WATER RELATION AND PHOTOSYNTHETIC PERFORMANCE OF EASTERN REDCEDAR (*JUNIPERUS VIRGINIANA*) AND POST OAK (*QUERCUS STELLATA*) IN THE CROSS TIMBERS FOREST

By

PATRICIA RETTONDINI TORQUATO

Bachelor in Forest Engineering

University of Sao Paulo (USP)

Piracicaba, Sao Paulo, Brazil

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WATER RELATION AND PHOTOSYNTHETIC PERFORMANCE OF EASTERN REDCEDAR (*JUNIPERUS VIRGINIANA*) AND POST OAK (*QUERCUS STELLATA*) IN THE CROSS TIMBERS FOREST

Thesis Approved:

Dr. Chris B. Zou

Thesis co-adviser

Dr. Rodney Will

Thesis co-adviser

Dr. Henry Adams

Name: Patricia Rettondini Torquato

Date of Degree: MAY, 2019

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Abstract: Eastern redcedar (*Juniperus virginiana*, redcedar) is rapidly encroaching and infilling the oak-dominated savannas and forest of the Cross Timbers of the central Great Plains. However, it remains unknown how this evergreen coniferous tree succeeds under the oak canopy and the hydrological impact associated with the transition of a deciduous oak forest to an oak-juniper mixed forest. I directly measured xylem water potential at predawn (Ψ_P) and midday (Ψ_M), net photosynthetic rate (P_n), stomatal conductance (g_s), and sap flux density of redcedars and post oaks (*Quercus stellata*) in a pure oak stand, pure redcedar stand, and oak and redcedar mixed stand from May 2017 to December 2018. I also measured soil water content within the soil profile during the study period. The Ψ, P_n and water use efficiency (WUE) of redcedar in the mixed stand were not significantly different from those in the redcedar stand. The P_n and g_s of post oak were always greater than those of redcedars. When soil moisture was low, post oak in the mixed stand had significantly higher Ψ_P compared with post oak growing in the post oak only stand. In the mixed stand, Ψ_P and Ψ_M were higher in post oak than in redcedar, although WUE was greater for redcedar. Sap flow density of redcedar was significantly higher than that of post oak but the water use of post oak was greater than that of redcedar of the same DBH. Relationships between Ψ_P and Ψ_M, and between relativized g_s and Ψ_M did not differ for redcedar and post oak on an annual basis. Post oak and redcedar mixed stand had higher water use than that of single species stand. Our results suggest that both redcedar and post oak tolerate episodic water stress while maintaining positive carbon assimilation and high WUE. The successful establishment of redcedar under oak savanna and forest and their co-existence may be due to the neutral interspecific interaction with post oak. At the ecosystem level, conversion from post oak savanna or forest to post oak-juniper mixed forest of a similar basal area may lead to an increase of transpiration.

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CHAPTER I

Introduction

The Cross Timbers ecoregion is located in the western edge of the eastern deciduous forest in the central and southern Great Plains. Its vegetation is characterized by a mosaic of prairie, oak savanna, and oak forest. The Cross Timbers ecoregion has a total area of 7.9 million hectares extending from eastern Kansas to central Texas (Therrell and Stahle 1998; Anderson et al. 2007). About 4.5 million hectares of the Cross Timbers are located in Oklahoma, and it is the most abundant woody vegetation type in the state (Therrell and Stahle 1998). The dominant woody species of the Cross Timbers are post oak (*Quercus stellata*) and blackjack oak (*Q. marilandica*), and the major grass species are little bluestem (*Schizachyrium scoparium*), big bluestem (*Andropogon gerardi*), and Indiangrass (*Sorghastrum nutans*) (Dyksterhuis 1948). The species composition of the Cross Timbers has been under a rapid change in the past decades due mainly to fire exclusion and increased drought episodes (DeSantis et al. 2010; DeSantis et al. 2011; Hoff et al. 2018a, Hoff et al. 2018b). With the decrease in fire frequency, fire-intolerant species have been increasing in number (Nowacki and Abrams 2008). Eastern redcedar (*Juniperus virginiana* L.) is the most successfully encroaching woody species in this region (DeSantis et al. 2011; Hoff et al. 2018a). The encroachment of eastern redcedar in Oklahoma expanded at a rate of approximately 48 km^2 per year since the 1980s and the most recent estimate is that eastern redcedar has encroached approximately 1300 km^2 of Oklahoma (Wang et al. 2018).

This change in species composition alters ecosystem structure and function (Coppedge et al.

2001; Caterina et al. 2014; Acharya 2018). The encroachment of eastern redcedar affected grassland biodiversity by eliminating some habitats critical for some wildlife species (Coppedge et al. 2001; Engle et al. 2008). The inclusion of a woody component in grassland and conversion of grassland to woodland increase water use at ecosystem-level (Awada et al. 2013; Caterina et al. 2014; Zou et al. 2014). In north-central Oklahoma, the closed canopy of eastern redcedar intercepted approximately 35% of rainfall (Zou et al. 2015) and was able to transpire over 95% of net precipitation (Caterina et al. 2014; Zou et al. 2015). The runoff coefficient averaged only a few percents, with over 80% reduction in annual streamflow compared with adjacent grassland (Zou et al. 2014). In Nebraska, an eastern redcedar stand transpired 413 mm in a year with total precipitation of 750 mm, and the soil water content was significantly lower than soil in grassland (Awada et al. 2013). Hence, eastern redcedar is effective in exploiting soil moisture to sustain high annual transpiration (Zou et al. 2014; Liu et al. 2017).

In the oak-dominated Cross Timbers forests, the encroachment and infilling of eastern redcedar is transforming these woodlands into mixed juniper-oak forests. The density of eastern redcedar in the oak-dominated forests increased from less than 1 to over 20 trees ha^{-1} from the 1950s to 2000s in central Oklahoma (DeSantis et al. 2011). In 2017, eastern redcedar averaged 57 trees ha^{-1} in north-central Oklahoma, representing about 20% of canopy cover (Hoff et al. 2018a). The presence of eastern redcedar in the midstory of oak forest increases flammable ladder fuel and the risk of crown fire (Hoff et al. 2018b). In addition, eastern redcedar was reported to increase litter that inhibits *Quercus spp*. recruitment, decreasing stand biodiversity (van Els et al. 2010). From the perspective of water budget, a study measuring water use in a mixed Ashe juniper (*J. ashei*) and live oak (*Q. virginiana*) forest in Texas reported that the daily water use of Ashe juniper was 58% greater than that of live oak (Owens 1996). In a stand level comparison, annual evapotranspiration of Ashe juniper savanna was 24 mm higher than that of live oak and Ashe juniper mixed savanna (Heilman et al. 2014). Therefore, woody encroachment and changes in species composition in oak woodland can have a significant impact on ecosystem processes including water budget. Yet the effect of eastern redcedar encroachment and infilling into the oak-dominated Cross Timbers on species-specific water use and ecosystem level water budget remains unknown.

The successful establishment of eastern redcedar in the midstory of the oak forests might be related to its physiological and morphological characteristics. Unlike deciduous species, eastern redcedar is able to maintain photosynthesis and transpiration nearly year round under the warm climate in the south-central Great Plains (Caterina et al. 2014). This characteristic affords eastern redcedar to properly function under much higher xylem tension than oak without cavitating (Bahari et al. 1985; Maherali et al. 2006). Soil moisture is highly variable in the Cross Timbers (Dyksterhuis 1948), and it is unknown how the physiological characteristics of eastern redcedar have assisted it to survive and expand in the water-limited environment.

Plants can regulate water use through stomata closure, reducing water loss under drought conditions. Eastern redcedar is able to maintain 50% of its hydraulic conductivity when its xylem water potential drops down to - 4.5 MPa in roots, and -7.1 MPa in the stem (Maherali et al. 2006). The ability to maintain carbon gain with high leaf-level water use efficiency under water stress makes eastern redcedar highly adaptive to water-limited conditions (Eggemeyer et al. 2006; Bihmidine et al. 2010). Post oak is considered a drought-tolerant species when compared to other oaks (Stransky 1990). Post oak has relatively low water use efficiency in seedlings grown in a greenhouse experiment, although it increases with water stress (Ni and Pallardy 1991). Interspecific interaction in mixed forests may complement resources use from niche stratification between species with different functional traits. However, how post oak and eastern redcedar could co-exist in the water-limited Cross Timbers remains unknown (Collins et al. 2013).

Although post oaks may adopt more conservative water use strategies when water becomes limited (Maherali et al. 2006), the root system of angiosperms is usually deeper than gymnosperms and able to reach deeper soil moisture (Renninger et al. 2015; Nardini et al. 2016). Thus, exploiting deeper soil moisture might display greater water use for post oak than eastern redcedar during dry periods. However, eastern redcedar is more flexible in its water extraction and is able to switch between shallow and deep soil layers depending on the availability of soil water (Eggemeyer et al. 2009; Awada et al. 2013). When post oak and eastern redcedar grow together, they may maximize the extraction of soil moisture. The potential impact of conversion of post-oak-dominated woodland to post oak and redcedar mixed forest on the ecosystem-level water use deserves further research (Zou et al. 2018).

The overall aim of this study is to understand how the co-occurring post oak and eastern redcedar balance carbon gain and water use and its implication of ecosystem-level water use in the Cross Timber. The specific objectives were to (1) determine if the physiological traits of eastern redcedar provide it a competitive advantage over post oak, and whether this is assisting its encroachment under the oak canopy, (2) understand the change of ecosystem-level transpiration after redcedar encroachment into the oak forest in the Cross Timbers.

