TRADEOFF BETWEEN WATER YIELD AND BIOMASS PRODUCTION ASSOCIATED WITH EASTERN REDCEDAR ENCROACHMENT INTO GRASSLAND ECOSYSTEMS

By

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"No one who achieves success does so without acknowledging the help of others. The wise and confident acknowledge this help with gratitude." Alfred North Whitehead

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Abstract: Eastern redcedar (*Juniperus virginiana*) is encroaching tallgrass prairie ecosystems in the southern Great Plains disrupting multiple ecosystem services provided by these ecosystems. While not suitable for row crop production, these lands could be restored to native prairie or planted with switchgrass (*Panicum virgatum*) for use as a biofuel feedstock. While removal of redcedar tends to increase runoff, the tradeoff is unknown between ecosystem productivity and water use among redcedar, oak stands, switchgrass, and native prairie ecosystems. My objective was to determine the water use efficiency (WUE), i.e., productivity/water use of redcedar woodland, Cross Timbers oak woodland, switchgrass and native tallgrass prairie ecosystems. Data were collected in northcentral Oklahoma on nine experimental watersheds, four of which were initially redcedar, three of which were oak, and two of which were native prairie. Redcedar was cut from two watersheds and removed. One watershed was allowed to reestablish as native prairie and the other was planted with switchgrass. Tree aboveground biomass was determined using annually measured diameters and calculated using allometric equations. Herbaceous biomass was determined with annual clip plots. Aboveground net primary production (ANPP) was the difference in tree biomass between successive years plus annual herbaceous biomass. Runoff was continuously measured on each watershed using H-flumes. Annual evapotranspiration (ET) was estimated as the difference between precipitation and runoff. Annual WUE was calculated as the ratio between ANPP and annual ET. In 2018, ANPP of the switchgrass growing on cut redcedar watershed was 10.1 Mg ha^{-1} which was greater than for the other watersheds (4.6 to 7.1 Mg ha^{-1}). Runoff was greater from the switchgrass watersheds (56.7 mm) and least from the redcedar (4.3 mm) and oak (2.7 mm) watersheds. WUE(s) of switchgrass watersheds (11.0 kg ha^{-1} mm^{-1}) were greater than those of native prairie (7.2 kg ha^{-1} mm^{-1}), oak (5.9 kg ha^{-1} mm^{-1}) and redcedar (6.6 kg ha^{-1} mm^{-1}) watersheds. Redcedar watersheds had higher ET, lower runoff and lower ANPP than switchgrass watersheds indicating that productivity, water yield and WUE can be increased by restoring encroached watersheds to native grassland or switchgrass systems.
KEY WORDS: eastern redcedar; switchgrass; tallgrass prairie; water use efficiency.

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CHAPTER I

GENERAL INTRODUCTION

Although a native species throughout the southern Great Plains, the encroachment of eastern redcedar (*Juniperus virginiana)* into native tallgrass prairie and Cross Timbers oak forest is an issue with severe ecological and societal implications. The Cross Timbers is a unique region on the western edge of the eastern deciduous forest. It is a mosaic of oak forest, woodland, savanna and prairie spanning parts of Texas, Oklahoma and Kansas. Historically, the Cross Timbers forests have been characterized by post oak (*Quercus stellata*) and blackjack oak (*Quercus marilandica*) and were maintained by regular fire (DeSantis et al. 2011). Because of its inability to resprout, eastern redcedar expansion was controlled until 1950s when fire exclusion regimes began (DeSantis et al. 2011). Between 1953 and 2007 redcedar density in the Cross Timbers of Oklahoma increased from less than 1 stem ha^{-1} to almost 24 stem ha^{-1} and redcedar basal area has increased from less than 1% to be 15% of the total basal area (Rice and Penfound 1959, DeSantis et al. 2010). In the Missouri Ozarks, eastern redcedar increased from an insignificant presence in historical surveys (1815 to 1850) to 9% in the current (2004-2008) USDA Forest Inventory and Assessment (FIA) surveys (Hanberry et al. 2012). While post oak basal area and dominance has increased in Oklahoma (DeSantis et al. 2011) decreased fire occurrence has also led to reduced oak recruitment and little oak regeneration (Stambaugh 2014, Hoff et al. 2018a). Post oak in the Missouri Ozarks had relative decreases of 7% and blackjack oak had a moderate decline of 3-4% (Hanberry et al. 2012). Eastern redcedar is also expanding into native tallgrass prairie in central Oklahoma at a rate of up to 8% per year from 1984 to 2010 (Wang et al. 2017) and may completely convert a grassland into closed canopy redcedar forest in as little as 40 years (Briggs et al. 2002).

Woody plant encroachment into the Great Plains is affecting productivity, water cycling, and vegetation structure (Briggs et al. 2005, Zou et al. 2014). Ecosystems with greater productivity are important in terms of removing carbon from the atmosphere and helping to mitigate the effects of climate change (Lal 2004). While forests and woodlands can store more aboveground carbon than grasslands (McKinley 2007) the conversion from grassland to woodland can also alter the water budget with runoff being substantially reduced in eastern redcedar stands (Zou et al. 2014). Although eastern redcedar woodland may have higher annual productivity than native prairie it can transpire most of the annual net precipitation (Caterina et al. 2014). In a region such as Oklahoma, provisioning of water is an important ecosystem service. Reduced runoff and stream flow associated with woody plant encroachment have an impact on the water available for agriculture, industry, municipal use and ecological flows.

However, with carbon dioxide rapidly increasing in the atmosphere, productivity is an important factor for increasing carbon uptake and sequestration. Species that can both have high levels of productivity and use water efficiently might be ideal to replace woody plants encroaching into the tallgrass prairie. Converting marginal lands to restorative land uses can help to increase soil organic carbon while having positive benefits on food security, water quality, and agro-industry (Lal 2004). One option is to replace eastern redcedar stands with switchgrass (*Panicum virgatum*). Switchgrass is a C_4, warm season perennial grass that is native to North America and consists of both lowland and upland ecotypes (Vogel et al. 2011).

Switchgrass was introduced as a research topic in screening trials for energy feedstocks funded by the USDA Department of Energy in the late 1980s to early 1990s. The herbaceous crops research (HECP) began in 1984 via the Oak Ridge National Laboratory (ORNL) with the goal to “develop data and information that will lead to commercially viable systems for producing herbaceous biomass for fuels and energy feedstocks” (Berger and Cushman 1984). They assessed 34 herbaceous species at 31 sites over 7 states in the crop producing regions of the United States with the goal to find a “model” crop species. The testing identified several species that had merit for further testing and development. Switchgrass was chosen as one of these species because of its high and reliable productivity, low requirements for water and nutrients, and its suitability for growth in marginal lands (Wright and Turhollow 2010). Because of these characteristics, switchgrass has been used for cellulosic ethanol production as well as biogas and direct combustion for thermal energy (NRCS fact sheet). Since switchgrass research began, there have been at least 24 cultivars developed and used across the country during the course of the last 35 years (NRCS fact sheet).

Precipitation in Oklahoma ranges from approximately 460 mm in the west to 1370 mm in the east (Brock et al. 1995, McPherson et al. 2007). Many places across the state experience water stress at some part of the year and drought occurs regularly (Harper 1961). Because of the importance of water in the region, the low water requirements of switchgrass make its potential even higher for production in the southern Great Plains. Species that use water efficiently are especially important to ensure water availability for human use and ecosystem services. Future climate change scenarios predict already dry areas to become even drier (Dore 2005, Trenberth 2011) so the importance of water use efficient plants will only increase in Oklahoma and similar regions.

The purpose of this study was to quantify the productivity and ecosystem water use of areas encroached by eastern redcedar as compared to oak forest, native tallgrass prairie and switchgrass stands in order to understand how land use can be used to increase future water availability. The objectives of this study were to 1) compare the aboveground net primary productivity (ANPP) of watersheds dominated by eastern redcedar woodland, native tallgrass prairie, switchgrass stands and native oak Cross Timbers forest and 2) compare the watershed-level water use efficiency (WUE), the ratio of ANPP and ET, of eastern redcedar woodland, native prairie, switchgrass stands and native oak Cross Timbers woodland. The goal of studying these objectives was to determine the feasibility of planting switchgrass as a dedicated biofuel feedstock.

Review of Literature

Eastern Redcedar Encroachment

Eastern redcedar (*Juniperus virginiana*) is a widely distributed, native species in the eastern United States (Meneguzzo and Liknes 2015). Since the 1950s, its prevalence in the grasslands of the Great Plains has increased due to its popularity as a windbreak species (Smith 2011), lack of fire and increased grazing of grassland (Briggs et al. 2002). Since 1984, redcedar forests in Oklahoma have expanded at a rate of 48 km^2 per year (Wang et al. 2018) and have been increasing in central Oklahoma at a rate of about 8% per year (Wang et al. 2017). This may be faster than redcedar encroachment on other areas, with Briggs et al. (2002) noting an average expansion rate of 2.3% of ground cover per year and a maximum of 5.8% per year on a grassland in central Kansas. In the late 1980s, redcedar forests covered approximately 350 km^2 in Oklahoma, which increased to over 800 km^2 by the late 1990s and were estimated to cover 1300 km^2 of the state in 2010 (Wang et al. 2018). Eastern redcedar encroachment has not been uniform across the state and has occurred primarily in western and central Oklahoma (Wang et al. 2018) and the most significant encroachment took place during the late 1990s and early 2000s (Wang et al. 2017). Estimates are that a native tallgrass prairie can be converted to closed canopy redcedar forest in as little as 40 years (Briggs et al. 2002).

Not only does eastern redcedar encroachment disturb native grassland, but it has also been related to a decline in oak (*Quercus spp*.) forest (Meneguzzo and Liknes 2015). Over the last 50 years upland forests in the forest-prairie ecotone have undergone major changes in woody species structure and succession appears to favor redcedar over the oak species that previously dominated the region (DeSantis et al. 2011). Post oak (*Quercus stellata*) and blackjack oak (*Quercus marilandica*) once accounted for the majority of trees in the prairie-forest ecotone (Rice and Penfound 1959). Since being measured in the 1950s, 6 regions across Oklahoma that were predominantly post and blackjack oak have had a 17% decrease in oak basal area, a 21% decrease in oak tree density and a 46% decrease in oak sapling density (DeSantis et al. 2010). These same regions had an increase in redcedar basal area, tree density and sapling density over the last 50 years (DeSantis et al. 2010) and an increase in redcedar recruitment as well (Clark et al. 2005). A combination of decreased fire frequency and drought induced tree mortality is the likely cause for changes in forest composition (DeSantis et al. 2011). Eastern redcedar is thought to be more drought tolerant than oak species because its xylem is made up entirely of tracheids, which resist drought-induced cavitation whereas the wider vessels in oak xylem are less resistant (Ginter-Whitehouse et al. 1983, Willson et al. 2008). Redcedar is also the longest lived species in some old growth stands within the northern range of the Cross Timbers, reaching ages over 400 years old while post and blackjack oak reach 100 to 200 years old (Clark et al. 2005).

In terms of redcedar control, many have cited fire as an important factor both before redcedar has established as well as after (DeSantis et al. 2011, Briggs et al. 2005, and Smith 2011). Fire benefits early successional, fire tolerant species such as oak and reduced fire frequency has caused reduced oak reproduction while improving conditions for mesophytic species such as redcedar, *Celtis spp.*, and *Ulmus spp.* (DeSantis et al. 2010, Hoff et al. 2018a).

Because of this, oak forests are shifting towards a closed canopy mesophytic forest with more shade tolerant species and less oak. Many mesophytic, encroaching species such as redcedar have less flammable litter than oak which will perpetuate the mesophication of forests, continue to exclude fire and worsen conditions for oak regeneration (Nowacki and Abrams 2008). Small redcedar are killed by fire because it does not re-sprout, therefore the primary control for redcedar before European-American settlement was fire set by Native Americans (Smith 2011). Eastern redcedar encroachment into oak forest may also result in wildfires that are much more severe and make fire management more difficult (Hoff et al. 2018b). Once redcedar reaches full canopy closure, understory biomass of herbaceous plants and woody seedlings has been measured as low as 0.18 g m^2 which is not enough fine fuel in the understory to carry a fire under safe prescribed burning conditions (Briggs et al. 2002). However, the encroachment of redcedar into the Cross Timbers adds approximately 6.3 Mg ha^{-1} of available fuel, which is a 38% increase of available fuel (Hoff et al. 2018b). This increased fuel load combined with decreased understory vegetation will not provide enough fuel load to reach a threshold necessary to kill redcedar during prescribed fires but may allow a wildfire to ignite redcedar and carry into the canopy creating a much more intense and severe fire. Also, as redcedar grows larger it becomes less vulnerable to surface fires and less likely to be killed by fire (Engle and Stritzke 1995).

