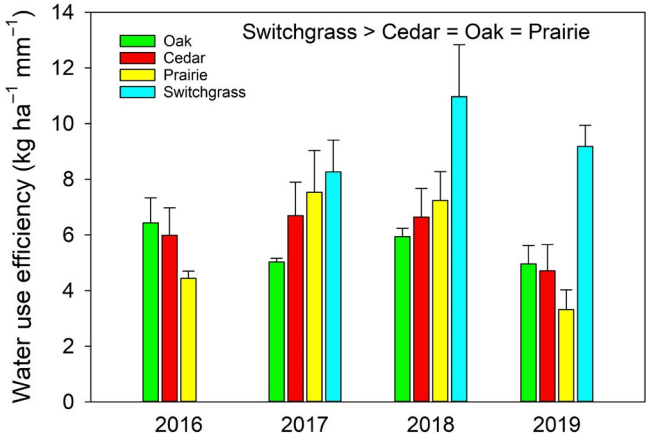


FIGURE 5 Water use efficiency for 2016–2019 water years calculated as the ratio of aboveground net primary production and evapotranspiration. No measurements were possible for the switchgrass watersheds in 2016 as they lacked vegetation. Vertical bars indicate SE. Statistical analysis only for 2017–2019

4 | DISCUSSION

We hypothesized that ANPP and WUE in the forested watersheds would generally be greater than or similar to the grassland watersheds. In contrast, we found that both ANPP and WUE were greatest for the switchgrass watersheds, with prairie mostly similar to the forest ecosystems. The greater WUE of the switchgrass watersheds was driven by both greater ANPP (numerator) and lower ET (denominator). Much of our initial expectation of greater WUE in forested ecosystems was based on previously reported rates of WUE using eddy flux and satellite-based estimates, e.g., Ponton et al. (2006) and Tian et al. (2010), and on a previous comparative study using direct measurement of runoff and ANPP (Webb et al., 1978). Webb et al. (1978) compared WUE of grassland and forest sites throughout the USA. They found WUE of grasslands to range from approximately 3 to 5 kg ha^{-1} mm^{-1} and that ANPP increased with ET. For forest sites, they found WUE ranging between 8 and 14 kg ha^{-1} mm^{-1}, but fairly constant ANPP of approximately 8 Mg ha^{-1} year^{-1} as ET increased from 500 to 1000 mm year^{-1}. One major difference between their meta-analysis and our research is that our watersheds were co-located in an area where precipitation is marginal for forests but adequate for tallgrass prairie and switchgrass stands. Webb et al. (1978) acknowledge that they did not address the transition between water abundance and water limitation for forest ecosystems. In our case, WUE was lower for forest systems and similar to prairie likely because of water limitation or because of the slower growth rate of the more drought-adapted tree species. In contrast, even without fertilizer application, a high-yielding cultivar of switchgrass outperformed both forest and prairie ecosystems. While we expected switchgrass ANPP to outperform prairie, they both used similar amounts of water. Likewise, switchgrass had higher WUE than native grass and a mix of alfalfa (*Medicago sativa*) and native grass in North Dakota, USA mostly due to greater ANPP of switchgrass (Hendrickson et al., 2013).

In locations where water limits productivity, like the southern Great Plains, WUE is an important consideration as it reflects the trade-off between carbon gain and water loss. Ecosystems with greater WUE may outperform those with lower WUE, especially in dry years. This may become more important with climate change as higher temperatures increase evaporative demand and water stress (Breshears et al., 2013; Will et al., 2013). In addition to greater productivity, ecosystems with higher WUE may have greater resistance and resilience of yield to drought.

To calculate WUE, we used the method like the "agronomical approach" described by Tallec et al. (2013) whereby we empirically measured ANPP and ET at an operational scale relevant to biofuel feedstock production that integrates all the processes operating across watershed for an annual time step. As we measured in our study, WUE within a given

ecosystem typically increases with reduced precipitation and increased water stress. Leaf-level estimates of WUE, i.e., photosynthesis divided by either transpiration or stomatal conductance, increased during periods of low soil moisture in eastern redcedar and post oak measured near our site (Torquato, Zou, et al., 2020) and increased with experimental decreases in throughfall for switchgrass (Deng et al., 2017). Likewise, WUE increased with decreasing ET when measured at the watershed scale for forests and tallgrass prairie systems (Webb et al., 1978).