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CHAPTER II

Tolerance to drought or competition avoidance? Key for successful establishment of eastern redcedar (*Juniperus virginiana*) in the oak-dominated Cross Timbers

Patricia R Torquato[1], Rodney Will[1], Chris B Zou[1], Henry Adams[2]

[1]*Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, OK 74078, USA*

[2]*Department of Plant Biology Ecology and Evolution, Oklahoma State University, Stillwater, OK 74078, USA*

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Abstract

Juniperus spp. are successfully encroaching grasslands and savannas of the Great Plains and changing the species composition and dynamics of these ecosystems. One well known case is the encroachment of eastern redcedar (*J. virginiana*) into the oak-dominated Cross Timbers forests of Oklahoma that is changing this ecoregion into a mixed juniper-oak forest. The overall objective of this study was to understand the inter-intraspecific interactions between eastern redcedar and post oak (*Quercus stellata*) for oak-redcedar forests of north-central Oklahoma Cross Timbers. Our specific objective was to understand how xylem water potential (Ψ), net photosynthetic rate (P_n), stomatal conductance (g_s), and water use efficiency (WUE) of eastern redcedar and post oak differed among single- and mixed-species stands. When growing together in mixed stands, Ψ at pre-dawn and midday was higher in oak than in eastern redcedar, although WUE was greater for eastern redcedar. When soil moisture was low, the oak growing in the mixed stand had significantly higher pre-dawn Ψ compared with oak in pure stands. The P_n and g_s of oaks declined during summer with high temperatures but was always greater than that of eastern redcedars. The P_n, g_s, and WUE of eastern redcedar in the mixed stand were not significantly different from those in the pure eastern redcedar stand, and Ψ was less negative for pure eastern redcedar stands during early spring but more negative during low soil moisture periods. Relationships between midday and pre-dawn Ψ and between relativized g_s and midday Ψ were similar for eastern redcedar and post oak. Our results suggest that eastern redcedar and post oaks have similar physiological responses regarding water use strategies during the growing season, both tolerating episodic water stress while maintaining positive carbon assimilation and high WUE. A neutral interspecific interaction with post oak may aid its successful encroach and co-existence into the forest midstory of the low stand density oak savanna and woodland.

Introduction

The Cross Timbers ecoregion is located on the dry western edge of the eastern deciduous forest and consists of a mosaic of prairie, savanna, and forest (Therrell and Stahle 1998; Anderson et al. 2007). It is located in the south-central Great Plains of the United States and covers almost five million hectares extending from Kansas across Oklahoma and into Texas (Therrell and Stahle 1998). The average annual precipitation in the western part of the Cross Timbers is 660 mm (Dyksterhuis 1948; Anderson et al. 2007), which is the lower bound to meet evapotranspiration requirements for the development of woodland or forest communities to the general exclusion of grasses species (Archer et al. 2017). As a result, the tree species within the Cross Timbers frequently experience water stress. The dominant tree species in the Cross Timbers are post oak (*Quercus stelatta*) and blackjack oak (*Quercus marilandica*) (Dyksterhuis 1948). However, woody species composition has been changing in the past century due largely to fire exclusion and increasing drought episodes (Burton et al. 2010; DeSantis et al. 2010; Rice and Penfound 1959). With the decrease in fire frequency, the stand density increases and fire-intolerant species are establishing and reaching the midstory (DeSantis et al. 2010; DeSantis et al. 2011; Hoff et al. 2018a; Hoff et al. 2018b).

The most common tree species encroaching into the Cross Timbers and present in the midstory is eastern redcedar (*Juniperus virginiana*) (DeSantis et al. 2011; Hoff et al. 2018a). Eastern redcedar is a non-sprouting, fire-intolerant, native evergreen species and is highly adaptable to water-limited conditions (Bahari et al. 1985; Maherali et al. 2006; Volder et al. 2013) in the Cross Timbers. The encroachment and infilling of eastern redcedar are transforming oak-dominated savannas and forests into oak and juniper mixed forests. This transformation in species composition and canopy structure is associated with the decrease in understory biodiversity (van Els et al. 2010), alteration in the watershed hydrological functions (Zou et al. 2016; Acharya et al.

2017), increase of wildfire risk (Hoff et al. 2018b) and elimination of some critical wildlife habitats (Horncastle et al. 2004).

The causes of eastern redcedar encroachment into the herbaceous dominated rangeland of the central Great Plains are well studied (Engle et al. 1996; Eggemeyer et al. 2006; Limb et al. 2010). However, there are fewer studies on the physiological mechanisms facilitating the evergreen eastern redcedar encroachment into oak-dominated forests (Volder et al. 2010). Eastern redcedar began to establish within the Cross Timbers in the middle of the 20th Century (DeSantis et al. 2010; Hoff et al. 2018a) concurrent with fire exclusion. From the 1950s to 2000s eastern redcedar within the Cross Timbers increased in stand density from <1 to 24 trees ha^{-1} in central Oklahoma (DeSantis et al. 2011) and averaged 57 trees ha^{-1} in north-central Oklahoma when measured in 2017 (Hoff et al. 2018a). Seedling recruitment of mesic fire-intolerant species and the evergreen species like eastern redcedar during these periods could have been facilitated by improved light and soil moisture conditions following gaps produced by drought-induced overstory mortality (DeSantis et al. 2011). However, the physiological mechanism remains unknown regarding how the shade intolerant evergreen eastern redcedar species is able to grow under the oak canopy and widely establish in the midstory in the water-stressed Cross Timbers region.

Eastern redcedar is able to maintain 50% of its hydraulic conductivity when its xylem water potential drops down to - 4.5 MPa in the roots and -7.1 MPa in the shoots (Maherali et al. 2006). This likely explains its ability to maintain carbon gain during periods of water deficit, and this in combination with its the high leaf-level water use efficiency (6 µmol m^{-2} s^{-1}) (Eggemeyer et al. 2006) makes eastern redcedar trees highly adaptive to semiarid conditions once fire is eliminated from the landscape (Eggemeyer et al. 2006; Bihmidine et al. 2010). Post oak is considered drought tolerant when compared to other oak species (Stransky 1990). Although its resistance to embolism has been characterized by Maherali et al. (2006), results from that research are problematic given recent artifact revelations for these methods with long-vessel species (Wheeler et al. 2013), such that these are inappropriate to compare directly to eastern redcedar. Post oak has been reported as having relatively low water use efficiency (near 0.10 µmol m^{-2} s^{-1}) in seedlings grown in a greenhouse experiment, although it increases with water stress (Ni and Pallardy 1991). I am not aware of any data available for mature post oaks.

Eastern redcedar morphological and physiological traits, such as extremely narrow xylem composed of tracheids, allow high xylem tensions to occur without cavitation, which assists eastern redcedar to tolerate and survive low soil moisture conditions (Eggemeyer et al. 2006; Maherali et al. 2006; Kannenberg et al. 2019). The water limited conditions and frequent droughts in the Cross Timbers might provide a competitive advantage for eastern redcedar over post oak, a condition that might intensify with predicted higher temperatures and more frequent droughts (Collins et al. 2013). However, there is limited information about how the co-occurring post oak and eastern redcedar balance carbon gain and water use, particularly under interspecific competition during low soil moisture availability.

The overall goal of this study was to answer the question whether the extreme drought tolerance of eastern redcedar lends it a competitive advantage over post oak and whether this is a key attribute facilitating its successful establishment in the midstory of the Cross Timbers. Specifically, I assessed the dynamics of xylem water potential (Ψ), photosynthetic rates (P_n), stomatal conductance (g_s), and water use efficiency (WUE) of these two species growing in single species stands and in mixed species stand. I hypothesized: (1) eastern redcedar maintains positive carbon gain across a broad range of soil water conditions and xylem water potentials which facilitates its competition with post oak during periods of low soil moisture; (2) when growing within stands of similar density, interspecific competition between oak and eastern redcedar for water is less than intraspecific competition when growing in single species stands. The competition was assessed by measuring water potential and leaf gas exchange decreases during dry periods. To test these hypotheses, I conducted a 17-month, field-based experiment in the Cross Timbers in north-central Oklahoma.

Material and methods

Study Site

The study was conducted at the Cross Timbers Experimental Range, a research and outreach facility owned by Oklahoma State University, 15 km southwest of Stillwater, Payne County, Oklahoma, USA. The site selected for the study is dominated by mature post oaks ranging from 6.2 to 30.7 cm diameter at breast height (DBH) and eastern redcedars ranging from 7.2 to 31.4 cm DBH (Table 2.1). The elevation is 331 m above the sea level, and the mean annual temperature is 15.5˚C. The soil is Stephenville series consisting moderately deep (approximate 1 m), well drained soils weathered from sandstone. The soil is mostly loamy fine sand in the upper 40 cm and sandy clay loam below 40 cm (Soil Survey Staff, 2018). Based on the Oklahoma Mesonet Marena Station located 2.1 km from the study site, the annual average precipitation is 887.9 mm with 66% falling during the growing season (April-September; Oklahoma Climatological Survey, 2018).

Experimental Design

I selected three stands representing different proportions of oak and eastern redcedar components in the early spring, 2017. The first stand was composed mainly of post oaks (OAK stand; 85% of basal area was post oak), the second stand was composed primarily of eastern redcedars (ERC stand; 82% of basal area was eastern redcedar), and the third stand was composed of post oaks (44% of basal area), and eastern redcedars (46% of basal area; MIX; Table 2.1). Each stand was demarked with 9.1 meters radius from the center point, totalizing 262.5 m^2 and they were less than 60 meters apart. Stands were selected based on a similarity of basal area and tree density (Table 2.1). I selected eastern redcedars and post oaks representing the range of DBH found in each stand for physiological measurements. There were seven post oaks selected within the OAK stand, seven eastern redcedars selected within the ERC stand, and five post oaks and five eastern redcedars selected within the MIX stand. The mean (± SD) basal area of the three different stands was 20.02 ±0.39 m^2 ha^{-1}.