Fire exclusion allowed redcedar to invade the tallgrass prairie as well. A decrease in fire can allow woody species to encroach in prairies and increase in density if fire is continuously excluded (DeSantis et al. 2011). Areas that are no longer regularly burned have had noticeable increases in redcedar; in a 20-year period at the Konza Prairie Biological Station, woody plant density increased by two- to tenfold except where the prairie was annually burned (Briggs et al. 2005). Grazing in the tallgrass prairie is also mentioned as a determining factor in redcedar encroachment. Four years after the addition of bison (*Bison bison*), Briggs et al (2005) found that woody plant abundance increased 4- to 40-fold compared to non-grazed areas which may be related to ineffective burning, depending on the intensity of grazing. Grazing by ungulates reduces the fuel load by as much as 33%, which affects the mortality of redcedar; in non-grazed sites, redcedar mortality averaged 94% while it was only 32% in grazed sites (Briggs et al. 2002).

Comparison of Biomass

Eastern Redcedar Biomass

The shift in dominant vegetation type from grassland to eastern redcedar causes changes in aboveground biomass and net primary productivity. Norris et al. (2001b) estimated biomass in a range from 114,000 kg ha^{-1} in younger eastern redcedar sites (approximately 35 years old) and up to 211,000 kg ha^{-1} of standing biomass at older sites (approaching 70 years old). McKinley (2007) had a lower projected range of 94,620 to 150,001 kg ha^{-1} for redcedar woodlands possibly because the stands were younger (30-55 years old). Estimates of aboveground carbon storage in redcedar forests can range from 61,563 to 106,192 kg C ha^{-1} using an average carbon concentration of 50% (Norris et al. 2001b). Annual net primary productivity (ANPP) of redcedar sites can range from 7,247 kg ha^{-1} y^{-1} in a 70 year-old stand to 10,442 kg ha^{-1} y^{-1} in a 35 year-old stand (Norris et al. 2001b). However, Norris et al. (2001b) did conclude that the estimates of total productivity for redcedar stands are below the average productivity of temperate forests, which have a mean ANPP of 12,500 kg ha^{-1} y^{-1} (Whittaker 1970), perhaps due to geographic location between grassland and eastern temperate deciduous forest where forest establishment can be limited by climate and fire.

Tallgrass Prairie Biomass

In the tallgrass prairie, productivity is affected by disturbance. Knapp et al. (1998) found that an annually burned prairie can have an average ANPP of 3,690 kg ha^{-1} y^{-1} and even reach 5,275 kg ha^{-1} y^{-1} on highly productive lowland sites and aboveground carbon storage of tallgrass prairie (with C content of 44.5%) can range from 1,730 to 4,110 kg C ha^{-1} (Norris et al. 2001b).

However, natural disturbances such as fire can have significant effects on biomass and productivity; ANPP on a grassland study site ranged from 462 to 624 g m^{-2} (4,620 to 6,240 kg ha^{-1}) on non-burned and burned plots, respectively (Harcombe et al. 1993). Knapp and Seastedt (1986) cite lack of fire, which leads to detritus accumulation in the tallgrass prairie, as the cause of decreased productivity because it reduces the amount of solar radiation that reaches new growth. Detritus accumulation is highly variable depending on the fire intensity, with data showing that standing dead biomass peaked on a non-burned plot at 1,113 g m^{-2} (11,130 kg ha^{-1}) and reached only 575 g m^{-2} (5,750 kg ha^{-1}) on a burned area (Harcombe et al 1993). Photosynthetically active radiation (PAR) that is available to new shoots may be reduced by as much as 58% in non-burned area; therefore, new shoots may have reduced maximum photosynthetic rate and represent a production loss (Knapp and Seastedt 1986). Rice and Parenti (1978) found higher soil temperatures in prairie that was burned and mowed and concluded this was responsible for an increase in productivity as compared with undisturbed prairie because the standing litter insulated the soil from radiation. Lower soil temperatures in undisturbed prairie can delay shoot emergence and reduce the growing season for grass species due to the increase in standing dead biomass (Knapp and Seastedt 1986). Fire can also differentially affect litter production, as Norris et al. (2001a) found mean annual litterfall was between 52 and 142 g m^{-2} y^{-1} (520 and 1,420 kg ha^{-1} y^{-1}) for burned and non-burned prairie, respectively.

Switchgrass Biomass

Switchgrass (*Panicum virgatum*) is currently in use as a cellulosic biofuel feedstock, due to its minimal management needs and ability to sequester carbon belowground (Hartman et al. 2011). Switchgrass is a prime candidate for a biofuel feedstock species because of its potential for high biomass and quality. Switchgrass is also a component of native tallgrass prairie, along with other herbaceous C_4 grass species. Various cultivars exist that make switchgrass adapted to most regions and a variety of water conditions. Regardless of variety, switchgrass monocultures using improved varieties produce high amounts of biomass that are often greater than that of native tallgrass prairie. Eggemeyer et al. (2006) found that switchgrass had higher photosynthetic rates than little bluestem (*Schizachyrium scoparium*), with single leaf photosynthetic rates attained by variety Alamo reaching a maximum of 34.1 μmol CO_2 m^{-2} s^{-1} (McLaughlin and Kszos 2005). However, another component of the tallgrass prairie, big bluestem (*Andropogon gerardii*), can sustain high rates of carbon gain over a broader range of temperatures than switchgrass and can have maximum photosynthetic rates similar to that of switchgrass (41.6 and 46 μmol CO_2 m^{-2} s^{-1} respectively) (Knapp 1985).

Switchgrass production is highly variable based on precipitation. In its native growing locations or areas that are climatically similar, switchgrass has no irrigation requirements (Wagle et al. 2016) although Koshi et al. (1982) found that maximum production of switchgrass occurred under the highest irrigation regime. With no irrigation, switchgrass yields may range from 4,030 kg ha^{-1} under severe drought to 13,000 kg ha^{-1} under moderate drought and up to 14,400 kg ha^{-1} in good growing conditions (Yimam et al. 2015). Nelson et al. (2006) used the Soil and Water Assessment Tool (SWAT) to simulate switchgrass yields with varying amounts of nitrogen fertilization (0-224 kg N ha^{-1}) and predicted harvests of 5,600 to 13,300 kg ha^{-1} in northeast Kansas. Certain switchgrass cultivars in Oklahoma have achieved sustained yields for more than 3 years that can exceed 20,000 kg ha^{-1} y^{-1} (Thomason et al. 2005). Parrish and Fike (2005) posited that it may be feasible to consistently produce more than 15,000 kg of biomass annually per hectare with well-developed cultivars in areas that receive more than 700 mm of rainfall per year.

Effects of Encroachment

The encroachment of woody plants into tallgrass prairie can have significant effects on the herbaceous vegetation in the area. Invading redcedar reduces the amount of herbaceous standing crop around an individual tree (Engle et al. 1987, Nunes et al. 2019) and can reduce herbaceous biomass from 5,300 kg ha^{-1} with no redcedar canopy cover to 1,500 kg ha^{-1} with 77% redcedar cover, which equates to a 460 kg ha^{-1} decline for every 10% increase in redcedar canopy cover (Limb et al. 2010). While herbaceous biomass decreases with woody plant encroachment, ANPP can have as much as a fourfold increase due to greater ANPP of woody plants as compared to herbaceous plants, and sites with high grassland ANPP have a large increase in relative and absolute ANPP after encroachment (Knapp et al. 2008). The Konza Prairie Biological Station saw a threefold increase in ANPP, from 300 g m^{-2} (3,000 kg ha^{-1}) to 900 g m^{-2} (9,000 kg ha^{-1}), after woody plant invasion (Knapp et al. 2008). Knapp et al. (2008) posited that conversion to shrub dominance in a grassland increases ANPP because the shrubs are able to support higher leaf area than the grasses grown in the same conditions which they supported with findings that leaf area index (LAI) and ANPP measured in shrub patches were higher than values given for most forests. Productivity, LAI and nitrogen cycling increase along a gradient of non-burned, tree dominant regions while these variables tend to be lower in grassland areas with more frequent fires (Reich et al. 2001).

Eastern redcedar encroachment into tallgrass prairie has significant effects on ecosystem composition and productivity. The production of herbaceous species may be reduced by as much as 99% when prairie is replaced by redcedar forest; understory biomass averaged 0.18 g m^{-2} (1.8 kg ha^{-1}) in redcedar while annually burned prairie production was 384 g m^{-2} (3,840 kg ha^{-1}) (Briggs et al. 2002). Understory stem density, species richness, forb cover, and grass cover are significantly lower under redcedar than in the non-burned central Oklahoma prairie and woody species tend to be more abundant below redcedar while grasses and forbs are more abundant in open grassland (Linneman and Palmer 2006). Redcedar canopies are linked to increased leaf litter, which further discourage the establishment of grass and forb species. Seeds from woody species tend to have larger mass and higher carbohydrate reserves than seeds from grasses and forbs, which allows them to better penetrate the deep litter layer below an redcedar tree

(Linneman and Palmer 2006). Species richness can undergo sharp declines with proximity to individual redcedar trees (van Els et al. 2010) and a higher species richness does not provide resistance to redcedar encroachment success (Ganguli et al. 2008).

Carbon storage in an redcedar woodland ranged from 61,563 to 106,192 kg C ha^{-1}, which is upwards of 20 times greater than the estimates for tallgrass prairie ranging from 1,730 to 4,110 kg C ha^{-1} (Norris et al. 2001b). Biomass C is known to increase as woody plants invade (300 to 44,000 kg C ha^{-1}) with the largest shift aboveground being at the wettest site (Jackson et al. 2002) but shifts such as this make carbon more available to loss from fire and harvest.

Comparison of Water Use

Interception and Throughfall

Plants have a physical impact on the distribution of rainfall through interception and evaporation. These processes direct the flow of precipitation and ultimately determine the fate of water. *Juniperus spp.* is especially suited to intercept and hold precipitation due to the scale like leaf structure and large amount of foliage (Owens 2008). The water that it holds in the canopy is then available to be evaporated into the atmosphere or distributed to other areas of the tree. Eastern redcedar trees have a canopy storage capacity ranging from 2.14 mm for open-canopy stands to 3.44 mm for closed-canopy stands while the canopy storage capacity of the tallgrass prairie is much more variable and can range from 0.27 mm during the early growing season to 3.86 mm at senescence (Zou et al. 2015). Rainfall interception by the tallgrass prairie is highly variable depending on the time of year due to the lifecycle of grasses. When newly emerged in March and April less than 10% of rainfall is intercepted by the grass canopy but this increases to 20-60% during the growing season May-September and can reach a peak at over 60% when grasses reach maturity and senesce (Zou et al. 2015). Because undisturbed prairie has a greater quantity of dead foliage and intercepts more rainfall than a burned prairie (40% and 20%

respectively) (Gilliam et al. 1987), if a prairie is left to accumulate detritus after senescence it can decrease runoff and reduce water quantity (Knapp and Seastedt 1986). Any rain that makes it through the canopy of the trees or grassland is able to reach the ground surface is termed throughfall. Zou et al. (2015) found that on average, annual throughfall for redcedar was 57.3% of an event's rainfall and 56% for grassland.

Runoff and Infiltration

Once rainfall reaches the soil surface, it either infiltrates the soil or is lost as runoff. Infiltrated water is available to be taken up by plants and transpired which in turn is related to net photosynthesis. Therefore, soil water content and storage is a key component of an ecosystem productivity. Under juniper canopy, initial and steady-state infiltration rates are almost three times greater than that of tallgrass prairie, but soil water content and storage were generally higher in the grassland than encroached stands (Zou et al. 2014). This is similar to findings by Qiao et al. (2017) that the soil profile rarely becomes saturated below redcedar canopy and that it does not stay above field capacity for any prolonged length even with significant rainfall.

Rainfall that does not infiltrate the soil surface becomes runoff which produces streamflow in a watershed. Encroachment of redcedar reduces runoff as compared to grassland; Zou et al. (2014) found that an encroached catchment averaged 2.1% annual runoff coefficient and grassland 10.6%. On the same site, Qiao et al. (2017) observed a 1.4% runoff coefficient in redcedar catchment and 4.4% in grassland but these differences are likely due to reduced precipitation in the later study. Total annual runoff was 22 mm from redcedar watersheds and predominantly took place when rainfall totaled more than 35 mm while runoff from grasslands could occur with as little as 5 mm of rainfall (Qiao et al. 2017). Zou et al. (2014) also observed reduced duration of streamflow, ranging from 80 to 250 hours annually for encroached watersheds and up to 800 hours for a grassland watershed. Reductions such as this may have important implications for streamflow and availability of water in redcedar encroached watersheds.

Evapotranspiration and Water Use

Rainfall that does not become runoff is returned to the atmosphere via evaporation or transpiration. Large redcedar are able to transpire up to 196 liters per day during the summer, which is higher than native grass species (for the same land surface area), while small redcedar transpiration rates are similar to that of native grasses (Starks et al. 2014). On an upland site in northcentral Oklahoma, daily water use of redcedar averaged 24 liters with a range from 1 to 66 liters per day, and when scaled to the hectare basis was equivalent to 4,308,817 liters ha^{-1} y^{-1} in total water use (431 mm rainfall) (Caterina et al. 2014). Not only can redcedar use large amounts of water during summer months, it is also able to transpire on any day above freezing, effectively increasing the growing season to 12 months (Wine and Hendrickx 2013). This means that in a hot year with average precipitation, a closed canopy stand of redcedar could wholly transpire (99.5%) the throughfall for that year (Caterina et al. 2014). Even when redcedar becomes water stressed it is able to maintain physiological activities; redcedar sustains a more negative xylem pressure potential and higher photosynthetic rates during drought than the common prairie grass big bluestem (*Andropogon gerardii*) (Axmann and Knapp 1993).