Aboveground net primary production of eastern redcedar watersheds ranged from 4.2 to 7.8 Mg ha^{-1} $year^{-1}$ which was lower than previous measurements in Kansas, USA. Norris et al. (2001) found that eastern redcedar stands in the Great Plains ranged from 7 Mg ha^{-1} $year^{-1}$ in a 70 year old stand to over 10 Mg ha^{-1} $year^{-1}$ for a 35 year old stand from an area with precipitation (average 835 mm per year) similar to our site. Based on aerial imagery and coring of several trees (Nunes Biral et al., 2019; Torquato, Will, et al., 2020), the eastern redcedar in our study were approximately 40 years old. The standing biomass of our eastern redcedar stands (61 and 112 Mg ha^{-1}) also was lower than estimates from Norris et al. (2001) where standing biomass ranged from 114 to 211 Mg ha^{-1}. The lower values of growth and standing biomass in our stands might reflect slower growth rates on the severely eroded upland soils or lower initial stand densities. Our estimates of standing biomass for eastern redcedar were more similar to McKinley (2007) who projected a range of 95–150 Mg ha^{-1} for stands age 30–55 years old in Kansas. Given the scope of eastern redcedar encroachment to the southern Great Plains, our biomass equations provide the basis to accurately estimate standing biomass from field-based measurements that include trees of all diameters. The ability to partition biomass into different components is important for determining not just bole biomass or ANPP, but also foliage and small branches which are important components of wildfire fuels (Hoff, Will, Zou, Weir, et al., 2018).

The ANPP of the oak watersheds in our study of 4.3–7.2 Mg ha^{-1} $year^{-1}$ was lower than the 14.9 Mg ha^{-1} $year^{-1}$ previously calculated for a Cross Timbers forest in central Oklahoma (Johnson & Risser, 1974). However, a survey measuring bole volume growth found a wide span of productivity in the Cross Timbers, from 0 to 4.5 m^3 ha^{-1} $year^{-1}$ (Rossen, 1989), indicating great variation in productivity depending on stand and site conditions. At a broader scale, Rodin and Bazilevich (1967) provided a range of ANPP estimates of 4–20 Mg ha^{-1} $year^{-1}$ for temperate deciduous forests and our oak watersheds fall within the lower part of this range. Post oak is a slow growing species and its growth is sensitive to low precipitation (Stahle & Hehr, 1984). A subset of post oaks measured at our site averaged 95 years old (Torquato, Will, et al., 2020). Another factor that impacted the productivity of the oak watersheds was the encroachment of eastern redcedar into the forest. Depending on the nature of interspecific competition, this could increase or decrease ANPP. At a location in our watersheds, Torquato, Zou, et al. (2020) found complementary interactions between eastern redcedar and post oak, possibly due to niche separation in depth of rooting and differential water uptake, i.e., eastern redcedar likely more shallow rooted and post oak more deeply rooted.

In the forested watersheds, standing bole biomass reached 70 Mg ha^{-1} and was increasing annually. In a biofuel feedstock production system that integrates woody and herbaceous biomass, the forest systems can provide large amounts of biomass if harvested periodically or as part of prairie restoration or switchgrass conversion. Eastern redcedar biomass is a viable biofuel option (e.g., Liua et al., 2015; Ramachandriya et al., 2013) that offers the advantage of temporal flexibility, both within and between years, as the wood continues to accumulate while biomass is "stored on the stump" until needed. While the forests provide flexibility regarding harvesting, not all of the biomass produced annually is available, i.e., foliage and branches are not typically harvested.