Microclimate and Soil Moisture

In the early spring of 2017, I randomly selected three locations at the OAK stand, three locations at ERC stand, and five locations at the MIX stand to monitor soil moisture. For each location, I inserted one pair of 15 cm long stainless steel rods (3.2 mm in diameter) about 3 cm apart perpendicular to the soil surface. I installed a second pair of 45 cm long rods close to the first pair in a similar method. Volumetric soil water contents (θ) for soil depths between 0-15 cm and 0-45 cm were estimated using a 1502B Metallic Cable Tester (Tektronix, Inc., Beaverton, Oregon, USA), following Evett (2003) methodology. Measurements were taken every 15 days from April 2017 to September 2018, except from October 2017 to March 2018 when measurements were taken every 30 days. The water storage θ from 15-45 cm layer was calculated by calculating the water content from the 0-15 and 0-45 cm layers. The amount of water (water depth, mm) held in 0-45 cm layer was calculated, then it was subtracted by the water depth in the 0-15 cm layer to estimate the water depth held in 15-45 cm. The water depth was converted back to volumetric water content for 15-45 cm layer ($\theta_{15\text{-}45}$). Daily precipitation, solar net radiation, air temperature, humidity, and vapor pressure deficit (VPD) were collected from the Oklahoma Mesonet Marena Station.

Physiological Responses

I measured midday xylem water potential (Ψ_M), leaf net photosynthetic rate (P_n), and stomatal conductance (g_s) of all selected eastern redcedar and post oak trees bi-weekly from April to September in both 2017 and 2018. From October 2017 to March 2018, I made monthly measurements of the selected eastern redcedar trees. I measured predawn xylem water potentials

(Ψ_P) monthly for all selected trees during the growing season and only for eastern redcedars during winter. To determine xylem water potential, I collected shoots from the mid-canopy from each tree with a pole pruner and stored in individually labeled plastic bags in a closed cooler with ice until the measurement was performed (less than 30 minutes). Shoots for Ψ_P measurement were collected before sunrise and shoots for Ψ_M measurement were collected between 1100 and 1300. I determined xylem water potentials using a Scholander pressure chamber (Soil Moisture Equipment Corp., Model 3005, Santa Barbara, CA) in the field.

I measured net photosynthesis and g_s using the LI-COR 6400 portable photosynthesis system (LI-COR, Inc., Lincoln, NE) for leaves on shoots clipped using a pole pruner. Prior to clipping, leaves were in the mid to upper canopy and mostly exposed to full sunlight. Gas exchange was measured immediately after clipping. A 2 x 3 cm opaque chamber (model 6400-02B, LICOR, Inc., Lincoln, NE) with a red/blue LED light source was used with photosynthetically active radiation (PAR) set to 1800 µmol m^{-2} s^{-1}. Carbon dioxide concentration entering the cuvette was set at 400 ppm and conditions of ambient temperature and humidity were maintained inside the cuvette. Four successive measurements were taken at 2 seconds interval and averaged for analyses. Measurements were made between 1000 and 1400 for all 24 trees on the same day for each collection date. After gas exchange measurement of eastern redcedar, the foliage sample in the cuvette was excised and stored in paper bags to be dried in an oven at 60 °C for 7 days to obtain dry weight. The equation from Cregg (1992) was used to calculate the leaf area from the dry weight, and P_n and g_s values were recalculated using the calculated areas. No calculations were necessary for post oaks as their leaves were large enough to cover the entire leaf chamber.

I calculated intrinsic water use efficiency (WUE) for each gas exchange measurement as the ratio of P_n and the corresponding g_s. Intrinsic WUE was chosen instead of instantaneous WUE (P_n /transpiration rate) because small VPD changes during the measurement period can affect leaf level transpiration rates (Yi et al. 2017), while g_s is generally not affected.

Data Analysis

I performed data analyses using SAS 9.4 (SAS Inc., Carey, NC, USA). I tested the following comparisons, 1) oak growing in the OAK stand vs oak growing in the MIX stand to determine the effects of intra- vs interspecific competition on oak physiology, 2) eastern redcedar growing in the ERC stand vs eastern redcedar growing in the MIX stand to determine the effects of intra- vs interspecific competition on eastern redcedar physiology, 3) oak in the MIX stand vs eastern redcedar in the MIX stand to determine how the two species differ when growing together. Because eastern redcedar was measured year round while post oak was only measured during the growing seasons, comparisons involving oak (1 and 3) used growing season data only while the comparison among eastern redcedar (2) included all data. From this point forward, the post oaks at the OAK site are abbreviated as “Oak” and the post oaks at the MIX site are abbreviated as “Moak”. Eastern redcedar trees at the ERC site are abbreviated as “Erc” and the eastern redcedar trees at the MIX site are abbreviated as “Merc”.

To determine whether Oak and Moak differ, Erc and Merc differ, and Moak and Merc differ, I tested for differences in Ψ_P, Ψ_M, P_n, g_s, and WUE using a PROC MIXED model with repeated measurements with autoregressive covariance structure. Date, species, and stand were considered fixed effects and individual trees were considered a random effect. The repeated θ measurements for each stand were analyzed using PROC MIXED with a similar model, testing for differences in date and stand as well as their interaction. The PDIFF option was used in all analyses to compare the LS-means of different treatment groups. To test whether the relationships between Ψ_P and Ψ_M differed between redcedar and post oak, analysis of covariance (ANCOVA) was used to test for differences in slopes or intercepts. Likewise, the relationship between Ψ_M and g_s was tested, Stomatal conductance values were relativized based on the maximum actual g_s reading of each species before analysis.

Results

Environmental Conditions

Environmental conditions during the study are presented summarized in Figure 2.1. During the study period (April 2017-September 2018), total precipitation was 1572.8 mm, with 977.4 mm from April 2017 to March 2018. There were 137 days with rain, of which 69 days had precipitation less than 5 mm and 13 days had precipitation greater than 25 mm. Of the total precipitation in both years, 45% occurred during spring. The largest daily precipitation was 125 mm on April 29, 2017. The longest period with no precipitation was 36 days between January 11 and February 15, 2018. From July 4 to September 25, 2017 (84 days), there was only 119.4 mm rainfall distributed in events smaller than 20 mm, and the study area experienced a drought during September 2017 classified as an abnormal, and another drought in July 2018, classified as a moderate by the Palmer Drought Severity Index (PDSI) (Dai, et al., 2017).

During the study period, the relative humidity had its lowest values during winter (December 2017 to March 2018), reaching 26.2% on January 25, 2018. The daily average temperature (±SD) was 17.8 ±9.2 °C, ranging from -12.4 to 32.8 °C. The daily average VPD ranged from 0.003 to 2.7 kPa. The annual mean temperature for the growing season (April to October) (±SD) was 22.5 ±9.64 °C in 2017 and 22.7 ±6.0 °C in 2018.

Volumetric Soil Water Content

For 0 - 15 cm soil layer, θ at the monthly scale varied across dates ($p < 0.0001$) and stands ($p < 0.003$) with date and stand interactions for OAK vs ERC and OAK vs MIX ($p < 0.05$, Table 2.2). The θ at the OAK stand was often greater than θ at MIX or ERC for the months when oaks were senescent ($p < 0.05$). Low θ occurred during the late growing season for both years and was not significantly different among stands (Fig. 2.2).

For 15 - 45 cm soil layer, θ varied across dates ($p < 0.0001$) and stands ($p < 0.0001$) but the interaction between date and stand was not significant ($p > 0.05$, Table 2.2). On average, θ (±SD) of the OAK stand (0.31 ±0.06 cm^3 cm^{-3}) was greater than θ at the MIX stand (0.23 ±0.07 cm^3 cm^{-3}) and the ERC stand (0.15 ±0.07 cm^3 cm^{-3}), while θ at the MIX stand was greater than θ at the ERC stand (Fig. 2.2, Table 2.2). For both years, the lowest θ occurred in the late growing season for all stands, and the lowest values of θ for OAK, MIX and ERC stands were 0.21, 0.12, and 0.06 cm^3 cm^{-3} in 2017 and 0.25, 0.15, 0.08 cm^3 cm^{-3} in 2018, respectively.

Physiological Responses

Comparisons for Ψ_P, Ψ_M, P_n, and g_s among post oaks (Oak vs Moak) were affected by date with a significant date and stand interaction (Table 2.3). The Ψ_P of Oak and Moak did not differ significantly when Ψ_P was higher than -1.6 MPa. The Ψ_P of Oak was significantly lower than that of Moak during the late growing season of 2017 when the overall Ψ_P and the soil moisture were very low (Fig. 2.2, 2.3a). Comparing Ψ_M of post oak in different stands, nine of eleven measurements presented no significant difference. Oak had significantly higher Ψ_M than Moak during the early growing season of 2017 when soil moisture was high, and in July 2018 (Fig. 2.2, 2.4a). The P_n and g_s for Moak and Oak comparisons, however, were inconsistently different in 2017 with Oak higher for P_n on two dates and for g_s on one date while Moak was higher for P_n and g_s on one date each (Fig. 2.5a, and 2.6a). The P_n and g_s followed the same trends and exhibited a decrease of 76% in P_n and 93% in g_s from June/July to September 2017. The WUE of Oak and Moak did not significantly differ among the stands and exhibited the highest values during the dry period of 2017 (Fig. 2.7a) (Table 2.3).

The Ψ_P, Ψ_M, P_n, and g_s of eastern redcedar (Erc vs Merc) were affected by date, but not by stand, however, there were significant date and stand interaction for Ψ_P and Ψ_M (Table 2.3). The differences in Ψ_P between Erc and Merc were generally small with more negative Ψ_P for Merc only in May 2017 and more negative Ψ_P for Erc in July 2018 (Fig. 2.3c; Table 2.3). For Ψ_M, there was one date in 2017 where Merc was more negative than Erc, but in 2018, there were four dates during the middle of the growing season where Erc was more negative than Merc (Fig. 2.4c; Table 2.3). The highest values for P_n and g_s occurred during early spring and declined during the season and reached the lowest values during the late growing season when eastern redcedar in both stands exhibited its highest values for WUE (Fig. 2.5c, 2.6c, and 2.7c).