When evaporation of water from the soil surface and canopy is considered along with transpiration associated with photosynthesis, evapotranspiration (ET) measures the amount of water returned directly to the atmosphere. Evapotranspiration appears to increase with woody encroachment with ET from redcedar ranging from 516-995 mm (average 798 mm) and ET for grassland ranging from 547-925 mm (average 787 mm) (Wine and Hendrickx 2013). This equates to ET consuming 97% and 95% of precipitation for redcedar and grassland respectively. Also, decreased runoff from redcedar indicates that more water is lost to ET since ET is the difference of precipitation and runoff (Zou et al. 2015, Qiao et al. 2017). Daily values of prairie ET during the growing season range from 3.5 to 5.0 mm day^{-1} (Burba and Verma 2005). Annually, grassland ET increased rapidly in the spring after vegetation began to green, reached a max during the summer when vegetation matured and then declined in the fall as prairie grass senesced and stopped transpiring and temperatures dropped (Wagle et al. 2014). Because redcedar is able to transpire year-round at the same or higher rates than native grasses and intercepts a significant portion of yearly precipitation, redcedar encroachment may reduce infiltration, runoff and ground water recharge to the point of affecting local water resources (Starks et al. 2014).

Ecosystem Water Use Efficiency

Transpiration and productivity can be related by calculating the water use efficiency (WUE), which is the ratio of biomass produced to water transpired. When based on ecosystem productivity and evapotranspiration, it is typically called ecosystem water use efficiency (EWUE). Emmerich (2007) defined EWUE as the net carbon uptake per amount of water lost from the ecosystem. Ecosystem water use efficiency is not a constant and can change significantly from year to year based on precipitation variability and climatic differences (Emmerich 2007). Increased precipitation may actually decrease EWUE when greater water supply increases soil moisture, causing a greater increase in ET than productivity (Wagle and Kakani 2014). However, productivity generally increases with ET, indicating that as more water is used for transpiration, more carbon is taken up by photosynthesis (Law et al. 2002).

Ecosystem water use efficiency can be measured in a variety of ways. The most common is through the use of eddy covariance (EC) towers that can measure the flux of CO_2, H_2O and heat and sometimes precipitation data from weather stations (Ponton et al. 2006, Abraha et al. 2016). Satellite remote sensing can be used to obtain MODIS-based estimates of GPP and ET (Tang et al. 2015). Both methods use the ratio of GPP to ET to find EWUE. Ecosystem water use efficiency can also be defined as the ratio of net ecosystem CO_2 exchange (NEE) and ET (Emmerich 2007) or as the ratio of photosynthetic CO_2 assimilation rate and ET rate (Ponton et al. 2006). Gross photosynthesis is calculated using daytime measurements of NEE and total ecosystem respiration which is estimated from the relationship of nighttime NEE and soil temperature.

Ecosystem water use efficiency is sometimes estimated using the ratio of ANPP to actual evapotranspiration (AET) from precipitation and outflow data. Webb et al. (1978) calculated WUE of grassland as the ratio of aboveground biomass and annual precipitation (assuming surface runoff and deep drainage as insignificant). For forest, ANPP was defined as change in aboveground biomass including the litter component and the AET was found by subtracting drainage from precipitation. Forest sites had a constant ANPP with increasing AET while grassland had an increasing ANPP with AET; however, biomass was much lower than that of forest sites (Webb et al. 1978). Trends indicated that forest ecosystems were more water use efficient than prairie systems, with forests ranging in WUE from 0.9 to 1.8 and prairie ranging 0.2 to 0.7 grams of ANPP per kilogram of water transpired.

Ecosystem water use efficiency can also be estimated using simulations such as the Dynamic Land Ecosystem Model (DLEM) which takes into account historic land-use and land cover maps, daily climate data, annual atmospheric CO_2 and daily ozone concentrations, annual nitrogen deposition, annual N fertilizer amounts, soil properties and topographic data. The integrated model simulates daily carbon, water and nitrogen cycles and can give estimates of GPP, NPP and ET which are then used to calculate EWUE (Tian et al. 2010).

From 1895 to 2007 the average water use efficiency (NPP/ET) in the southern United States was 0.71 g C kg^{-1} H_2O and increased about 25% based on simulations using DLEM (Tian et al. 2010). During this time period, WUE of different ecosystems had an order of forest >

wetland > grassland > cropland > shrubland. Tian et al. (2010) found a WUE of 0.93 g C kg^{-1} H_2O for forests, 0.58 g C kg^{-1} H_2O for grassland and 0.45 g C kg^{-1} H_2O for shrubland in the southern United States. This agrees with data from Emmerich (2007) who used the ratio of daily daytime NEE to ET and the regression of daily daytime CO_2 flux and ET to find that grass dominated ecosystems are 1.4 to 1.6 times more water use efficient than a shrub ecosystem in southeastern Arizona. Maximum EWUE for the growing season was achieved when plant growth and environmental conditions were most favorable and reached 7.35 g CO_2 mm^{-1} ET for grassland and 4.68 g CO_2 mm^{-1} ET for shrubland (Emmerich 2007). Net daytime growing season EWUE was 1.74 g CO_2 mm^{-1} ET and 1.28 g CO_2 mm^{-1} ET for grassland and shrubland respectively (Emmerich 2007). Using the slope of the relationship between gross ecosystem productivity (GEP) and ET in a worldwide study, Law et al. (2002) found that grasslands had a higher EWUE than deciduous broadleaf forests and evergreen conifers, with values of 3.4 g CO_2 kg^{-1} H_2O for grasslands, 3.24 g CO_2 kg^{-1} H_2O for broadleaf and 2.4 g CO_2 kg^{-1} H_2O for conifer. However, the forests in this study were not representative of those in the southern United States.

Differences between Switchgrass and Tallgrass Prairie

Carbon Sequestration

Due to current trends in climate and atmospheric CO_2, mitigating the effects of global climate change has become the interest of many fields. Sequestering carbon through the use of crops has been the focus of much current research. Bioenergy crops have carbon sequestration rates ranging from 600 to 3,000 kg C ha^{-1} y^{-1} (Lemus and Lal 2005). Switchgrass has the potential to annually produce 7,400 kg C ha^{-1} of aboveground biomass and sequester up to 400 kg C Mg^{-1} of aboveground biomass in both organic and inorganic forms (Cook and Beyea 2000). The amount of carbon sequestered is affected by the rate of microbial activity that removes carbon from the soil (Williams et al. 2004). Additionally, switchgrass may be able to input 2,200 kg C ha^{-1} y^{-1} into soils through belowground biomass (Zan et al. 1997).

Initially after conversion to perennial vegetation (switchgrass or native tallgrass prairie), maximum rates of soil carbon sequestration are low, typically around 33 g C m^{-2} y^{-1} (330 kg C ha^{-1} y^{-1}) (Post and Kwon 2000). Switchgrass may need up to 10 years to accrue significant carbon gains (Lemus and Lal 2005) with predicted soil sequestration rates over the first 10 years averaging 1,400 kg of C ha^{-1} y^{-1} (McLaughlin et al. 2002).

Water Use

Northcentral Oklahoma sites at the drier, western edge of the southern forest region, is an area where water quantity is an important ecological factor. Near Stillwater specifically, the long term (50 year) annual average precipitation is 880 mm (Yimam et al. 2015). The difference in water use between native tallgrass prairie and switchgrass is an important factor to consider in terms of water availability for human use.

Evapotranspiration (ET) is a dominant form of water loss to an ecosystem and by reducing ET runoff can be increased. Daily ET for switchgrass ranges from 1.0 to 6.2 mm with peak growing season ET from a switchgrass field averaging 6 mm day^{-1} and seasonal ET ranging 653 to 740 mm (Wagle et al. 2016). This daily ET range for switchgrass is greater than what has been observed for native tallgrass prairie which ranges from 3.5 to 5 mm and tallgrass seasonal ET between 465 and 553 mm makes it lower than that of switchgrass (Burba and Verma 2005). Also, during the growing season March to November switchgrass ET averages 521-786 mm (Yimam et al. 2015). Evapotranspiration may be lower in tallgrass prairie than switchgrass based on disturbance and cutting regime. Undisturbed prairie may have reduced ET because of the detritus accumulation that keeps soil cooler, effectively increasing soil water content (Knapp and Seastedt 1986). This may be important during periods of water stress by allowing undisturbed prairie to be more productive than regularly harvested switchgrass. Although not a major component, soil evaporation is an important part of total ET. For harvested switchgrass, growing season soil evaporation ranged from 28 to 69 mm, most of which occurred during the early growing season when canopy cover is low and water was available to be evaporated from the soil surface (Yimam et al. 2015). After 80% canopy closure, soil evaporation is a minimal part of ET; however, canopy interception losses can range from 103 to 171 mm, which accounts for 28% of growing season ET when combined with soil evaporation (Yimam et al. 2015). Transpiration is the largest component of ET during the growing season, accounting for up to 76% of total ET (Yimam et al. 2015).

On a leaf level, measurements of water use efficiency indicate that switchgrass is able to use low levels of water and the most productive varieties have the highest water use efficiency (McLaughlin and Kszos 2005). Mature switchgrass is able to reduce water cost aboveground during moderate drought by moving carbon from belowground to increase aboveground growth and has good potential for growth under dry conditions (Eichelmann et al. 2015). However, during dry conditions switchgrass transpired more water than the amount of precipitation it received in a year because it was able to access deep water with its extensive root system (Eichelmann et al. 2016). When precipitation is adequate, switchgrass is able to fix more atmospheric carbon per unit of water transpired than in a year with drought because it uses stored carbon to reduce water loss (Eichelmann et al. 2016).

Abraha et al. (2016) observed similar EWUE's for switchgrass and restored native tallgrass prairie over 4 years using eddy covariance. Switchgrass ranged 3.0-3.3 g C kg^{-1} H_2O while prairie was slightly lower at 2.5-3.0 g C kg^{-1} H_2O. EWUE's of both native prairie and switchgrass increased over the 4 years, possibly due to establishment of perennial grasses following planting. Kiniry et al. (2008) measured WUE as plant dry weight increase per the unit of water transpired and found that for four different switchgrass varieties the means ranged from

3 to 5 mg C g^{-1} H_2O. Using the ratio of seasonal GPP to ET, Wagle et al. (2016) yielded an EWUE of 9.41 to 11.32 grams of CO_2 per millimeter of water lost through ET for switchgrass. Seasonal EWUE based on gross ecosystem production on a mature switchgrass field was 13.3 and 14.0 g CO_2 kg^{-1} H_2O in a dry year and wet year, respectively (Eichelmann et al. 2016). Based on calculations using kilograms per hectare of aboveground dry biomass per millimeter ET, Yimam et al. (2015) found seasonal WUE for switchgrass to be from 8 to 21 kg ha^{-1} mm^{-1}.

CHAPTER II

TRADEOFF BETWEEN WATER YIELD AND BIOMASS PRODUCTION ASSOCIATED WITH EASTERN REDCEDAR ENCROACHMENT INTO GRASSLAND ECOSYSTEMS

Introduction

The encroachment of woody plants into native tallgrass prairie is a well-documented issue currently facing the southern Great Plains (e.g., Bragg and Hulbert 1976, Briggs et al. 2005, DeSantis et al. 2010, Engle et al. 1996). Fire exclusion, habitat fragmentation, increased grazing, shift in land use, and climate change, among other factors, have all been cited as causes of the increased woody plant abundance in the 20th century (e.g., Briggs et al. 2002, Briggs et al. 2005, DeSantis et al. 2011, Smith 2011). Changes in precipitation intensity that are associated with climate change have the ability to further facilitate woody plant encroachment into grassland ecosystems by allowing deeper water infiltration in the soil where it is only available for use by woody plants (Kulmatiski and Beard 2013). This conversion from a C_4 grassland to a C_3 woody species-dominated ecosystem could cause dramatic changes in terms of productivity, community structure, and community composition (Briggs et al. 2005). In addition, woody plant encroachment can impact carbon and nitrogen cycling (Hughes et al. 2006), modify streamflow (Huxman et al. 2005), and decrease diversity (Ratajczak et al. 2012).

Eastern redcedar (*Juniperus virginiana*) has been of particular concern in Oklahoma, Texas, Nebraska and Kansas. Eastern redcedar is a shade-intolerant, evergreen, drought resistant species with a long growing season (Burns and Honkala 1990). Even in winter, eastern redcedar is physiologically active as long as temperatures are above freezing (Caterina et al. 2014). Eastern redcedar does not typically establish in forests because it is shade intolerant. However, it has encroached into the midstory of the Cross Timbers in Oklahoma, likely taking advantage of leaf-off periods for the oaks (Lassoie et al. 1983), to the extent that it comprised 21% of the canopy cover within the post oak (*Quercus stellata*) dominated Cross Timbers forest when recently measured in northcentral Oklahoma (Hoff et al. 2018). 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. (2018) estimated that eastern redcedar encroachment in Oklahoma is expanding by 8% per year and since 1984, eastern redcedar has expanded by 40 km^2 annually (Wang et al. 2018). 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).