The ANPP of the tallgrass prairie watersheds ranged from 2.5 to 7.5 Mg ha^{-1} $year^{-1}$ depending on the year and watershed which is similar to other estimates of non-grazed and non-burned tallgrass prairie that ranged from 0.5 to 6 Mg ha^{-1} (Abrams et al., 1986; Norris et al., 2001; Sala et al., 1988; Sims & Singh, 1978). Aboveground net primary production of the eastern redcedar watershed converted to prairie reached a peak in 2018 which was the third year after harvesting the eastern redcedar. This dynamic may have been related to a lag in productivity with establishment and then a decrease in 2019 as the pulse of nutrients available post disturbance declined and litter accumulated. Our estimates of ANPP in the prairie would likely be higher with either fire or harvesting to reduce interference from litter and to release nutrients (Knapp & Seastedt, 1986; Ojima et al., 1994).

After the first year, ANPP of the switchgrass watersheds averaged 8.6 Mg ha^{-1} $year^{-1}$ which was similar to the Alamo cultivar planted operationally at other upland locations in Oklahoma with similar precipitation (5.7–7.6 Mg ha^{-1} $year^{-1}$; Caddel et al., 2010) but much lower than the 16.0–19.7 Mg ha^{-1} achieved with fertilization and irrigation in southern Oklahoma (Kering et al., 2012). Our switchgrass stands were not fertilized and were planted on upland sites severely eroded from previous agriculture. Future productivity may become nutrient limited as the pulse of nutrient availability post disturbance declines and nutrients contained in aboveground biomass are removed during annual harvest.

Trends in ANPP of the various vegetation cover types in relation to precipitation were not obvious. For instance, 2019 had >50% more precipitation than the other years, but ANPP was not substantially higher. Part could be a lack

of sensitivity. For instance, Deng et al. (2017) experimentally reduced throughfall and switchgrass only showed a decrease in ANPP at a 50% reduction (~600 mm). Likewise, post oak and eastern redcedar are relatively slow growing and possibly less able to take advantage of above average precipitation. In addition, ANPP is often influenced by previous-year (e.g., Oesterheld et al., 2001; Sala et al., 2012) as well as current-year precipitation such that the benefits of higher precipitation in 2019 may partially manifest in 2020.

Evapotranspiration is the combination of transpiration and evaporation. Given there was very little bare ground, most of the evaporation component came from evaporation of water intercepted by the canopies and litter layers. At these same sites, Zou et al. (2015) measured canopy interception of 36% for eastern redcedar that was fairly consistent throughout the year. Interception by intact tallgrass prairie vegetation increased with canopy development during the growing season and the annual interception loss could be as high as eastern redcedar. In our study, switchgrass was harvested in November which would reduce some of the losses to interception during winter. We did not estimate interception in oak, but annual estimates may be lower than in eastern redcedar because oak is deciduous.

The effects of vegetation cover type on runoff for these watersheds have been previously discussed for results through 2018 (Qiao et al., 2017; Zhong et al., 2020; Zou et al., 2014). The extremely wet 2019 resulted in runoff that was by far greater than previous years indicating that precipitation likely exceeded potential ET for most of the year. Therefore, the ET results from 2019 likely indicate near maximum ET for the various vegetation cover types, i.e., 1200–1300 mm for the forested watersheds and 900–1000 mm for the grassland watersheds. These differences are in the range reported by Liu et al. (2014) who measured annual ET 10% greater from forests than adjacent grasslands. However, we did not measure deep recharge such that our calculations of ET in 2019 might be overestimated if recharge was greater during 2019 than other years.

The factors contributing to differences in the transpiration component of ET among vegetation cover types in our study were very complicated. Among vegetation cover types there are differences in canopy leaf area, timing of transpiration, and leaf-level rates of transpiration. For instance, eastern redcedar can transpire year-round in Oklahoma given its evergreen nature (Caterina et al., 2014) while the grasses and oak do not transpire following first frost (grassland) or leaf drop (oak). Leaf area-based rates of transpiration are approximately 10x greater for post oak than eastern redcedar (Torquato, Zou, et al., 2020) while forb transpiration is greater than grasses or broadleaf woody plants (O'Keefe & Nippert, 2018). While mechanisms driving differences in ET are difficult to tease apart at the spatial and temporal scale we addressed, our measurements are robust for estimating whole ecosystem ET at an annual time scale which is of most relevance for our research questions.