For the MIX stand (Moak vs Merc), the Ψ_P, Ψ_M, P_n, g_s, and WUE were affected by date, species (except for WUE) with a significant date and species interactions (Table 2.3). The Ψ_P of Merc was significantly more negative ($p < 0.05$) than that of Moak on nine of eleven dates, all except for the first and last measurement of 2018 (Fig. 2.3b). The Ψ_M of the Merc was more negative than Moak only during the dry seasons (5 out of 17 measurement date) (Fig. 2.4b). By contrast, P_n and g_s of the Moak were significantly higher than the Merc for the all data collection period, except for a late growing season date in 2017 when the entire soil profile was very dry (Fig 2.5b, and 2.6b). In addition, WUE of the Moak was significantly lower than Merc during the early spring and the dry season of 2017 (Fig. 2.7b).

When the relationship between Ψ_M and Ψ_P were compared, the slopes for post oak (0.80) and eastern redcedar (0.79) were similar for the entire study period (Fig. 2.8), with no significant difference in slope or intercept ($p > 0.05$). For the nonlinear relationship between relativized g_s and Ψ_M (Fig. 2.9), decrease in g_s for post oak was similar for eastern redcedar. Therefore, even though eastern redcedar tended to have lower water potentials, the degree to which stomata close per unit change in Ψ_M was similar.

Discussion

In general, eastern redcedar had lower P_n, g_s, and Ψ, and higher WUE relative to post oaks. However, there was no evidence in our study to support the hypothesis that eastern redcedar is able to maintain carbon gain at a wider range of water potential than the post oak. The slope of leaf Ψ_P and Ψ_M (Ψ_M/Ψ_P) can be used to characterize the water stress response strategy of co-occurring tree species along the anisohydric and isohydric spectrum, and a lower Ψ_M/Ψ_P indicates a higher stomatal conductance sensitivity to drought (MartínezVilalta et al. 2014). *Pinus sylvestris*, a coniferous species, and *Q. pubescens*, a white oak, growing in a Mediterranean-type transition zone, exhibited Ψ_M/Ψ_P slopes of 0.64 and 0.33, respectively (Poyatos et al. 2008), with *Q. pubescens* exhibiting a more anisohydric behavior than the post oak species in our study. However, *J. osteosperma* during a summer drought in Utah reported Ψ_M/Ψ_P with a slope close to 1.0 (Linton et al. 1998). In addition, the slopes between relativized g_s and Ψ_M were similar for post oak and eastern redcedar in our study, which indicates a similar percent decreases in stomatal conductance per decrease in water potential. Even with eastern redcedar generally maintaining more negative Ψ_M, our analysis included the non-stressed periods such that the response of g_s to declining Ψ_M was assessed across a full range of water availability. Likewise, the absolute value of g_s in both species approached zero during the driest period, further supporting that both species do close their stomata to prevent water potentials from becoming excessively negative and the embolism risk (Maherali et al. 2006; Bihmidine et al. 2010; Volder et al. 2010).

Past studies have found that eastern redcedar was capable of maintaining 50% of its hydraulic conductivity when its xylem water potential drops down to -7.1 in shoots (Maherali et al. 2006), which is much lower than the most negative xylem water potential recorded in this study. In greenhouse studies, Parker and Pallardy (1988) and Kwon and Pallardy (1989) reported turgor loss in seedlings of post oak at leaf Ψ of -2.8 MPa and -2.0 MPa. However, in our study, post oak reached lower Ψ_M than these values, can indicate that mature trees are more tolerant of low water potentials or that the post oak growing in the Cross Timbers forest is more drought tolerant, or even that post oak species can adjust its turgor loss point depending to the water conditions it is exposed to. The period that I performed the data collection had only moderate drought, which did not cause conditions sufficient to cause irreversible damage to the leaf physiology of either species.

For our second hypothesis involving cross stand comparisons, Ψ of post oak in the mixed stand (Moak) was not reduced by replacing about half the oak basal area with eastern redcedar. In fact, oak Ψ_P was higher in the mixed stand than the single-species stand under moderate water stress perhaps indicating more intense competition for water in pure oak stands. Likewise, Ψ_M tended to be lower for eastern redcedar in the single-species stand than in the mixed stand. However, these differences were infrequent and inconsistent, as were the responses of P_n and g_s which indicates transient response or a Type I error which is quite possible given the number of comparisons made. The effects of interspecific competition can be less intense than the intraspecific competition if there are differences in rooting structure and rooting depth among species (Davis et al. 1998; Nardini et al. 2016). The rooting structure of a beech-oak forest differed between the monospecific stand and a mixed stand, with beech growing more roots in the upper most soil when growing with oaks (Leuschner et al. 2001). It is possible that eastern redcedar at the mixed stand concentrated on developing a shallow root system which reduces competition for deep soil moisture with oak. As a result, eastern redcedar may lessen competition for water with oak and more easily recruit into the middle canopy than oak saplings. Despite our measured variation in Ψ_P among stands, the differences could not be explained by soil moisture differences among the three stands. I measured the highest soil moisture within the upper 45 cm in the oak stands which seem to support oak accessing deeper water. I suggest further investigation of the effective rooting depth of eastern redcedar and post oak under intra- and inter-specific competition.

When P_n and g_s were compared between species, the P_n and g_s of post oak were substantially higher than eastern redcedar during the growing season, independent of the stand. This finding is consistent with the results from a study in Texas, where post oak seedlings had rates of P_n and g_s that were almost double those of eastern redcedar seedlings (Volder et al. 2010). Also, Owens

(1996) reported the average conductance of *Q. virginiana* was 0.11 mol m^{-2} s^{-1}, twice as much as the 0.05 mol m^{-2} s^{-1} measured for *J. ashei* (closely related to *J. virginiana*), and *Q. virginiana* exhibited 30% higher P_n than *J. ashei*. The WUE of eastern redcedar was higher than post oak in the early spring and during the drought condition in September in 2017. During the early spring 2017, the relatively lower WUE of post oak compared to the eastern redcedar may have been due to the high water use of post oak at this time of the year. Granier et al. (1994) found that oaks produce wide diameter vessels (usually larger than tracheids) in the early wood which easily embolize. I speculate that the low WUE of post oak observed during spring might be associated with abundant water use when the soil moisture is high and the larger diameter vessels functional. During the dry season of 2017, WUE increased for both post oak and eastern redcedar. The higher WUE during low soil moisture is a result of the increase in WUE of both species during drought (Ni and Pallardy 1991; Eggemeyer et al. 2006).

Even though species had similar physiological behavior, they have different xylem anatomy. Junipers are known for extremely narrow xylem composed of tracheids. The diameter of tracheids in juniper species ranges from 8 to 9.5 µm, enabling these trees to withstand the effect of low water potentials without experiencing cavitation; Ψ values of -7.1, -8 and -13.4 MPa have been reported at 50% conductivity loss in eastern redcedar (Maherali et al. 2006), Utah juniper (*J. scopulorum*), and Ashe juniper (McElrone et al. 2004; Pittermann and Sperry 2006), respectively. Post oaks have tracheids and vessels as xylem elements, ranging from 14.9 to 27.2 µm diameter, and their much wider conduits should make them more vulnerable to embolism (Bares and Holbrook 2001). The similarity of species g_s in the mixed stand during the driest period of 2017 highlights the fact that post oak is also very drought tolerant. Its xylem anatomy allows large water transport when water is available, but it can still move water when water becomes limiting and the largest vessels cavitate (Abrams 1990).

The Cross Timbers is located in the climate transition zone between forest and grassland. Climate is highly variable and the frequency and severity of episodic droughts are predicted to increase (Cook et al. 2015). Post oak is a deciduous tree that can avoid extreme drought stress by dropping leaves to eliminate transpiration (Baldocchi and Xu 2007). As an evergreen, *Juniperus spp*. has to tolerate low soil moisture through physiological regulation or suffer mortality during protracted droughts as observed in 2011 and 2012 in some places of north-central Oklahoma (Twidwell et al. 2014). Drought tolerance might be essential for the survival of eastern redcedar during low soil moisture condition but the successful establishment of eastern redcedar in the middle canopy may have resulted from its ability to reduce competition for soil water with oaks by spatially partitioning water uptake via different rooting depths and by gaining carbon year round, taking advantage of higher light conditions in the midstory during the leaf-off period for oaks.

Our result shows that replacement of post oak by equal basal area of eastern redcedar resulted in improvement of the water potential status of both species during the driest periods. This neutral to facilitative interspecific interaction or niche separation may permit the co-existence of post oak and eastern redcedar and the successful establishment of eastern redcedar into the middle canopy of the low stand density oak savanna and woodland, as widely observed in the Cross Timbers.

Conclusion

Eastern redcedar has successfully established into the midstory of the oak dominated savanna and forest of the Cross Timbers. Eastern redcedar had similar physiological traits compared to post oaks. Both species were equally effective and responsive to moderate water stress through water regulation with similar Ψ_M/Ψ_P ratios, and tolerating episodic water stress while maintaining positive carbon assimilation and high water use efficiency. A neutral to facilitative interspecific interaction with post oak under moderate water stress may aid its successful establishment and co-existence into the middle canopy of the low stand density oak savanna and woodland.

The information on the physiological responses and interspecific competition between encroaching eastern redcedar and post oak is fundamental for projecting the change in species composition of the Cross Timbers under predicted increase in climate variability for this general region. Also, the future successional trajectory in the structure and function of the Cross Timbers are important for the prediction of carbon and water dynamics for the Cross Timbers ecoregion. The future research needs to focus on the impact of an oak-dominated ecosystem to an oak-eastern redcedar co-dominated ecosystem on the water budget, carbon cycle, wildlife habitat, and a broader social and economic impact.

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Table 2.1. Mean diameter at breast height (DBH), basal area (BA), and trees per hectare (TPH) for each stand for stems greater than 5 cm DBH. Each stand had an area of 262.5 m^2 (0.026 ha).

