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

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

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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 that 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.](image-url)
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 diame-
ter measurements. Initial measurements were taken in early

| Table 1 Watershed name, vegetation, area, and soil series* of nine watersheds located at Oklahoma State University Cross Timbers Experimental Range near Stillwater, Oklahoma, USA |

| Watershed | Vegetation           | Area (m²) | Soil series                                                                 |
|-----------|----------------------|-----------|------------------------------------------------------------------------------|
| 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                   |

*Soil series were obtained from the NRCS Web Soil Survey.
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 smaller trees, we destructively sampled eight trees ranging in DBH from 1.1 to 7.2 cm. These data were combined with in DBH from 1.1 to 7.2 cm. These data were combined with in DBH from 1.1 to 7.2 cm. These data were combined with in DBH from 1.1 to 7.2 cm. These data were combined with in DBH from 1.1 to 7.2 cm. These data were combined with in DBH from 1.1 to 7.2 cm. These data were combined with in DBH from 1.1 to 7.2 cm. These data were combined with in DBH from 1.1 to 7.2 cm. These data were combined with equations 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 m² 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 m² 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, \( \text{ET} = \text{precipitation} - \text{runoff} - \text{deep recharge} - \text{change in soil water storage} \). 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
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.

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 ($p < 0.001$), 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 redecder, and oak cover types (Figure 5).

![Figure 5](image_url) 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., Liu 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 30% for 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 forested 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 CO₂ (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.

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**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](https://orcid.org/0000-0002-4649-8858)

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

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