Switchgrass is a component of native tallgrass prairie in the Great Plains and has the potential to be used in a restorative capacity. Converting from eastern redcedar to switchgrass production recreates a grassland ecosystem and may restore many of the ecosystem services that native prairie provide with an additional service of biofuel feedstock production. In terms of water quantity, the switchgrass stands had similar, if not greater, runoff compared to prairie or forest watersheds. Therefore, removing eastern redcedar and planting switchgrass may have the capacity to restore streamflow and groundwater recharge. The oak-dominated Cross Timbers forest historically occurred throughout the region, but at lower stand densities and more open canopy structure (DeSantis et al., 2010, 2011; Hoff, Will, Zou, Weir, et al., 2018). Harvest of the oaks as part of thinning or forest regeneration operations could capture a source of biofuel feedstock while enhancing important ecosystem services related to wildlife, wildfire fuels reduction, recreation, and water yield (Joshi et al., 2019).

At the transition zone between the subhumid and arid region in the southern Great Plains, switchgrass out-produced the relatively slow-growing Cross Timbers oak forest and eastern redcedar woodlands. When compared to forest ecosystems, switchgrass yields may be more resilient to climate change and variation in precipitation (Deng et al., 2017) and may thrive in warmer temperatures and elevated CO_2 (Brown et al., 2000). In contrast, climate change has been pushing the boundary of the humid region capable of supporting trees eastward (Seager, Feldman, et al., 2018). Native tallgrass prairie, which is dominated by warm season (C4) grasses, including switchgrass, may be more resilient than pure switchgrass stands due to its greater biodiversity. However, prairie had yields significantly lower than switchgrass in both dry and wet years. Overall, our findings indicate that an integrated biofuel feedstock system that includes converting eastern redcedar encroached areas to switchgrass, as well as thinning the oak forest, can increase productivity, increase runoff to streams, and generally improve ecosystem services. However, continued study of the long-term effects are necessary.

ACKNOWLEDGEMENTS

Funding was provided by National Institute of Food and Agriculture AFRI Sustainable Bioenergy program (2014-67010-21653), National Science Foundation (OIA-1946093), McIntire-Stennis (OKL0 2931 and OKL0 2929), and the Oklahoma Agricultural Experiment Station. We thank Chris Stansberry and Adam Gourley for help in cutting the eastern redcedar. We thank Jay Prater for help in

planting switchgrass. We also thank Chris Stansberry, Erich Wehrenberg, Chet Venard, and Jason Walker for help maintaining watersheds. We thank Nick Brooks, Jake Hammons, Josh Everett, Wade Fisher, Christian Hayes, Katelyn Jeffries, Travis Reddout, and David Wall for assistance collecting field data.

AUTHOR CONTRIBUTION

R.E.W., C.B.Z., and V.G.K. conceived the research idea. K.N.S. and Y.Z. collected data. K.N.S. and R.E.W. analyzed data. K.N.S., R.E.W., C.B.Z., Y.Z., and V.G.K. wrote the manuscript. C.B.Z., R.E.W., and V.G.K. managed and maintained the research site.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ORCID

Rodney E. Will https://orcid.org/0000-0002-4649-8858

REFERENCES

Abrams, M. D., Knapp, A. K., & Hulbert, L. C. (1986). A ten-year record of aboveground biomass in a Kansas tallgrass prairie: Effects of fire and topographic position. *American Journal of Botany*, *73*, 1509–1515.

Acharya, B. S., Hao, Y. H., Ochsner, T. E., & Zou, C. B. (2017). Woody plant encroachment alters soil hydrological properties and reduces downward flux of water in tallgrass prairie. *Plant and Soil*, *414*, 379–391.