Stand	Species	DBH (±SD)	BA (m^2 ha^{-1})	TPH
OAK	Post oak	18.6 (±4.5)	17.5	609
	Eastern redcedar	11.4 (±3.0)	1.6	152
	Other	11.8 (±1.9)	1.3	114
	Total		**20.5**	**876**
MIX	Post oak	19.9 (±10.1)	8.9	229
	Eastern redcedar	14.8 (±8.2)	9.3	419
	Blackjack oak	13.1 (±7.8)	1.5	190
	Other	6.9 (±0.9)	0.4	114
	Total		**20.1**	**952**
ERC	Eastern redcedar	13.7 (±7.4)	16.0	838
	Post oak	18.9 (±0)	1.1	38
	Blackjack oak	14.4 (±6.0)	2.2	114
	Other	10.0 (±0)	0.3	38
	Total		**19.5**	**1028**

Table 2.1. Results of PROC MIXED model with repeated measurements with autoregressive covariance structure for date, stand and their interaction on soil water content (θ) in 0-15 and 15-45 cm depth

Stand	θ (cm)	0-15	15-45
ERC vs MIX	Date	**<0.0001**	**<0.0001**
	Stand	**0.0028**	**<0.0001**
	Date x Stand	0.3604	0.4285
ERC vs OAK	Date	**<0.0001**	**<0.0001**
	Stand	**0.0007**	**<0.0001**
	Date x Stand	**0.0043**	0.072
OAK vs MIX	Date	**<0.0001**	**<0.0001**
	Stand	**<0.0001**	**<0.0001**
	Date x Stand	**0.0024**	0.382

Table 2.2. Results of PROC MIXED model with repeated measurements with autoregressive covariance structure for the date, stand and species and their interaction on photosynthesis and leaf water status

Species	Variable	P_n	g_s	Ψ_P	Ψ_M	WUE
Post oak (Oak vs Moak)	Date	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
	Stand	0.0724	0.0877	0.5425	0.878	0.0805
	Date x stand	**0.0463**	**0.0154**	**0.008**	**0.006**	0.94
Eastern redcedar (Erc vs Merc)	Date	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
	Stand	0.2153	0.4241	0.8168	0.1078	0.4857
	Date x stand	0.2997	0.3076	**0.0002**	**<0.0001**	0.1302
Post oak vs Eastern redcedar (Moak vs Merc)	Date	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
	Species	**<0.0001**	**<0.0001**	**<0.0001**	**0.0302**	0.1889
	Date x species	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**0.001**

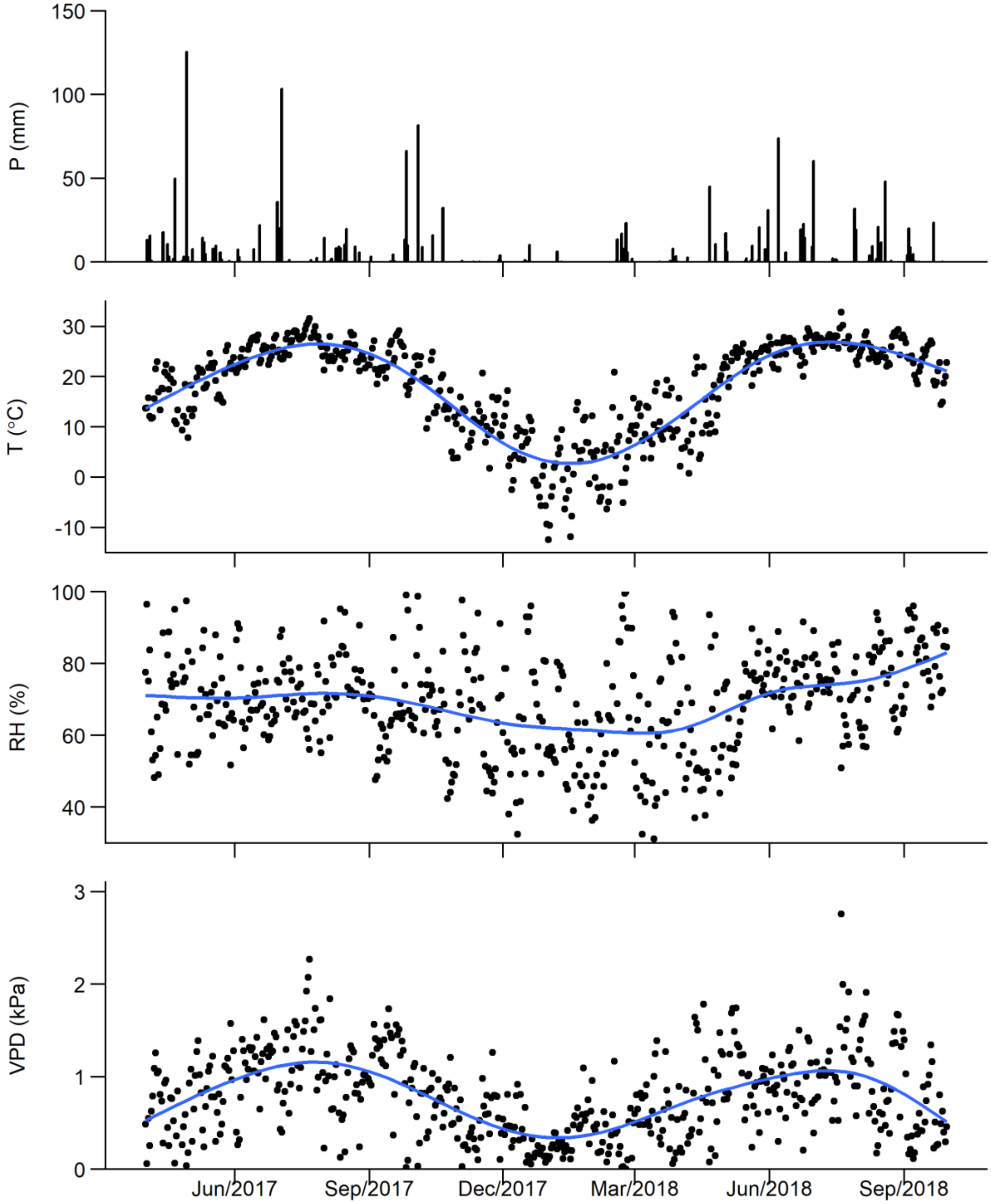

Figure 2.1. Daily precipitation (P), and daily average temperature (T), relative humidity (RH), and vapor pressure deficit (VPD) from April 2017 to September 2018. The blue line is the locally weighted regression using local neighborhood with size of 5 days.

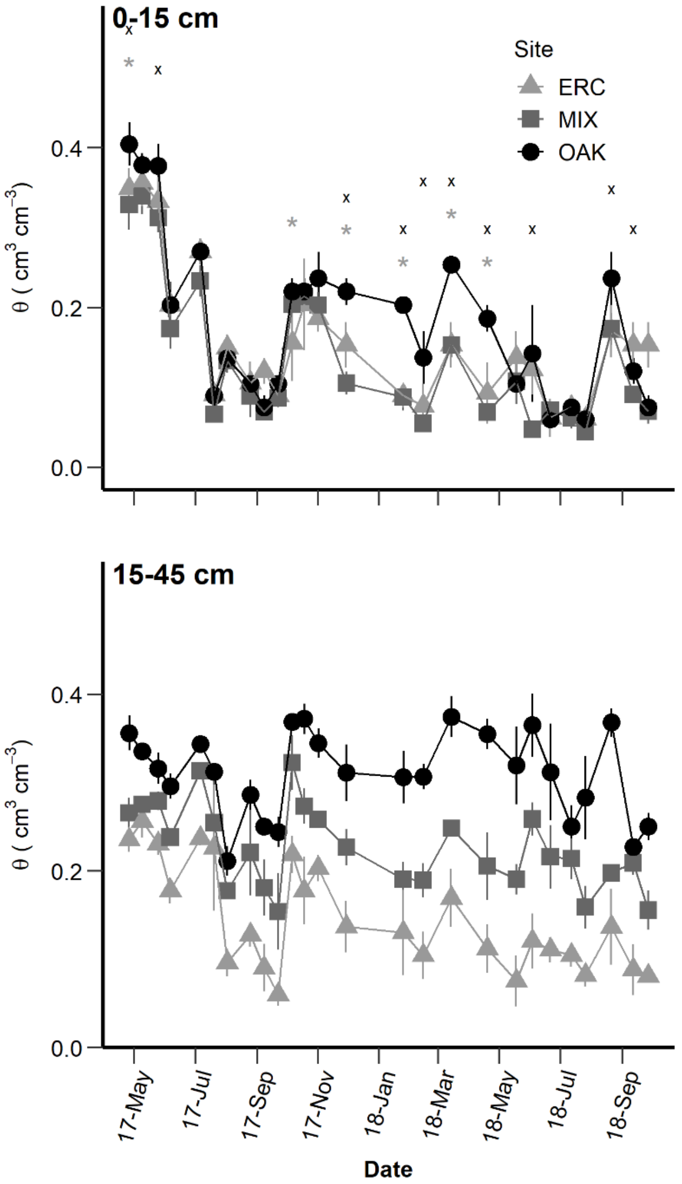

Figure 2.2. Volumetric soil water content (θ) for the 0-15 cm and 15-45 cm soil depth intervals for the oak stand (OAK), mixed stand (MIX), and eastern redcedar stand (ERC) measured between April 2017 and September 2018. For the 0-15 cm layer asterisks (*) indicates significant differences ($p < 0.05$) between OAK and ERC, and the letter "x" indicates significant differences ($p < 0.05$) between OAK and MIX. For the 15-45 cm layer, significant differences were OAK stand > MIX stand > ERC stand ($p < 0.05$). Vertical bars represent sthe tandard error of each measurement.