While forests and woodlands can sequester more carbon than grasslands, primarily due to greater aboveground storage (McKinley 2007), transitions from herbaceous to woody species alters the water budget. For instance, woody plant encroachment can increase evapotranspiration, decrease stream flow and reduce runoff and groundwater recharge (Zou et al. 2014). Afforestation has the potential to decrease stream flow by more than 50% and may even cause streams to go completely dry for periods of a year or longer, which is even more likely in drier regions like the southern Great Plains (Jackson et al. 2005). Specifically related to eastern redcedar encroachment, Qiao et al. (2017) found a large difference in runoff coefficients between eastern redcedar watersheds (1.4%) and grassland watersheds (4.4%) during a four-year study and reported a greater threshold of rainfall intensity was necessary to generate runoff in a redcedar watershed as opposed to grassland watersheds. Eastern redcedar encroachment also increases the evapotranspiration (ET) of the watershed because it maintains higher water requirements and a year round growing season (Wine and Hendrickx 2013). A redcedar stand with full canopy closure can completely transpire (99.5%) the net throughfall during a year that was hot and dry (Caterina et al. 2014). The combination of decreased runoff and increased ET associated with eastern redcedar encroachment can significantly reduce water availability of regions that already commonly experience water stress.

The purpose of this study was to better quantify the productivity and ecosystem water use of areas encroached by eastern redcedar as compared to Cross Timbers oak forest, native tallgrass prairie and switchgrass (*Panicum virgatum)* stands. Water use efficiency, i.e., carbon gain per water loss, is critical to assess the tradeoff between carbon uptake and water use. Especially in the southern Great Plains, where water is often scarce, the amount of water consumed by vegetation is of great importance. Because predictions of future climate changes include increases in temperature and drought in semiarid regions, species that can assimilate carbon while consuming less water will be more important to optimize water use. While global forests can sequester more carbon than grasslands (De Deyn et al. 2008, Post and Kwon 2000), transitions from herbaceous to woody species can have impacts on evapotranspiration and lead to decreased stream flow and runoff (Caterina et al. 2014, Qiao et al. 2017, Zou et al. 2014) which results in less water available for human uses and ecological flow. Therefore, determining the water use efficiency of each land cover type is necessary to understand how land use can be used to increase future water available for human and ecosystem use while potentially providing the additional benefit of carbon uptake.

Encroachment by eastern redcedar is not irreversible and these areas can be converted back to prairie. An alternative is to convert encroached areas into switchgrass stands for biofuel feedstock production which could restore a grassland ecosystem and possibly increase water yield. Therefore, I determined the feasibility of planting switchgrass as a dedicated biofuel feedstock. Traditional biofuels from maize (*Zea mays*) need extensive irrigation which is not practical or sustainable; producing a single liter of ethanol from maize grain requires anywhere from 21 to 958 liters of irrigation water (Wagle et al. 2016). In contrast, using switchgrass as a biofuel feedstock for cellulosic-based biofuels may restore grasslands and increase water yield.

Objectives

The objectives of this study were to 1) compare the aboveground net primary productivity (ANPP) of watersheds dominated by eastern redcedar woodland, native tallgrass prairie, switchgrass stands and native oak Cross Timbers forest and 2) compare the watershed-level water use efficiency (WUE), the ratio of ANPP and ET, of eastern redcedar woodland, native prairie, switchgrass stands and native oak Cross Timbers woodland. My first hypothesis was that ANPP would be greatest in the oak-dominated forest followed by eastern redcedar encroached areas, switchgrass and then native prairie. Although there are few estimates of the productivity of the Cross Timbers, Johnson and Risser (1974) found ANPP of approximately 14,900 kg ha^{-1} y^{-1} while estimates of ANPP for eastern redcedar ranges from 7,250 to 10,440 kg ha^{-1} y^{-1} (Norris et al. 2001). Standing biomass of eastern redcedar encroached areas will be greater than that of switchgrass or native prairie, but switchgrass is very productive and can in some cases can have higher ANPP than that reported for eastern redcedar (McLaughlin and Kszos 2005, Nelson et. al. 2006). Yields reported for switchgrass stands can range from 5,600 to 13,300 kg ha^{-1} y^{-1} while comparable estimates for upland tallgrass prairie sites are 3,690 kg ha^{-1} y^{-1} (Nelson et al. 2006).

My second hypothesis was that eastern redcedar encroached areas would have higher watershed-level WUE than switchgrass and native prairie because of proportionally larger increases in ANPP compared to ET but that oak forest WUE would be greater than eastern redcedar forest. Water use efficiency is the ratio between carbon gain and ET. We expected that the increase in productivity with redcedar encroachment into grassland is enough to offset the increased ET and previous research indicates that forested ecosystems tend to use water more efficiently than grassland ecosystems (Webb et al. 1978). Therefore, we expected that eastern redcedar would be more water use efficient than switchgrass or tallgrass prairie. Because of its longer growing season and higher rates of carbon sequestration, a switchgrass stand is likely more water use efficient than tallgrass prairie (Zeri et al. 2013). Switchgrass also had lower rates of ET than other ecosystems (Wagle and Kakani 2014). Because eastern redcedar retains its needles and is able to transpire year round (Lassoie et al. 1983) we expected that ET would be greater in eastern redcedar and that even with similar values of ANPP, the oak-dominated Cross Timbers forest would have greater WUE than eastern redcedar.

Due to current trends in climate and atmospheric CO_2, investigating the potential to mitigate the effects of global climate change is important. Atmospheric CO_2 concentrations have increased by 30 percent since the industrial era (CHANGE 2001) and enhancing carbon sequestration through the use of high biomass producing crops could have the potential to offset 1000 to 2000 Mt C yr^{-1} (Cannell 2003). Therefore, sequestering carbon through the use of crops has been the focus of much research (Mathews 2008, Lemus and Lal 2005). Switchgrass has the potential to sequester up to 400 kg C Mg^{-1} of aboveground biomass in both organic and inorganic forms (Lemus and Lal 2005) and annually produce 7,400 kg C ha^{-1} of aboveground biomass (Cook and Beyea 2000). Also, CO_2 emissions from using switchgrass as a biofuel is potentially lower than gas, petroleum and coal (Lemus and Lal 2005).

Switchgrass has the potential to be grown in a large swath of marginal land in the southern Great Plains. Although this area has adequate precipitation to support switchgrass production, water stress is a frequent occurrence. Because the encroachment of eastern redcedar into the area has the potential to impact water resources, it is important to understand the dynamic between vegetation type and water use to determine which cover type will have the least impact on water resources. Human consumption of water is an important issue in the southern Great Plains and water availability is a vital ecosystem service. Understanding the productivity, carbon sequestration and water use is important for determining the impacts of eastern redcedar encroachment and removal and the sustainable management of the Great Plains.

Methods

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 above sea level). Average annual mean temperature is 15°C with an average minimum of -3.2°C in January and an average maximum of 33.3°C in July. Average annual precipitation was approximately 900 mm during the study and long term annual average precipitation was 880 mm over the last 50 years (Yimam et al. 2015). Cross Timbers Experimental Range sits along the ecotone between the eastern deciduous forest and the southern Great Plains. Following the Land Run (1889), the prairie at this location was plowed to grow cotton (*Gossypium spp.)* which was 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 redcedar had an estimated woody cover of 75% in areas where it had encroached. There are 9 experimental watersheds present on CTER: two originally grassland watersheds (G1, G2), four watersheds originally encroached by redcedar (F1-F4), and three oak watersheds (D1-D3) (Figure 1). In July 2015, eastern redcedar was cut from two of the four encroached watersheds (F3, F4), allowed to dry for 6 months and then chipped and removed. One of the two cut watersheds was allowed to revegetate naturally (F4). 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 of 2017, switchgrass was planted on these two watersheds using the upland variety “Alamo”. 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).

Aboveground Net Primary Production

Aboveground tree biomass

Twenty 0.04 ha plots were located within each of the oak and eastern redcedar encroached watersheds and trees within plots were permanently tagged to allow for annual diameter measurements. Initial measurements were taken in early 2016 when trees were tagged and identified by species. All tree measurements were taken between growing seasons, i.e., November and January. Diameter was measured at breast height (DBH) using a diameter tape to the nearest mm. Erroneous measurements, of which there were approximately 40, were resolved as the average of 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 12.7 centimeters to 48.3 centimeters. To calculate equations for smaller trees in the study, I destructively sampled 8 trees ranging in DBH from 1.1 centimeters to 7.2 centimeters. Data were combined with those from Lykins and equations were fit for the various tree components.

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. Eastern redcedar biomass was broken into the components of bole, total branch, foliage and dead branch and total tree was calculated independently ($R^2 > 0.95$) (Table 3).

Aboveground dry biomass for oak and remaining species was calculated using prediction equations from Clark et al. (1986) (Table 4 and Table 5) which were divided based on tree DBH less than or greater than 11 inches.

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 six weeks throughout the year and dried at 60°C in a drying oven 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. Annual foliage production of eastern redcedar was then calculated by multiplying standing foliage by this value.

For all trees, ANPP for the growing season 2016-2018 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 and converted to kilograms. Per hectare ANPP was calculated by summing ANPP of trees within plots, averaging the plots within a watershed, and multiplying by 25.

Aboveground herbaceous biomass

Herbaceous biomass 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 depending on vegetation type (grasses, forbs, or new woody understory growth). 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 2016-2018 and converted to Mg ha^{-1}.

Precipitation, Runoff and Evapotranspiration

Precipitation was measured using an automatic tipping bucket rain gauge (model TAB3, Hydrological Services America, Lake Worth, FL, USA). 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 averaged across the four separate gauge locations.

Water yield was continuously measured on all 9 watersheds. H-flumes were installed at the outlet of each watershed which measure discharge rates and stage measurements using stilling wells equipped with floats and optical shaft encoders with 0.25 mm resolution (50386SE-105 HydroLynx, West Sacramento, CA, USA). Water level in the flumes was recorded every 5 minutes using CR200 or CR1000 dataloggers (Campbell Scientific, Logan, UT, USA). Annual runoff depth was calculated by dividing the total runoff volume by the area of the watershed. Annual ET was estimated as the difference between annual precipitation and annual runoff.

Precipitation and runoff events were grouped by water year for 2016-2018 which runs from October 1st to September 30th to best capture the changes in precipitation and streamflow and have negligible changes in storage. For instance, the 2016 water year included rainfall and runoff collected from October 2015 until September 2016 and corresponded to biomass data from the 2016 growing season. Water-use efficiency (WUE) was evaluated at the watershed level as opposed to leaf level and was calculated as the ratio between ANPP (kg ha^{-1} y^{-1}) and ET (mm y^{-1}).

Data analysis

Data was analyzed using SAS software. I ran a mixed effects model and used the watersheds as replicates of the four treatments: eastern redcedar, oak, switchgrass and prairie. The significance level was set at α=0.01.

Results

Standing Biomass

In total 3,571 trees were measured annually for DBH across the five forested watersheds. Average DBH of all trees in 2018 was 13.5 cm (Table 6). From 2015 to 2018, 28 trees died. Mean tree DBH among the watersheds in 2018 ranged from 10.9 cm in the Oak 1 watershed to 15.1 cm in the Oak 3 watershed. The average DBH of all trees increased from 12.5 cm in 2015 to 13.5 cm in 2018.

Basal area (BA) was greatest in the Cedar 1 watershed for all four years (Table 7) and in 2018, was 26.70 m2 ha^{-1}. The smallest was 9.54 m^2 ha^{-1} in the Oak 1 watershed in 2018. Average BA grew from 14.11 m^2 ha^{-1} to 16.17 m^2 ha^{-1} between the end of 2015 to the end of the 2018 growing seasons.

Standing biomass in 2018 ranged from 41.25 Mg ha^{-1} in the Oak 1 watershed to 111.81 Mg ha^{-1} in the Cedar 1 watershed (Figure 2). Total standing biomass of the oak watersheds averaged 62.97 Mg ha^{-1} and the cedar watersheds averaged 86.28 Mg ha^{-1} in 2018. The biomass of the Cedar 1 watersheds was significantly greater than all other forested watersheds ($p<0.0001$) and the Cedar 2 was significantly greater than Oak 1 ($p<0.0001$). Oak 2 and Oak 3 were significantly greater than Cedar 2 and Oak 1 ($p>0.001$) but were not significantly different from one another. Average standing biomass increased from 62.8 Mg ha^{-1} after the 2015 growing season to 72.29 Mg ha^{-1} after the 2018 growing season (Table 8).