Bragg, T. B., & Hulbert, L. C. (1976). Woody plant invasion of unburned Kansas bluestem prairie. *Rangeland Ecology & Management/Journal of Range Management Archives*, *29*, 19–24.

Breshears, D. D., Adams, H. D., Eamus, D., McDowell, N. G., Law, D. J., Will, R. E., Williams, A. P., & Zou, C. B. (2013). The crucial amplifying role of increasing atmospheric moisture demand on tree mortality associated with regional die off. *Frontiers in Plant Science*, *4*, 266. https://doi.org/10.3389/fpls.2013.00266

Briggs, J. M., Hoch, G. A., & Johnson, L. C. (2002). Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. *Ecosystems*, *5*, 578–586.

Briggs, J. M., Knapp, A. K., Blair, J. M., Heisler, J. L., Hoch, G. A., Lett, M. S., & McCarron, J. K. (2005). An ecosystem in transition: Causes and consequences of the conversion of mesic grassland to shrubland. *BioScience*, *55*, 243–254.

Brown, R., Rosenberg, N., Hays, C. J., Easterling, W. E., & Mearns, L. (2000). Potential production and environmental effects of switchgrass and traditional crops under current and greenhouse-altered climate in the central United States: A simulation study. *Agriculture, Ecosystems & Environment*, *78*, 31–47.

Caddel, J., Kakani, G., Porter, D., Redfearn, D., Walker, N., Warren, J., Wu, Y., & Zhang, H. (2010). *Switchgrass production guide for Oklahoma:* E-1012 *Oklahoma Cooperative Extension Service*. Division of Agricultural Sciences and Natural Resources, Oklahoma State University.

Caterina, G. L., Will, R. E., Turton, D. J., Wilson, D. S., & Zou, C. B. (2014). Water use of *Juniperus virginiana* trees encroached into mesic prairies in Oklahoma, USA. *Ecohydrology*, *7*, 1124–1134.

Clark, A., Phillips, D. R., & Frederick, D. J. (1986). *Weight, volume, and physical properties of major hardwood species in the upland-south. Res. Pap. SE-257*. USDA Forest Service, Southeastern Forest Experiment Station, 61 pp.

Collins, S. L., Knapp, A. K., Briggs, J. M., Blair, J. M., & Steinauer, E. M. (1998). Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science*, *280*, 745–747.

Deng, Q., Aras, S., Yu, C.-L., Dzantor, E. K., Fay, P. A., Luo, Y., Shen, W., & Hui, D. (2017). Effects of precipitation changes on aboveground net primary production and soil respiration in a switchgrass field. *Agriculture, Ecosystems & Environment*, *248*, 29–37.

DeSantis, R. D., Hallgren, S. W., Lynch, T. B., Burton, J. A., & Palmer, M. W. (2010). Long-term directional changes in upland *Quercus* forests throughout Oklahoma, USA. *Journal of Vegetation Science*, *21*, 606–618.

DeSantis, R. D., Hallgren, S. W., & Stahle, D. W. (2011). Drought and fire suppression lead to rapid forest composition change in a forest-prairie ecotone. *Forest Ecology and Management*, *261*, 1833–1840.

Engle, D. M., Bidwell, T. G., Moseley, M. E., & Masters, R. E. (1996). *Invasion of Oklahoma rangelands and forests by eastern redcedar and Ashe juniper,* Circular E-947. Oklahoma Cooperative Extension Service, Division of Agricultural Sciences and Natural Resources, Oklahoma State University.

Hendrickson, J. R., Schmer, M. R., & Sanderson, M. A. (2013). Water use efficiency by switchgrass compared to a native grass or a native grass alfalfa mixture. *Bioenergy Research*, *6*, 746–754.