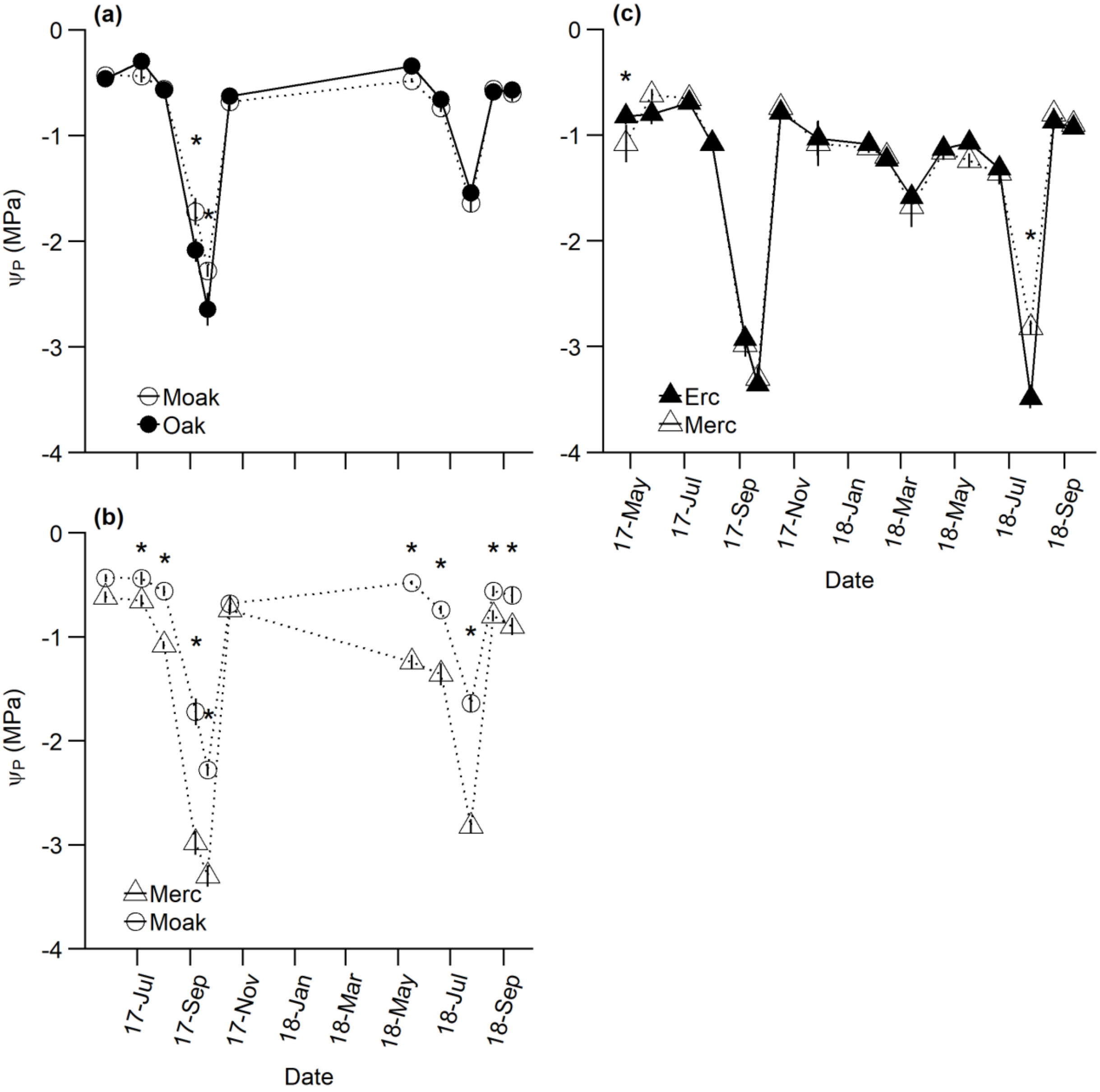

Figure 2.3. Predawn water potential (Ψ_P) measured during the study period for three comparisons; Moak vs. Oak (a); Merc vs. Moak (b) and Erc vs. Merc (c). Merc and Moak are eastern redcedar and post oak trees growing in a mixed species stand while Erc and Oak are eastern redcedar and post oak growing in single species stands. An asterisk (*) indicates significant differences ($p<0.05$). Vertical bars represent, standard error of each measurement.

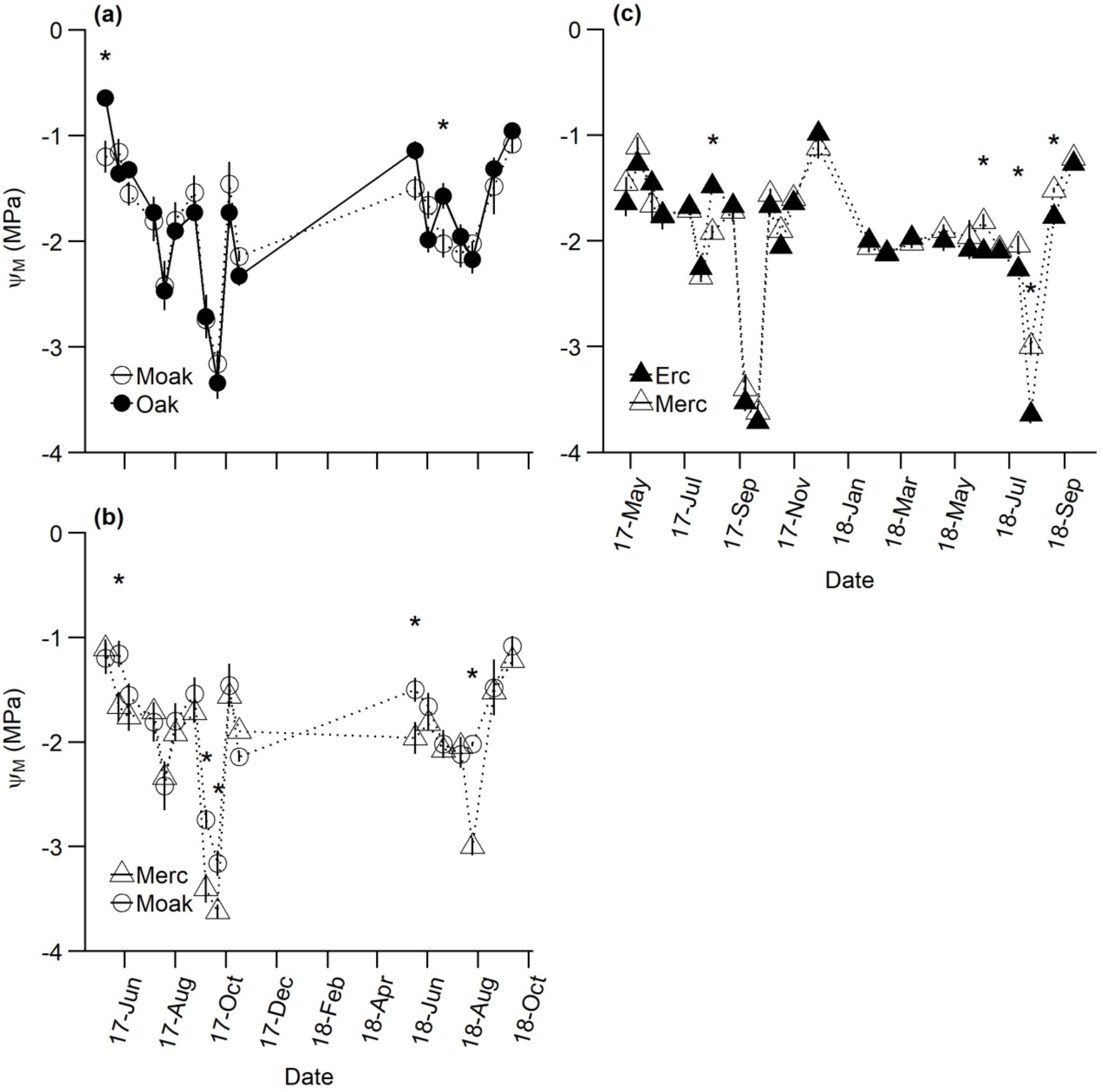

Figure 2.4. Midday water potential (Ψ_M) measured during the study period for three comparisons; Moak vs. Oak (a); Merc vs. Moak (b) and Erc vs. Merc (c). Merc and Moak are eastern redcedar and post oak trees growing in a mixed species stand while erc and oak are eastern redcedar and post oak growing in single species stands. An asterisk (*) indicates significant differences ($p<0.05$). Vertical bars represent, standard error of each measurement.