In the cedar watersheds, about 58% of the biomass was composed of the bole, 11% by branches, 17% by dead branches and 14% by foliage. In the oak watersheds, about 66% of the biomass was composed of the bole, 23% by branches, 3% by dead branches and 7% by foliage (Figure 2). In 2018, the standing biomass of the bole of the Cedar 1 was 29 to 55% greater than the other watersheds. The branch biomass of the Cedar 1 watershed was 18.56 Mg ha^{-1} which was the greatest and was 9 to 46% greater than the other watersheds. Finally, the Cedar 1 watershed had the greatest standing foliage biomass at 14.19 Mg ha^{-1} which was 35 to 91% greater than the remaining watersheds.

The Cedar 1 watershed had the greatest redcedar biomass with 101.93 Mg ha^{-1} in 2018. Oak biomass was greatest in the Oak 3 watershed in 2018 (47.22 Mg ha^{-1}) (Figure 3). In 2018, the percent of total biomass made up by eastern redcedar of Cedar 1 and Cedar 2 watersheds was 91 and 99% respectively. The oak species made up 95% and 66% of the Oak 1 and Oak 3 watersheds respectively. The Oak 2 watershed was made up of 62% eastern redcedar and 36% oak in 2018. The standing tree biomass of watersheds ranged from 0.1 to 7% of non-cedar and non-oak species.

Aboveground Net Primary Production

No measure of ANPP is 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 Oak 1 and in 2017 for the Oak 2 and Oak 3 watersheds. For all three growing seasons, the ANPP of the prairie and switchgrass watersheds was composed entirely of herbaceous plants. For the cedar and oak watersheds, the percent of herbaceous ANPP ranged from 0.5 to 16% (Figure 4).

For the 2016 growing season, the ANPP of the oak watersheds averaged 5.4 Mg ha^{-1}, the cedar watersheds averaged 5.2 Mg ha^{-1} and the prairie watersheds averaged 3.5 Mg ha^{-1}. These differences were not significant ($p>0.10$). For the 2017 growing season, ANPP averaged 4.5 Mg ha^{-1} for the oak watersheds, 6.4 Mg ha^{-1} for the cedar watersheds, 6.3 Mg ha^{-1} for the prairie watersheds and 6.2 Mg ha^{-1} for the switchgrass watersheds. Cedar ANPP was significantly greater than ANPP in the oak watersheds ($p=0.095$). For the 2018 growing season, ANPP of the oak watersheds averaged 5.0 Mg ha^{-1}, the cedar watersheds averaged 5.6 Mg ha^{-1}, the prairie watersheds averaged 5.8 Mg ha^{-1} and the switchgrass watersheds averaged 8.6 Mg ha^{-1}. Switchgrass ANPP was significantly greater than ANPP of the oak ($p=0.048$) and cedar ($p=0.091$) watersheds.

Precipitation, Runoff and Evapotranspiration

Precipitation averaged 900 mm for 2016-2018. The wettest year was 2017 with 993 mm and the driest year was 2018 with 840 mm (Figure 5). Runoff for the 2016 water year averaged 8.4 mm for the oak watersheds, 7.9 mm for the cedar watersheds, 80.9 mm for the prairie watersheds and 97.0 mm for the watersheds that were kept clear in preparation for planting switchgrass. Runoff was significantly greater for the prairie and future switchgrass watersheds than for the oak and cedar watersheds ($p<0.004$). Runoff for the 2017 water year averaged 45.5 mm for the oak watersheds, 37.8 mm for the cedar watersheds, 159.8 mm for the prairie watersheds and 239.5 mm for the switchgrass watersheds. Runoff was significantly greater in the switchgrass watersheds than all other watersheds ($p<0.04$) and prairie watershed runoff was significantly greater than that from oak and cedar watersheds ($p<0.02$). Runoff for the 2018 water year was 2.7 mm for the oak watersheds, 4.3 mm for the cedar, 43.0 mm for the prairie and 56.7 mm for the switchgrass watersheds. Again, runoff was significantly greater from the switchgrass watersheds than all others ($p<0.01$) and prairie watershed runoff was significantly greater than oak and cedar watershed runoff ($p<0.001$).

The lower rates of runoff for the cedar and oak watersheds translated to greater ET (ET = precipitation – runoff) (Figure 5). Across all three water years ET for the cedar watersheds was 98% of total precipitation, for the oak watersheds was 98%, for the prairie watersheds was 89% and for the switchgrass watersheds was 86%.

Water-Use Efficiency

Water use efficiency for the 2016 water year averaged 6.3 kg ha^{-1} mm^{-1} for the oak, 6.0 kg ha^{-1} mm^{-1} for the cedar, 4.4 kg ha^{-1} mm^{-1} for the prairie watersheds ($p>0.05$) (Figure 6). Because switchgrass was not yet planted, there was no WUE measurement for switchgrass stands in 2016. Water use efficiency for the 2017 water year averaged 4.7 kg ha^{-1} mm^{-1} for the oak, 6.7 kg ha^{-1} mm^{-1} for the cedar, 7.5 kg ha^{-1} mm^{-1} for the prairie and 8.3 kg ha^{-1} mm^{-1} for the switchgrass watersheds. Switchgrass WUE was significantly greater than oak WUE in 2017 ($p<0.071$). Water use efficiency for the 2018 water year averaged 5.9 kg ha^{-1} mm^{-1} for the oak, 6.6 kg ha^{-1} mm^{-1} for the cedar, 7.2 kg ha^{-1} mm^{-1} for the prairie and 11.0 kg ha^{-1} mm^{-1} for the switchgrass watersheds. WUE of switchgrass was significantly greater in 2018 than all other watersheds ($p<0.046$).

Discussion

The water use efficiency of oak and eastern redcedar watersheds was not greater than grassland watersheds which contradicted my hypothesis. Although forested ecosystems are expected to be more water use efficient (Webb et al. 1978), the results of my study found that the switchgrass stands were the most efficient ecosystem type and that tallgrass prairie WUE was similar to, if not greater than, the forested watersheds. Water use efficiency is a function of ANPP (numerator) and ET (denominator). While over the course of the entire study there was variability in which watershed had the greatest ANPP for each year, in the final year (2018) ANPP was significantly greater in the switchgrass watersheds than the oak or redcedar watersheds which largely contributes to the higher WUE of the switchgrass in 2018. This also contradicts my first hypothesis that ANPP of eastern redcedar watersheds would be greatest. Water use efficiency was also greater in the switchgrass stands due to significantly more runoff (lower ET) than the other watersheds. This was as expected based on studies showing a decrease in runoff from eastern redcedar encroached watersheds as compared to prairie watersheds (Zou et al. 2014, Qiao et al. 2017). However, switchgrass had significantly greater runoff than the prairie watersheds in 2017 and 2018.

Water use efficiency is often expected to be greater in forests because of higher levels of productivity, even if ET of forests is greater than grasslands (Ponton et al. 2006, Tian et al. 2010). Documented WUE for forests ranges from 9 to 18 kg ANPP ha-1 mm-1 water which is greater than the 4.6 to 7.8 kg ANPP ha^{-1} mm^{-1} water measured in my study for eastern redcedar and oak watersheds. However, these forests measured with greater WUE than my study were in regions with greater rainfall (1230 - 2300 mm y^{-1}) and composed of different species (*Pseudotsuga menziesii, Acer saccharum, Carya spp., Q. prinus, Tsuga heterophylla, Betula lutea, Q. alba, A. rubrum*) (Webb et al. 1978) than my site. The Cross Timbers forest used in my study faces significant water stress which may constrain ANPP. The eastern deciduous forest does not extend any farther west than the Cross Timbers because declining precipitation cannot support a forest ecosystem. Long-term drought occurs approximately every 20 years and this region has had several severe droughts with Palmer Drought Severity Indexes (PDSI) of -4.68 (1911), -3.30 (1936) -4.11 (1956) and -3.06 (2006) (Bendixsen et al. 2015). Palmer Drought Severity Index values ranges from -6 to 6 and the more negative numbers indicate a more extreme drought year while positive numbers indicate a wet year (Palmer 1965). Post oak and blackjack oak (*Q. marilandica*) are species typically associated with the Cross Timbers and they can be particularly sensitive to climate with their productivity declining with decreased precipitation and drought events (Stahle and Hehr 1984). Therefore, WUE may be lower for the forests I studied than for others in more humid regions.

Aboveground net primary production of eastern redcedar for my study ranged from 4.2 – 7.8 Mg ha^{-1} y^{-1} which was generally lower than most other estimates. Norris et al. (2001) found that eastern redcedar stands in the Great Plains could range from 7 Mg ha^{-1} y^{-1} in a 70-year-old stand to over 10 Mg ha^{-1} y^{-1} for a 35-year-old stand. Based on aerial imagery, my eastern redcedar stands are most likely younger than 40 as individuals began appearing on the landscape in the 1970s. Because of their younger age, the standing biomass of my eastern redcedar stands (60.7 and 111.8 Mg ha^{-1}) was also lower than estimates from Norris et al. (2001) where standing biomass ranged from 114 Mg ha^{-1} in younger sites to 211 Mg ha^{-1} in older sites. My estimates of standing biomass for eastern redcedar are more similar to McKinley (2006) who projected a range of 95 to 150 Mg ha^{-1} for stands age 30 to 55 years old near the Konza Prairie Biological Station, Kansas, USA.

The ANPP of the oak watersheds of my study were lower than other estimates for the Cross Timbers. For instance, oak ANPP for my watersheds ranged from 4.1 to 6.4 Mg ha^{-1} y^{-1} while Johnson and Risser (1974) measured ANPP of 14.9 Mg ha^{-1} y^{-1} which was two to three times greater. Aboveground net primary production estimates of 4 to 20 Mg ha^{-1} $year^{-1}$ for temperate deciduous forests were given by Rodin and Bazilevich (1967) and while my oak estimates fall within this range, they are all at the lower end. The productivity of these stands may decrease as oak is replaced by eastern redcedar and more mesic species (Fralish 2004). Overall, productivity estimates of the oaks in the Cross Timbers are limited and those that are available predate much of the woody plant encroachment into the region. Post oak in particular is a slow growing species and its growth tends to decrease with decreasing precipitation (Stahle and Hehr 1984) so the oak forests from my study may not meet the expectations set by other forests.

Another factor that could impact the productivity of the oak species in my watersheds is the large percent of the oak watersheds being encroached by eastern redcedar. Throughout the course of the study, there were marginal declines in the percent oak composition of about 2% in the Oak 2 and Oak 3 watersheds coupled with slight increases in percent eastern redcedar biomass on these watersheds. The biomass of the Oak 2 watershed was made up of 62% eastern redcedar in 2018 and it made up 27% of the Oak 3 watershed as well. While the encroachment of eastern redcedar will increase total ANPP, it may decrease the productivity of other tree species through competition (Hanberry et al. 2012). Lack of fire that allowed encroachment to proceed can also have negative impacts on oak regeneration and productivity in the long term (Van Lear et al. 2000).

The increasing productivity of switchgrass from the first year of production (2017) to the second (2018) corresponds with several studies that measured increasing productivity of switchgrass through the first three years of production (Sharma et al. 2003, Caddel et al. 2010, de Koff and Tyler 2012). Typically, in the second year switchgrass will produce 2/3 of its full yield which is an increase from the 1/4 to 1/3 of a full yield produced in the first year. In Oklahoma, the Alamo variety of switchgrass has average annual yields ranging from 12.7 to 17.0 Mg ha^{-1} over a 7-year period when grown under 830 and 1,100 mm of rainfall respectively (Caddel et al. 2010). While the two-year averages of 8.6 and 6.3 Mg ha^{-1} (Figure 4) for my study were below this, it could be due to the immaturity of the stands in my study and lack of fertilizer application. With fertilizer application and irrigation, the Alamo cultivar of switchgrass reached yields of 19.7 Mg ha^{-1} in Oklahoma (Kering et al. 2012). An increase in productivity of switchgrass stands would also cause an increase in water use efficiency, given similar runoff. This increasing productivity between 2017 and 2018 explains the increasing separation for WUE of switchgrass in 2018 compared to the other watersheds.

The ANPP of both switchgrass watersheds and the Cedar → Prairie watershed was greater in 2018 as opposed to 2017. This could simply be due to the establishment of the stands after redcedar removal. ANPP of the tallgrass prairie was similar to other estimates of ungrazed and unburned tallgrass prairie ranging from 0.54 to 6 Mg ha^{-1} (Sims et al. 1978, Sala et al. 1988, Abrams et al. 1986, Norris et al. 2001). In 2017 ANPP of the prairie watershed was 7.5 Mg ha^{-1}, which was above average for most tallgrass prairie estimates. One explanation may be the precipitation measured in 2016 and 2017 at the study site. Oesterheld et al. (2001) observed that the current-year ANPP of grasslands can be explained by the precipitation of the previous two years. Legacies of rainfall from the previous two years can account for up to 20% of the variation in ANPP of the third year and up to 80% of annual variability in grassland ANPP can be accounted for by the current and previous year precipitation (Reichmann et al. 2013). In my study, the 2016 total (869 mm) was similar to the long term average of 880 mm and the 2017 total (993 mm) was above average and this may have helped to increase the prairie ANPP. Precipitation in 2018 was below average (840 mm) and this was reflected in the lower ANPP of the prairie watershed in 2018.