Hoff, D., Will, R., Zou, C., & Lillie, N. (2018). Encroachment dynamics of *Juniperus virginiana* L. and mesic hardwood species into cross timbers forests of North-Central Oklahoma, USA. *Forests*, *9*, 75. https://doi.org/10.3390/f9020075

Hoff, D. L., Will, R. E., Zou, C. B., Weir, J. R., Gregory, M. S., & Lillie, N. D. (2018). Estimating increased fuel loading within the Cross Timbers forest matrix of Oklahoma, USA due to an encroaching conifer, *Juniperus virginiana*, using leaf-off satellite imagery. *Forest Ecology and Management*, *409*, 215–224.

Johnson, F. L., & Risser, P. G. (1974). Biomass, annual net primary production, and dynamics of six mineral elements in a post oak-blackjack oak forest. *Ecology*, *55*, 1246–1258.

Joshi, O., Will, R. E., Zou, C. B., & Kharel, G. (2019). Cross-timbers forest resources: Current knowledge and future research needs. *Sustainability*, *11*, 4703. https://doi.org/10.3390/su11174703

Kang, W., & Kang, S. (2019). On the use of alternative water use efficiency parameters in dryland ecosystems: A review. *Journal of Ecology and Environment*, *43*, 24. https://doi.org/10.1186/s41610-019-0122-7

Kering, M., Butler, T., Biermacher, J., & Guretzky, J. A. (2012). Biomass yield and nutrient removal rates of perennial grasses under nitrogen fertilization. *BioEnergy Research*, *5*, 61–70.

Knapp, A., & Seastedt, T. (1986). Detritus accumulation limits productivity of tallgrass prairie. *BioScience*, *36*, 662–668.

Knight, C. L., Briggs, J. M., & Nellis, M. D. (1994). Expansion of gallery forest on Konza Prairie Research Natural Area, Kansas USA. *Landscape Ecology*, *9*, 117–125.

Lawson, E. R. (1990). Eastern redcedar. In R. M. Burns & B. H. Honkala (Eds.), *Silvics of North America*. Vol. 1. Conifers. USDA Agric. Handb, 654 pp.

Liu, Z., Yao, Z., Huang, H., Wu, S., & Liu, G. (2014). Land use and climate changes and their impacts on runoff in the Yarlung Zangbo river basin, China. *Land Degradation & Development*, *25*, 203–215.

Liua, K., Atiyeha, H. K., Pardo-Planasa, O., Ramachandriyaa, K. D., Wilkins, M. R., Ezejib, T. C., Ujorb, V., & Tanner, R. S. (2015). Process development for biological production of butanol from eastern redcedar. *Bioresource Technology*, *176*, 88–97.

Lykins, R. W. (1995). *Estimation of aboveground eastern redcedar biomass*. MS thesis, Oklahoma State University.

McKinley, D. C. (2007). *Consequences of conversion of native mesic grassland to coniferous forest on soil processes and ecosystem C and N storage*. PhD dissertation, Kansas State University.

McKinley, D. C., Norris, M. D., Blair, J. M., & Johnson, L. C. (2008) Altered ecosystem processes as a consequence of *Juniperus virginiana* L. encroachment into North American tallgrass prairie. In O. W. Van Auken (Ed.), *Western North American Juniperus Communities*. Ecological Studies, vol. 196. Springer.

Nelson, R. G., Ascough II, J. C., & Langemeier, M. R. (2006). Environmental and economic analysis of switchgrass production for water quality improvement in northeast Kansas. *Journal of Environmental Management*, *79*, 336–347.

Norris, M. D., Blair, J. M., Johnson, L. C., & McKane, R. B. (2001). Assessing changes in biomass, productivity, and C and N stores following *Juniperus virginiana* forest expansion into tallgrass prairie. *Canadian Journal of Forest Research*, *31*, 1940–1946.

Nunes Biral, V. C., Will, R. E., & Zou, C. B. (2019). Establishment of *Quercus marilandica* Muenchh. and *Juniperus virginiana* L. in the tallgrass prairie of Oklahoma, USA increases litter inputs and soil organic carbon. *Forests*, *10*, 329. https://doi.org/10.3390/f10040329

O'Keefe, K., & Nippert, J. B. (2018). Drivers of nocturnal water loss in a tallgrass prairie. *Functional Ecology*, *32*, 1155–1167.