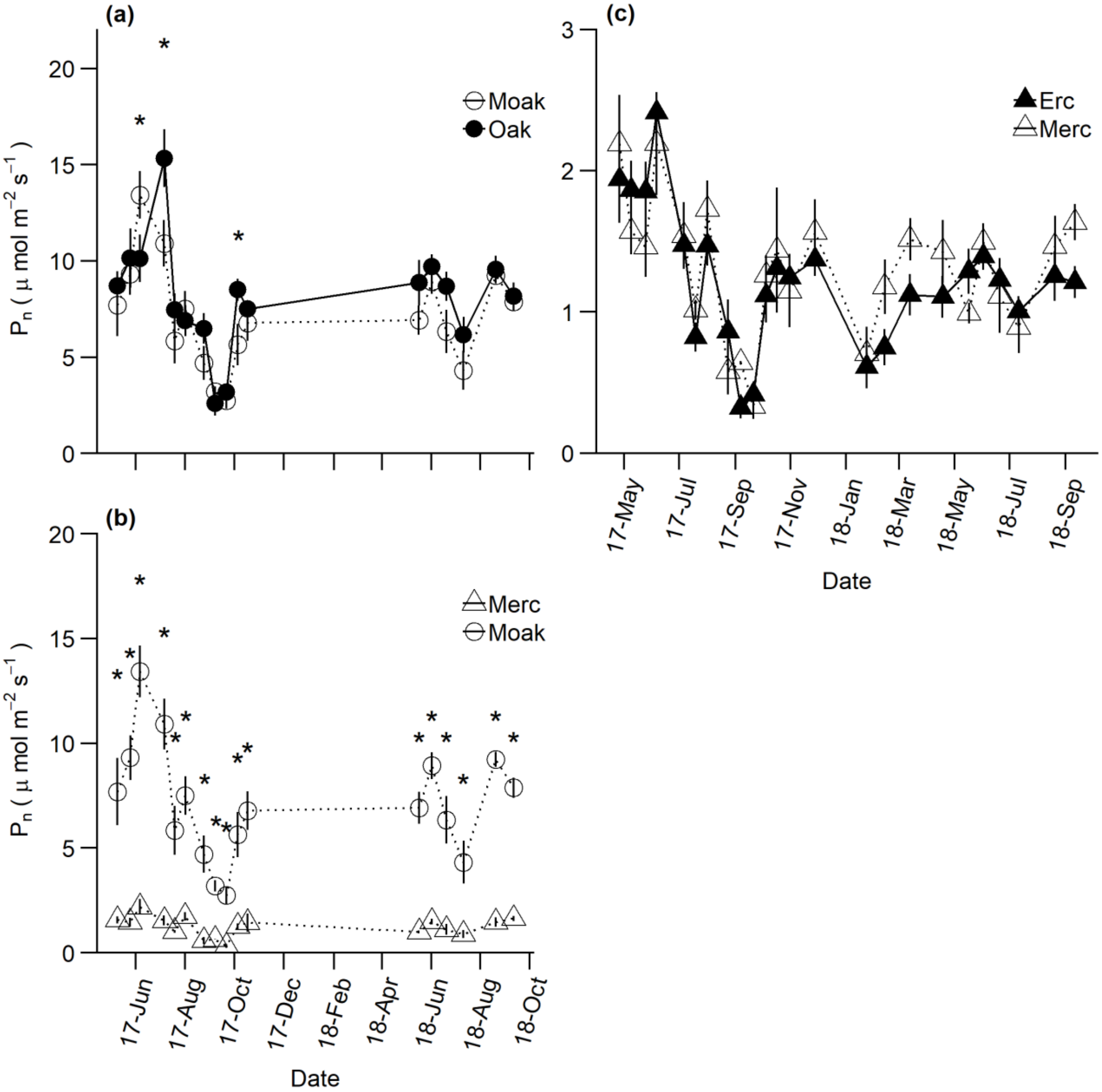

Figure 2.5. Photosynthetic rate (P_n) measured during the study period for three comparisons; Moak vs. Oak (a); Merc vs. Moak (b) and Erc vs. Merc (c). Merc and Moak are eastern redcedar and post oak trees growing in a mixed species stand while erc and oak are eastern redcedar and post oak growing in single species stands. An asterisk (*) indicates significant differences ($p<0.05$). Vertical bars represent, standard error of each measurement.

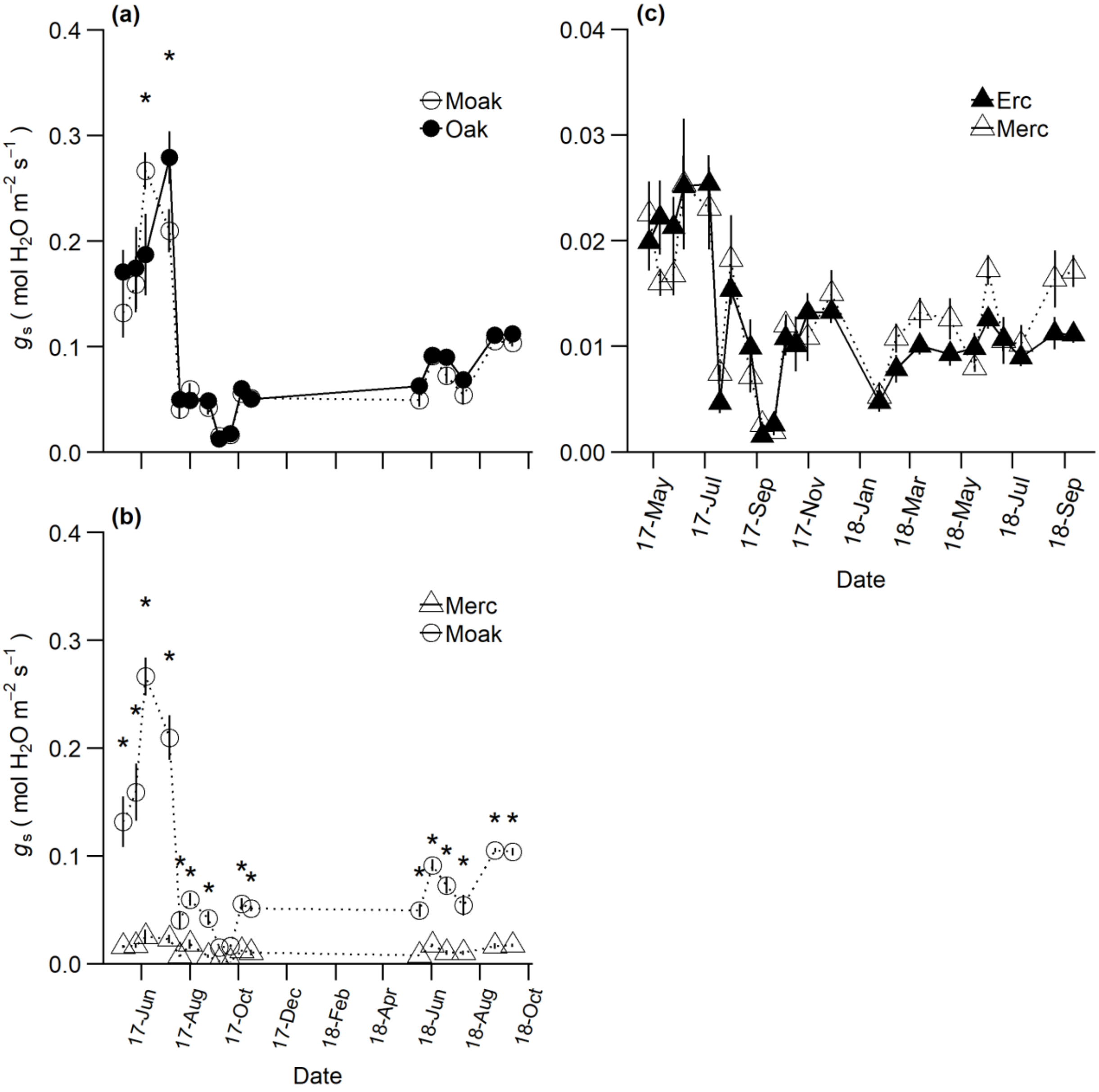

Figure 2.6. Stomatal conductance (g_s) measured during the study period for three comparisons; Moak vs. Oak (a); Merc vs. Moak (b) and Erc vs. Merc (c). Merc and Moak are eastern redcedar and post oak trees growing in a mixed species stand while erc and oak are eastern redcedar and post oak growing in single species stands. An asterisk (*) indicates significant differences ($p<0.05$). Vertical bars represent, standard error of each measurement.

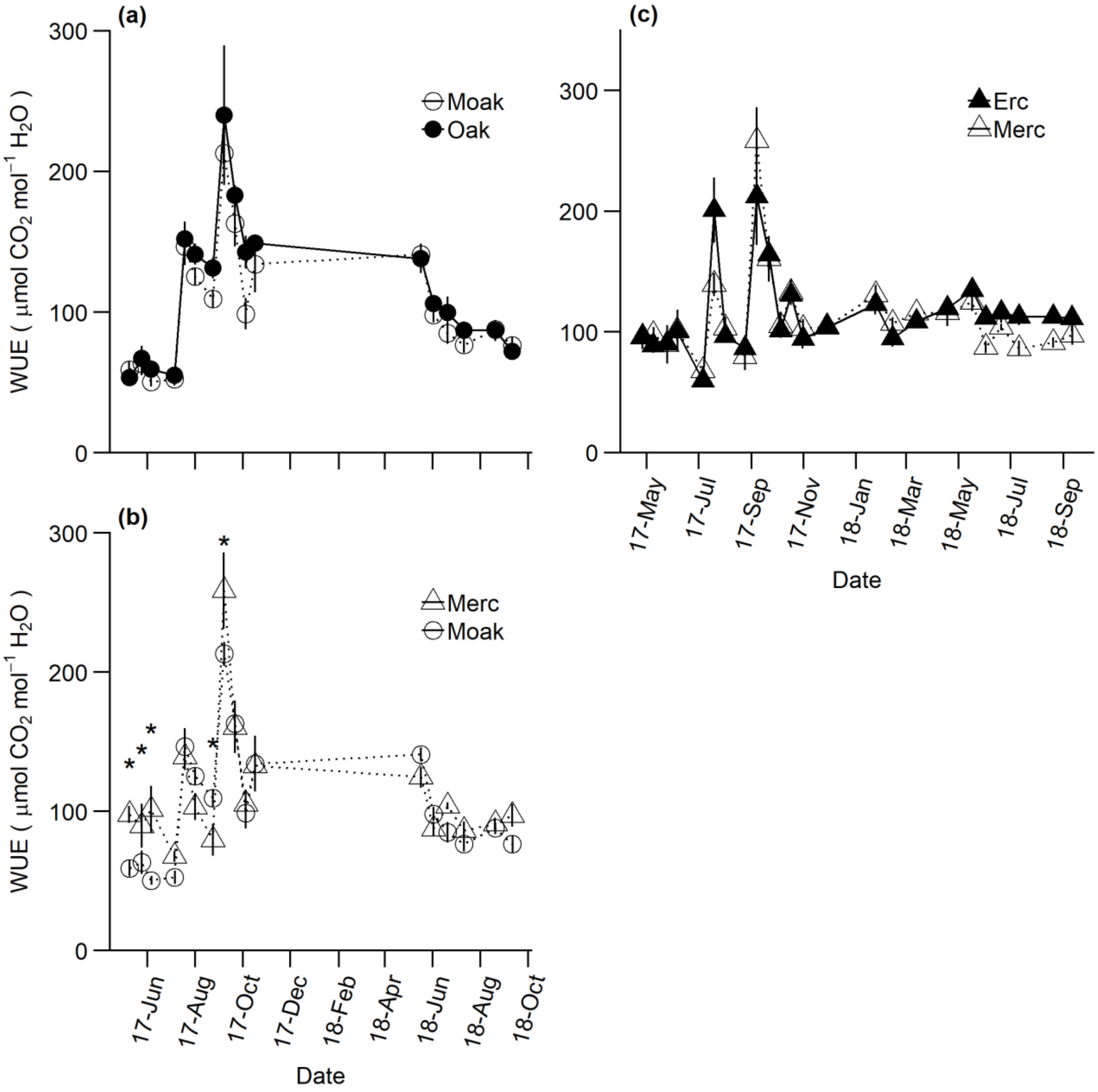

Figure 2.7. Water use efficiency (WUE) measured during the study period for three comparisons; Moak vs. Oak (a); Merc vs. Moak (b) and Erc vs. Merc (c). Merc and Moak are eastern redcedar and post oak trees growing in a mixed species stand while erc and oak are eastern redcedar and post oak growing in single species stands. An asterisk (*) indicates significant differences ($p<0.05$). Vertical bars represent, standard error of each measurement.