As ET increases, WUE decreases given the same ANPP. I measured runoff and calculated ET by subtracting runoff from precipitation. Runoff from oak and redcedar watersheds was less than that of prairie and switchgrass watersheds, which was expected based on previous research (Zou et al. 2014, Qiao et al. 2017). Runoff coefficients calculated in my study as the average of the years 2016-2018 ranged from 1.7% for redcedar, 2% for oak, 10.2% for prairie and 14% for switchgrass. These compare well with estimates from the same site in 2009 to 2011 that found an average of 2.1% annual runoff coefficient from watersheds encroached with redcedar and an average runoff coefficient of 10.6% for prairie (Zou et al. 2014). On the same site, Qiao et al. (2017) observed a 1.4% runoff coefficient in redcedar catchment and 4.4% in prairie, for 2011-2014 which was lower than that reported by Zou et al. (2014) due to an average annual precipitation of 726 mm across the four years. In general, forests will have less runoff as compared to grasslands due to greater interception, transpiration and evaporation (Owens et al. 2006, Baldocchi et al. 2004). Annual ET can be up to 10% greater from forests than adjacent grasslands (Liu et al. 2014) which indicates a reduction in the amount of precipitation going towards runoff. Eastern redcedar water use may be even greater than deciduous species such as oaks because it retains its leaves during the winter thus capturing more throughfall and using water year round (Caterina et al. 2014). Redcedar is able to maintain positive daily carbon uptake for the majority of the year and may only be limited when freezing temperatures limit gas exchange (Lassoie et al. 1983)

What is particularly interesting from my study is that ET was significantly greater from tallgrass prairie watersheds than from the switchgrass watersheds due to greater runoff from the switchgrass. During the growing season, daily ET of switchgrass can range from 0.5 to 4.8 mm in northcentral Oklahoma (Wagle and Kakani 2014) while native tallgrass prairie can range from 3.5 to 5.0 mm (Burba and Verma 2005). This may be due to the composition of native tallgrass prairie that includes not only grasses but also forb and woody species while switchgrass stands are typically a grass monoculture. A higher rate of transpiration or increased interception of incoming precipitation from the native prairie stands would decrease the runoff and WUE of these watersheds as compared to switchgrass. Another consideration that could impact runoff is the harvest of switchgrass as a biofuel. While ungrazed native prairie senesces and is left as standing dead biomass unless burned, switchgrass is typically cut from the stand which leaves the watershed with a reduced canopy cover. However, switchgrass litter biomass significantly decreases after harvest and is not likely to affect runoff amounts from cut switchgrass stands (Self-Davis et al. 2003).

Switchgrass is a component in 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, while not returning to a traditional native tallgrass prairie, does recreate a grassland ecosystem and may restore some of the ecosystem services that a native prairie provides while providing an additional service of biofuel production. In terms of water quantity, the switchgrass stands had similar, if not greater, levels of runoff compared to the native intact and restored prairies and significantly greater runoff than eastern redcedar watersheds. Therefore, removing eastern redcedar and planting switchgrass may have the capacity to restore streamflow and even groundwater recharge that was decreased by the encroachment of eastern redcedar. Switchgrass also has benefits for wildlife habitat and animal grazing and forage (Wolf and Fiske 2009, Guretzky et al. 2011). Planting switchgrass could restore habitat opportunities and increase local diversity for game and non-game bird species that typically utilize grasslands by providing a greater prey abundance and breeding opportunities that are not supported by eastern redcedar woodlands (Murray et al. 2003, Roth et al. 2005) and it has the potential to be viable wildlife habitat for small mammal species as well (Schwer 2011).

When compared to traditional row crops, switchgrass production may be more resilient to climate change and variation in precipitation. Increases in precipitation had little effect on switchgrass ANPP and it was not affected by drought until a 50 percent decrease in precipitation led to decreased transpiration (Deng et al. 2017). Simulated yields of switchgrass grown in the Missouri-Iowa-Nebraska-Kansas region under climate altered scenarios predicted an increase of 5.0 Mg ha-1 with temperature increases of 3.0 – 8.0°C and increases in atmospheric CO_2 increased annual switchgrass yields on average by an additional 2.6 Mg ha^{-1} over 30 years because of an improved WUE of the C_4 plant especially in already water scarce regions. (Brown et al. 2000). Switchgrass may be especially important in terms of runoff. The runoff coefficient for switchgrass in my study was 14%, which was significantly greater than the others. As well as increasing runoff, switchgrass has the potential to reduce sediment loss in surface runoff by 66% as compared to traditional row crops and can be used as a filter strip to reduce non-point source pollution (Rankins et al. 2001). Under certain global change scenarios runoff may be decreased by as much as 50% with a 10°C increase due to an accelerated rate of ET (Bell et al. 2010). The increased runoff from switchgrass and its ability to reduce soil loss may be even more valuable with the changing climate scenarios.

Switchgrass has the potential to make a significant impact in terms of carbon sequestration as well. Although forests can be good sinks for CO_2 as compared to native prairie, the encroachment of eastern redcedar into tallgrass prairie does not provide much additional soil carbon storage (Smith and Johnson 2003) and any increased soil carbon is primarily focused directly under encroaching tree canopies (Nunes et al. 2019). The encroachment of eastern redcedar into grasslands can have a significant impact on carbon allocations, such that carbon storage can shift from 96% belowground in grasslands to 52% aboveground in eastern redcedar stands (Norris et al. 2001, McKinley 2006). Removing eastern redcedar and planting switchgrass may be able to return some of the carbon input to soils as it is able to input 2,200 kg C ha^{-1} y^{-1} into soils through belowground biomass (Zan et al. 1997). Moving forward, these factors could be important in terms of water use and carbon sequestration as climate continues to change, water becomes scarcer and CO_2 levels rise.

These findings lead to many implications for the future. Allowing the encroachment of eastern redcedar to continue will further reduce water availability for human consumption and ecosystem functions. Reduced streamflow can not only impact humans but native wildlife and fisheries as well. Especially in the subhumid regions of the country such as Oklahoma, minimizing water loss is an important factor when considering land use. The planting of switchgrass and restoration of native prairie will allow more water to be available for these services. Switchgrass may provide the additional benefit of increasing the amount of carbon that sequestered from the atmosphere.

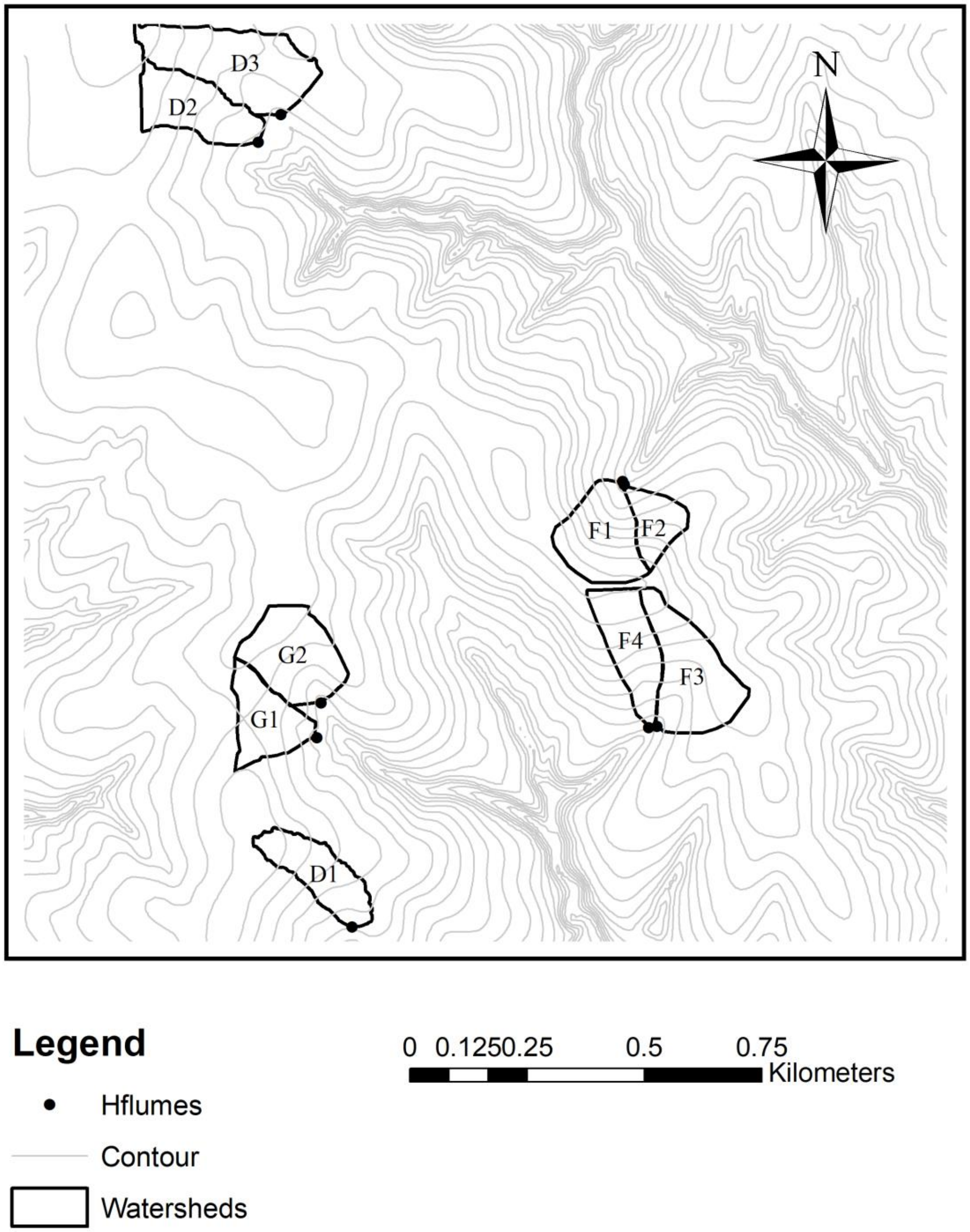

Figure 1. Topographic imagery of the ten experimental watersheds at the Oklahoma State University Cross Timbers Experimental Range (CTER) near Stillwater, Oklahoma. Refer to Table 1 for description of each watershed. Created on June 21st, 2019.

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

Watershed	Vegetation	Area (m^2)	Soil series	Watershed Percentage (%)
D1	Oak 1	23853	-Stephenville-Darnell complex, 3 to 8 percent slopes, rocky	100
D2	Oak 2	28297	-Doolin silt loam, 1 to 3 percent slopes	4
			-Coyle loam, 3 to 5 percent slopes, eroded	47
			-Coyle and Zaneis soils, 3 to 5 percent slopes, severely	12
			eroded	35
			-Stephenville fine sandy loam, 3 to 5 percent slopes	2
			-Renfrow loam, 3 to 5 percent slopes, eroded	
D3	Oak 3	46528	-Renfrow loam, 3 to 5 percent slopes, eroded	8
			-Coyle and Zaneis soils, 3 to 5 percent slopes, severely	1
			eroded	23
			-Coyle loam, 3 to 5 percent slopes, eroded	68
			-Stephenville fine sandy loam, 3 to 5 percent slopes	
G1	Prairie	22872	-Coyle Loam, 1 to 3 percent slopes	20
			-Harrah-Pulaski complex, 0 to 12 percent slopes, very rocky	15
			-Stephenville-Darnell complex, 3 to 8 percent slopes, rocky	64
			-Zaneis-Huska complex, 1 to 5 percent slopes	1
G2	Prairie →	33211	-Coyle Loam, 3 to 5 percent slopes	18
	Switchgrass		-Coyle Loam, 1 to 3 percent slopes	15
			-Stephenville-Darnell complex, 3 to 8 percent slopes, rocky	67
F1	Cedar 1	29866	-Coyle and Zaneis soils, 3 to 5 percent slopes, severely	2
			eroded	7
			-Grainola-Lucien complex, 5 to 12 percent slopes	91
			-Stephenville-Darnell complex, 3 to 8 percent slopes, rocky	
F2	Cedar 2	13449	-Coyle and Zaneis soils, 3 to 5 percent slopes, severely	56
			eroded	22
			-Grainola-Lucien complex, 5 to 12 percent slopes	22
			-Stephenville-Darnell complex, 3 to 8 percent slopes, rocky	
F3	Cedar →	37899	-Renfrow and Grainola, 3 to 8 percent slopes, severely	29
	Switchgrass		eroded	9
			-Stephenville fine sandy loam, 3 to 5 percent slopes, severely	20
			eroded	13
			-Coyle-Lucien complex, 1 to 5 percent slopes	29
			-Grainola-Lucien complex, 5 to 12 percent slopes, rocky	
			-Stephenville-Darnell complex, 3 to 8 percent slopes, rocky	
F4	Cedar →	25737	-Renfrow and Grainola soils, 3 to 8 percent slopes, severely	11
	Prairie		eroded	8
			-Stephenville fine sandy loam, 3 to 5 percent slopes, severely	3
			eroded	78
			-Grainola-Lucien complex, 5 to 12 percent slopes, rocky	
			- Stephenville-Darnell complex, 3 to 8 percent slopes, rocky	

1. Soil series were obtained from the NRCS Web Soil Survey.

Table 2: Taxonomic classification of the soils found at Oklahoma State University Cross Timbers Experimental Range near Stillwater, Oklahoma[1]

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

1. Soil descriptions were obtained from the NRCS Web Soil Survey.

Table 3. Prediction equations for standing dry biomass of eastern redcedar[1]

Open Grown[2]

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
Total Branch	-40.7	585	31.9	11.1	0.956
Foliage	0	209	18.9	4.64	0.973[3]

Closed Grown[4]

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
Total 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

1. From Lykins (1995) and our destructive sampling

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

3. Equation for open grown dead branches: $Y = -3.2526 + 0.5668*DBH + (-0.0302)*DBH^2 + 0.0006*DBH^3$. $R^2 = 0.8963$

4. $Y = y^0 + a * DBH^b$. Y is predicted biomass in kilograms and diameter in centimeters.