Oesterheld, M., Loreti, J., Semmartin, M., & Sala, O. E. (2001). Inter-annual variation in primary production of a semi-arid grassland related to previous-year production. *Journal of Vegetation Science*, *12*, 137–142.

Ojima, D. S., Schimel, D. S., Parton, W. J., & Owensby, C. E. (1994). Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. *Biogeochemistry*, *24*, 67–84.

Ponton, S., Flanagan, L. B., Alstad, K. P., Johnson, B. G., Morgenstern, K., Kljun, N., Black, T. A., & Barr, A. G. (2006). Comparison of ecosystem water-use efficiency among Douglas-fir forest, aspen forest and grassland using eddy covariance and carbon isotope techniques. *Global Change Biology*, *12*, 294–310.

Qiao, L., Zou, C. B., Stebler, E., & Will, R. E. (2017). Woody plant encroachment reduces annual runoff and shifts runoff mechanisms in the tallgrass prairie, USA. *Water Resources Research*, *53*, 4838–4849.

Ramachandriya, K. D., Wilkins, M., Atiyeha, H. K., Dunforda, N. T., & Hiziroglu, S. (2013). Effects of high dry solids loading on enzymatic hydrolysis of acid bisulfite pretreated eastern redcedar. *Bioresource Technology*, *147*, 168–176.

Rodin, L. E., & Bazilevich, N. I. (1967). *Production and mineral cycling in terrestrial vegetation*. Oliver and Boyd.

Rossen Jr, J. F. (1989). *The timberland and woodland resources of central and western Oklahoma*. USDA, Forest Service, Southern Forest Experiment Station. SO-193.

Sala, O. E., Gherardi, L. A., Reichmann, L., Jobbagy, E., & Peters, D. (2012). Legacies of precipitation fluctuations on primary production: Theory and data synthesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*, 3135–3144.

Sala, O. E., Parton, W. J., Joyce, L., & Lauenroth, W. (1988). Primary production of the central grassland region of the United States. *Ecology*, *69*, 40–45.

Seager, R., Feldman, J., Lis, N., Mingfang, T., Williams, A. P., Nakamura, J., Liu, H., & Henderson, N. (2018). Whither the 100th Meridian? The once and future physical and human geography of America's arid-humid divide. Part II: The meridian moves east. *Earth Interactions*, *22*, 1–24. https://doi.org/10.1175/EI-D-17-0012.1

Seager, R., Lis, N., Feldman, J., Mingfang, T., Williams, A. P., Nakamura, J., Liu, H., & Henderson, N. (2018). Whither the 100th Meridian? The once and future physical and human geography of America's arid-humid divide. Part I: What we know so far. *Earth Interactions*, *22*, 1–22. https://doi.org/10.1175/EI-D-17-0011.1

Sims, P. L., & Singh, J. (1978). The structure and function of ten western North American grasslands: III. Net primary production, turnover and efficiencies of energy capture and water use. *The Journal of Ecology*, *66*, 573–597.

Stahle, D. W., & Hehr, J. G. (1984). Dendroclimatic relationships of post oak across a precipitation gradient in the southcentral United States. *Annals of the Association of American Geographers*, *74*, 561–573.

Tallec, T., Béziat, P., Jarosz, N., Rivalland, V., & Ceschia, E. (2013). Crops' water use efficiencies in temperate climate: Comparison of stand, ecosystem and agronomical approaches. *Agricultural and Forest Meteorology*, *168*, 69–81.

Thomason, W., Raun, W., Johnson, G., Taliaferro, C., Freeman, K., Wynn, K., & Mullen, R. (2005). Switchgrass response to harvest frequency and time and rate of applied nitrogen. *Journal of Plant Nutrition*, *27*, 1199–1226.

Tian, H., Chen, G., Liu, M., Zhang, C., Sun, G., Lu, C., Xu, X., Ren, W., Pan, S., & Chappelka, A. (2010). Model estimates of net primary productivity, evapotranspiration, and water use efficiency in the terrestrial ecosystems of the southern United States during 1895–2007. *Forest Ecology and Management*, *259*, 1311–1327.

Torquato, P. R., Will, R. E., Zhang, B., & Zou, C. B. (2020). Stand-level transpiration increases after eastern redcedar (*Juniperus virginiana*) encroachment into the midstory of oak forest. *Forests*, *11*, 901. https://doi.org/10.3390/f11090901

Torquato, P. R., Zou, C. B., Adhikari, A., Adams, H., & Will, R. E. (2020). Drought tolerance and competition in eastern redcedar (*Juniperus virginiana*) encroachment of the oak-dominated Cross Timbers. *Frontiers in Plant Science*, *11*, 59. https://doi.org/10.3389/fpls.2020.00059

van Els, P., Will, R. E., Palmer, M. W., & Hickman, K. R. (2010). Changes in forest understory associated with Juniperus encroachment in Oklahoma, USA. *Applied Vegetation Science*, *13*, 356–368.

Wagle, P., & Kakani, V. G. (2014). Growing season variability in evapotranspiration, ecosystem water use efficiency, and energy partitioning in switchgrass. *Ecohydrology*, *7*, 64–72.

Wagle, P., Kakani, V. G., & Huhnke, R. L. (2016). Evapotranspiration and ecosystem water use efficiency of switchgrass and high biomass sorghum. *Agronomy Journal*, *108*, 1007–1019.

Wang, J., Xiao, X., Qin, Y., Dong, J., Geissler, G., Zhang, G., Cejda, N., Alikhani, B., & Doughty, R. B. (2017). Mapping the dynamics of eastern redcedar encroachment into grasslands during 1984–2010

through PALSAR and time series Landsat images. *Remote Sensing of Environment*, *190*, 233–246.

Webb, W., Szarek, S., Lauenroth, W., Kinerson, R., & Smith, M. (1978). Primary productivity and water use in native forest, grassland, and desert ecosystems. *Ecology*, *59*, 1239–1247.

Will, R. E., Wilson, S. M., Zou, C. B., & Hennessey, T. C. (2013). Increased VPD due to higher temperature leads to greater transpiration and faster mortality during drought for tree seedlings common to the forest-grassland ecotone. *New Phytologist*, *200*, 366–374.

Yimam, Y. T., Ochsner, T. E., & Kakani, V. G. (2015). Evapotranspiration partitioning and water use efficiency of switchgrass and biomass sorghum managed for biofuel. *Agricultural Water Management*, *155*, 40–47.

Zeri, M., Hussain, M. Z., Anderson-Teixeira, K. J., DeLucia, E., & Bernacchi, C. J. (2013). Water use efficiency of perennial and annual bioenergy crops in central Illinois. *Journal of Geophysical Research: Biogeosciences*, *118*, 581–589.

Zhong, Y., Zou, C. B., Saenz, A., Stebler, E., Kakani, G., & Will, R. E. (2020). Conversion of encroached juniper woodland back to native prairie and to switchgrass increases root zone soil moisture and watershed runoff. *Journal of Hydrology*, *584*, 124640. https://doi.org/10.1016/j.jhydrol.2020.124640

Zou, C. B., Caterina, G. L., Will, R. E., Stebler, E., & Turton, D. (2015). Canopy interception for a tallgrass prairie under juniper encroachment. *PLoS ONE*, *10*, e0141422.

Zou, C. B., Turton, D. J., Will, R. E., Engle, D. M., & Fuhlendorf, S. D. (2014). Alteration of hydrological processes and streamflow with juniper (*Juniperus virginiana*) encroachment in a mesic grassland catchment. *Hydrological Processes*, *28*, 6173–6182.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Schmidt KN, Zou CB, Kakani VG, Zhong Y, Will RE. Improved productivity, water yield, and water use efficiency by incorporating switchgrass cultivation and native ecosystems in an integrated biofuel feedstock system. *GCB Bioenergy*. 2021;13:369–381. https://doi.org/10.1111/gcbb.12787