Table 4[1]. Prediction equations for calculation of post oak dry biomass[2]

	DBH < 11 in			DBH ≥ 11 in		
Component	a	b	R^2	a	b	R^2
Total Tree[3]	2.24	1.24	0.98	6.79	1.01	0.98
Wood & Bark	2.18	1.24	0.98	6.65	1.01	0.98
Bole	1.69	1.23	0.98	7.48	0.922	0.98

1. $Y = a * (DBH^2)^b$. Y is predicted biomass in pounds and DBH is in inches.

2. From Clark et al. (1986)

3. Total tree is wood, bark and foliage

Table 5[1]. Prediction equations for dry biomass of all species[2]

	DBH < 11 in			DBH ≥ 11 in		
Component	a	b	R^2	a	b	R^2
Total Tree	2.40	1.23	0.99	2.77	1.20	0.99
Wood & Bark	2.278	1.24	0.99	2.61	1.21	0.99
Bole	1.87	1.23	0.99	4.04	1.07	0.99

1. $Y = a * (DBH^2)^b$. Y is predicted biomass in pounds and DBH is in inches.

2. From Clark et al. (1986)

3. Total tree is wood, bark and foliage

Table 6. Average diameter at breast height (DBH) for trees measured within each forested watershed measured after the growing seasons 2015 to 2018. SE is the standard error of the mean.

		Average DBH (cm)							
Watershed	No. Trees	2015	SE	2016	SE	2017	SE	2018	SE
Oak 1	587	9.4	0.2	9.9	0.2	10.5	0.2	10.9	0.2
Oak 2	560	14.0	0.3	14.3	0.3	14.6	0.3	14.9	0.3
Oak 3	501	14.1	0.3	14.6	0.3	14.9	0.3	15.1	0.3
Cedar 1	1162	12.8	0.2	12.9	0.2	13.3	0.2	13.5	0.2
Cedar 2	761	12.2	0.2	12.5	0.2	12.8	0.2	13.1	0.2
Average	714	12.5	0.2	12.8	0.2	13.2	0.2	13.5	0.2

Table 7. Basal area of forested watersheds following the growing season from 2015 to 2018. SE is the standard error of the mean.

	Basal Area (m^2 ha^{-1})							
Watershed	2015	SE	2016	SE	2017	SE	2018	SE
Oak 1	6.72	3.85	7.36	4.06	7.99	4.21	9.54	6.08
Oak 2	13.97	11.46	14.51	11.63	15.00	11.90	15.48	12.05
Oak 3	12.36	11.79	13.00	12.36	13.43	12.72	13.76	12.97
Cedar 1	24.00	5.71	24.76	5.85	25.89	6.11	26.70	6.24
Cedar 2	13.49	8.50	14.09	8.76	14.77	9.11	15.38	9.37
Average	14.11	8.26	14.74	8.53	15.42	8.81	16.17	9.34

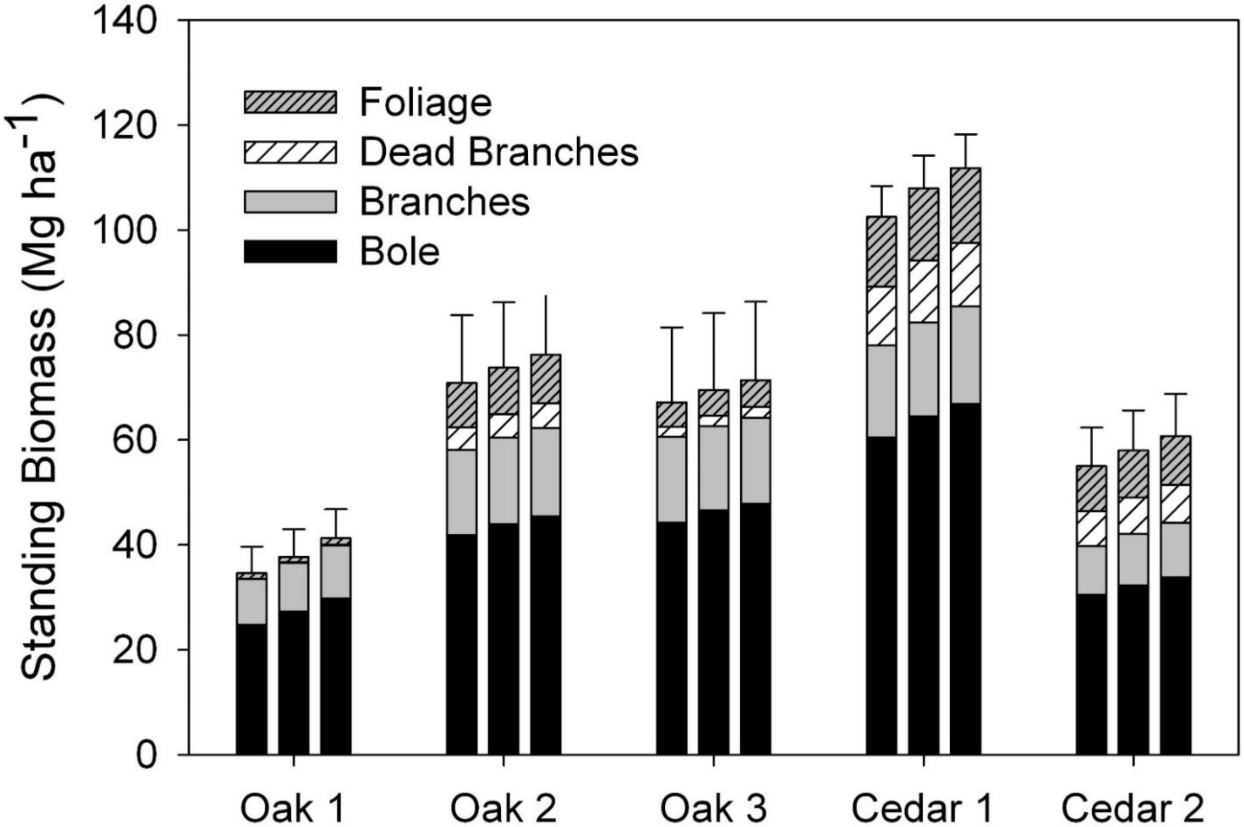

Figure 2. Standing biomass (Mg ha^{-1}) of forested watersheds broken into components of bole, branches, dead branches, and foliage. Bars represent the individual years 2015 to 2018 from left to right. Dead branch was only calculated for eastern redcedar because they retain dead branches. Vertical bars represent + SE of total biomass.

Table 8. Standing biomass for each forested watershed following the growing season from 2015 to 2018. SE is the standard error of the mean.

	Standing Biomass (Mg ha^{-1})							
Watershed	2015	SE	2016	SE	2017	SE	2018	SE
Oak 1	31.40	4.90	34.59	5.12	37.71	5.26	41.25	5.51
Oak 2	68.00	12.69	70.92	12.87	73.81	12.44	76.26	13.42
Oak 3	63.61	13.55	67.22	14.24	69.53	14.67	71.40	14.97
Cedar 1	98.79	5.75	102.52	5.91	107.96	6.26	111.81	6.44
Cedar 2	52.26	7.16	54.99	7.40	57.99	7.68	60.75	8.03
Average	62.81	8.81	66.05	9.11	69.40	9.26	72.29	9.67

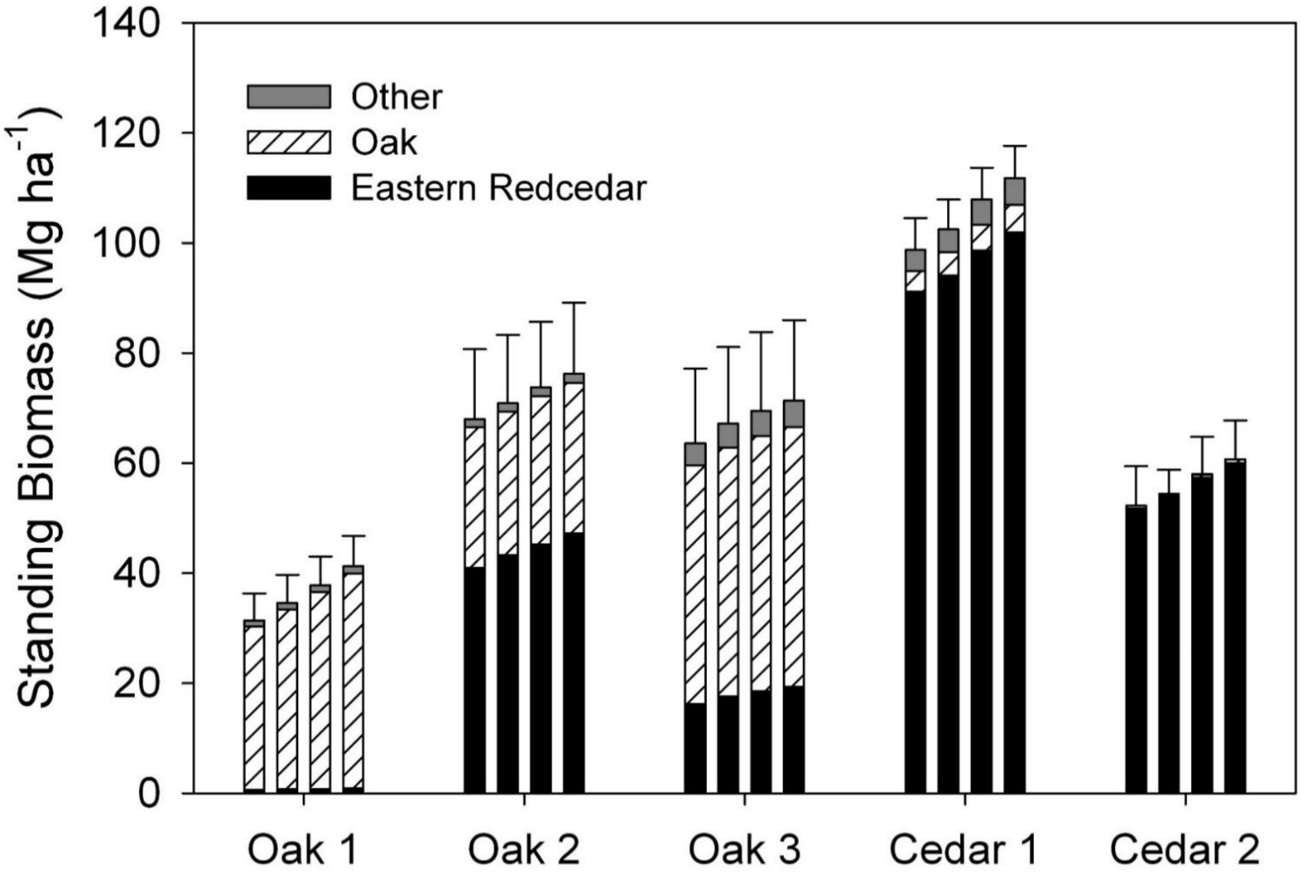

Figure 3. Standing biomass (Mg ha^{-1}) of forested watersheds broken down into categories of eastern redcedar, oak, and other species. Bars represent individual years 2015 to 2018 from left to right. Vertical bars denote + SE of total biomass.

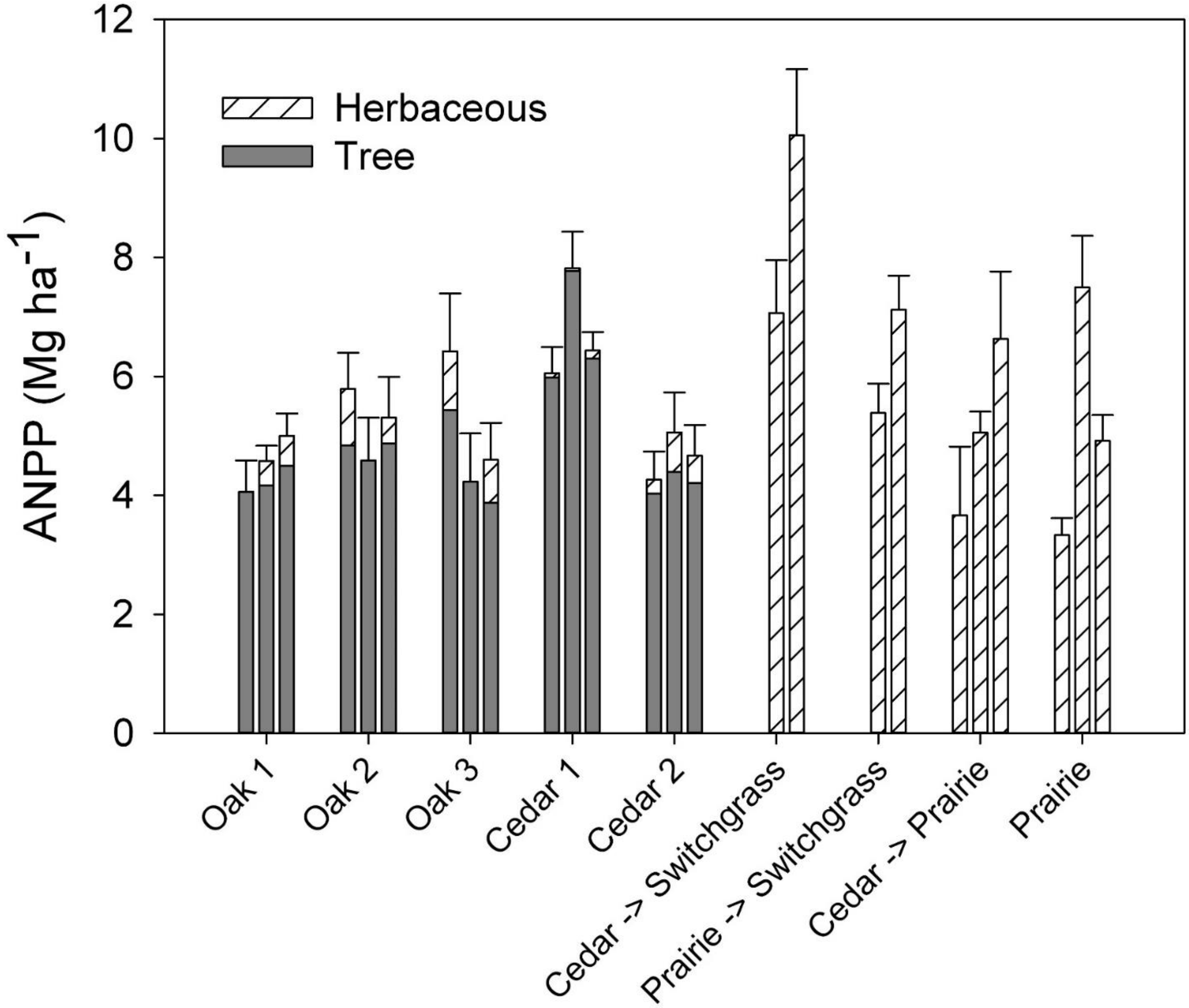

Figure 4. Annual net primary productivity (ANPP) (Mg ha^{-1}) of each watershed for individual growing seasons 2016 to 2018 broken into tree and herbaceous components. Cedar → Switchgrass and Prairie → Switchgrass have no ANPP for 2016 because switchgrass was not planted until 2017.Vertical bars indicate + SE of total productivity.

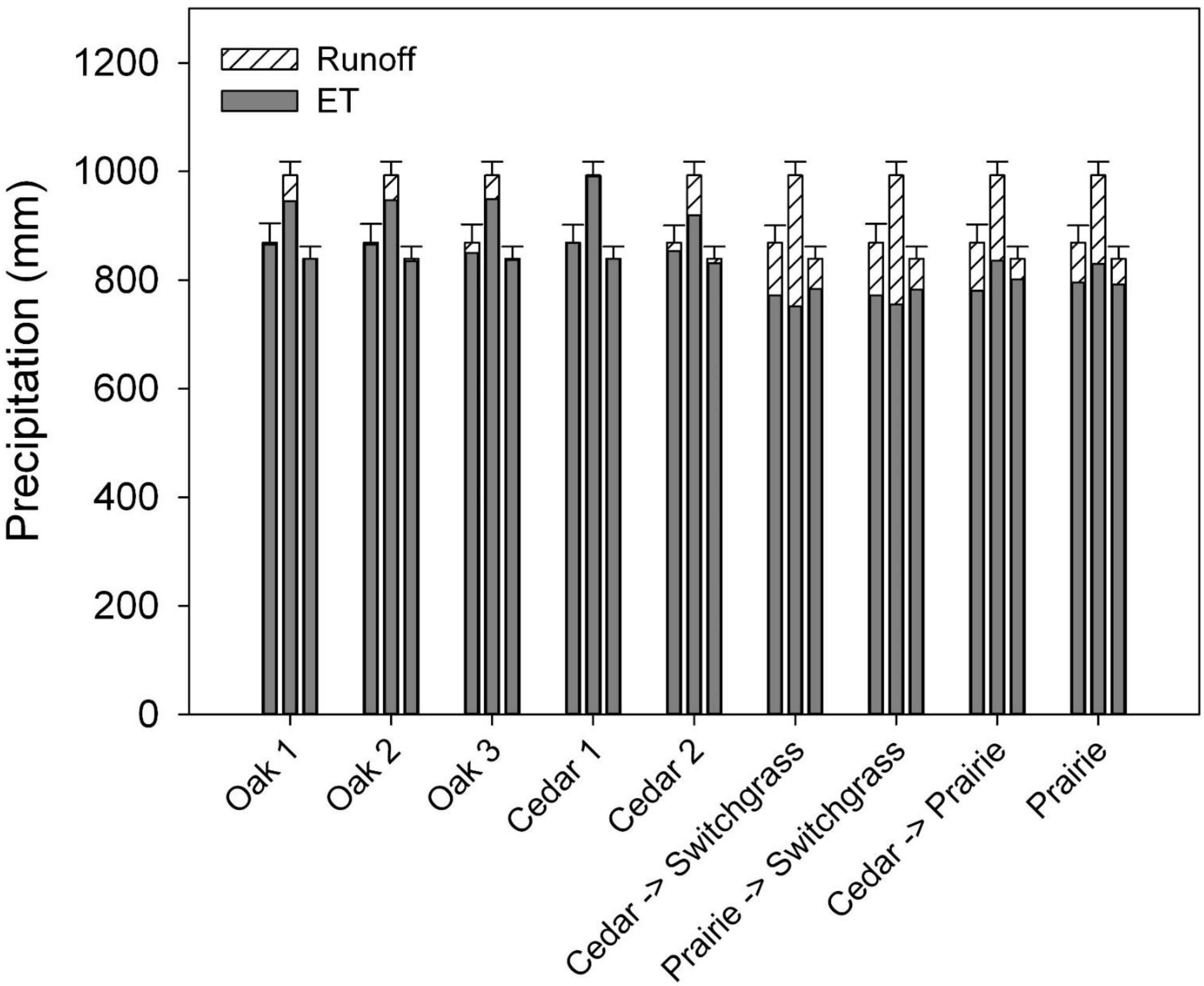

Figure 5. Total precipitation (mm) for the years 2016 to 2018 separated into runoff and evapotranspiration (ET). Total precipitation is calculated based on water year (October to September) and vertical bars indicate + SE of total precipitation.

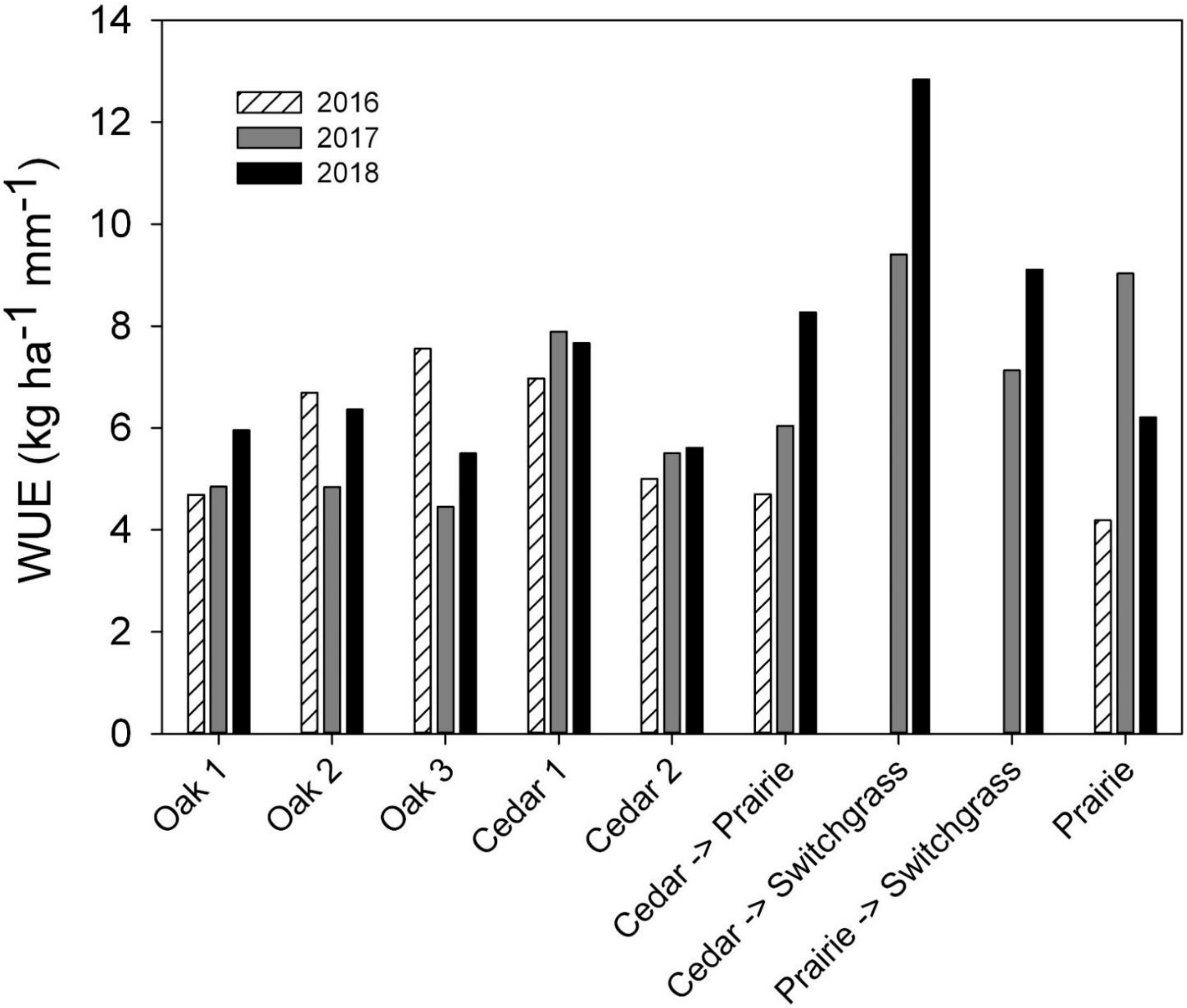

Figure 6. Water use efficiency (kg ha^{-1} mm^{-1}) of each watershed for 2016, 2017, and 2018 calculated as the ratio of ANPP and ET.

CHAPTER III

CONCLUSION

The encroachment of eastern redcedar and other woody species into the native tallgrass prairies and woodlands of the southern Great Plains is undeniably impacting water resources and ecosystem functions. Unless fire regimes are reinstated on the landscape or other management practices are undertaken, the invasion of eastern redcedar will not slow. But this encroachment is reversible and active management solutions are present for mitigating its impacts. Planting switchgrass could be both economically and environmentally beneficial to plant as a biofuel feedstock in the marginal lands of the Great Plains that are currently encroached by woody plants. My study found that switchgrass can have significantly greater productivity, runoff and water-use efficiency than redcedar. Higher productivity translates to greater CO_2 sequestration and greater runoff provides more streamflow for human uses and environmental services. Economically, switchgrass can be harvested for profit as a biofuel or used for forage for livestock with low cost to produce (Vadas et al. 2008, Aravindhakshan et al. 2010). Although switchgrass may not have the highest yields compared to other energy crops it does have reliably high yields for a variety of climate conditions which reduces risk for growers (Wright and Turhollow 2010).

Current climate change scenarios are expected to impact water resources so that already dry regions become drier (Dore 2005, Trenberth 2011) therefore the importance of water conservation will only increase with time. My study found that restored native prairie can also have significantly greater runoff and water use efficiency than encroached watersheds and could also be considered for management when removing eastern redcedar. However, runoff from switchgrass watersheds was significantly greater than that from native prairie due to greater evapotranspiration from native prairie which could have important implications for future land use decisions.

Because future climate change scenarios predict an increase in temperature and drought in semiarid regions, determining which species can provide the most ecological benefits are important. My study sought to quantify the productivity and ecosystem water use of lands encroached by eastern redcedar as compared to oak forest, native tallgrass prairie and switchgrass stands. I found that switchgrass has high productivity and runoff as compared to other local ecosystems which makes it a good choice in terms of carbon sequestration and water consumption.

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