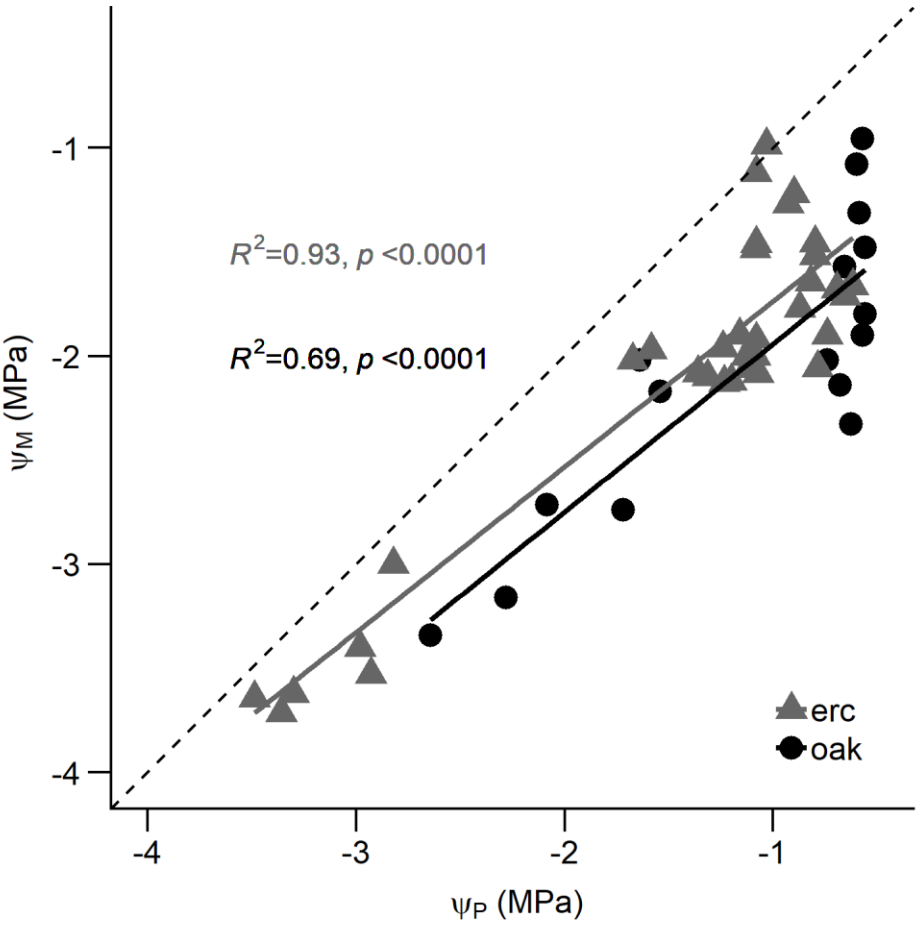

Figure 2.8. Linear regressions between the predawn water potential (Ψ_P) and midday water potential (Ψ_M) for post oak (circles) and eastern redcedar (triangles). The 1:1 relationship is indicated by a dashed line. Equations are as follow: Ψ_M oak = 0.80 Ψ_P - 1.13; Ψ_M erc = 0.79 Ψ_P - 0.93

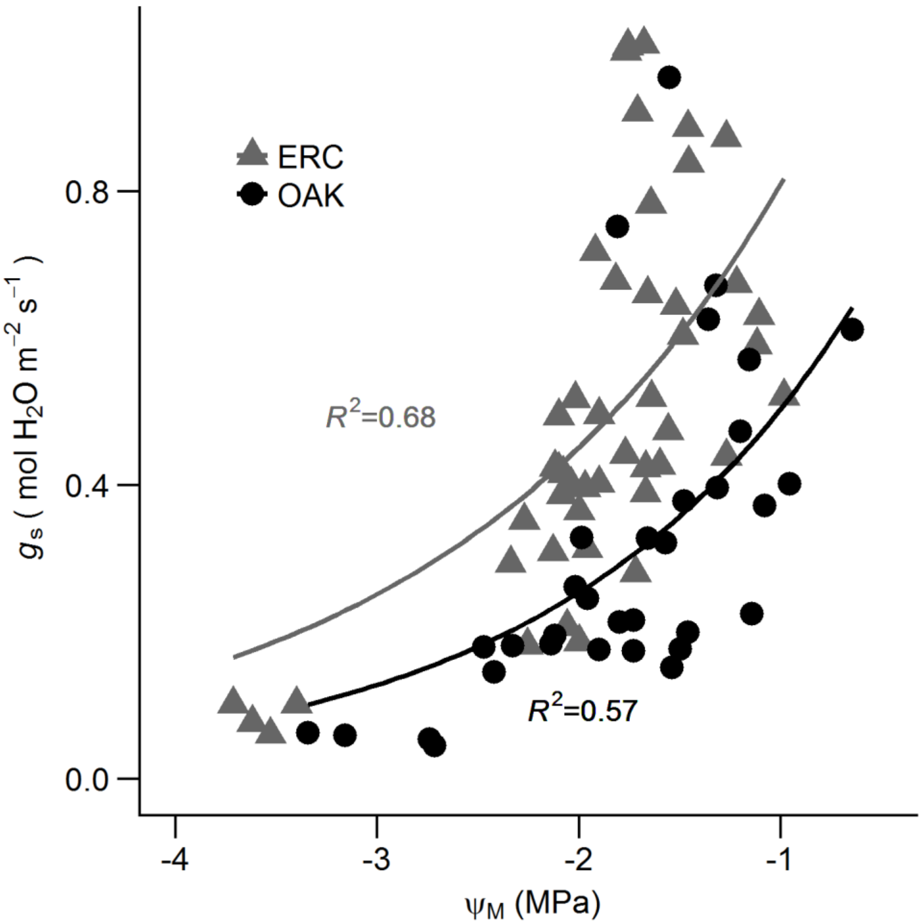

Figure 2.9. Relationship between the stomatal conductance (g_s) midday water potential (Ψ_M) for post oak (circles) and eastern redcedar (triangles). Equations are as follow: $g_{s\ oak} = 1.47\ e^{0.97\ \Psi}$; $g_{s\ erc} = 2.33\ e^{0.89\Psi}$

CHAPTER III

Water use of eastern redcedar (*Juniperus virginiana*) and post oak (*Quercus stellata*) in a mixed forest.

Patricia R. Torquato[1], Chris B. Zou[1], Rodney E. Will[1]

[1]Oklahoma State University, Department of Natural Resource Ecology and Management, Stillwater, OK 74078, USA

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encroachment, sap flow density, transpiration, Cross Timbers

Abstract

Rapid encroachment and infilling of *Juniperus virginiana* (redcedar) within the Cross Timbers ecoregion are drastically changing the species composition, midstory canopy structure, and the phenology of the oak-dominated ecosystem. Our objective was to determine how these changes affect species-specific water use and competition, and ultimately ecosystem-level water use and potentially water availability for streams and groundwater. I selected three stands representative of different post oak and redcedar compositions in the Cross Timbers Experimental Range, near Stillwater in Payne County, Oklahoma. Sap flow of selected trees was monitored continuously using the commercially available thermal dissipation probes (TDPs) from May 2017 to December 2018. Our results show that sap flow density of redcedar was generally higher than the post oaks, independent of the stand. However, the average water use of the post oaks was higher than redcedar with the overall daily water use of 7.9 L day^{-1} for redcedar and 13.3 L day^{-1} for post oaks during the two growing seasons. When growing in the mixed stand, both post oak and redcedar had higher water use than growing in the single-species stand. For 2018, the total water use was 635, 557, 498 mm for the mixed stand, the oak stand, and redcedar stand, respectively. Empirical models to simulate water use from temperature, solar radiation, and vapor pressure deficit, and soil moisture were established for post oak and redcedar. Our results suggest replacement of post oak by redcedar of a similar basal area will increase the total transpiration on the annual scale. The increase in ecosystem water use may lead to a reduction in streamflow, the loss of a major ecosystem service of the Cross Timbers. Direct quantification of streamflow response using a watershed approach will improve the assessment of the runoff responses to change in vegetation composition and guide effective silvicultural practices for sustainable management of Cross Timbers for optimizing water resources.

Introduction

The Cross Timbers is a vegetation mosaic composed of open prairie, oak savannas, and oak-dominated forests extending from Kansas to Texas (Therrell and Stahle 1998; Anderson et al. 2007). The oak savanna and forest mostly occur on coarsely textured soils, and the dominant canopy tree species are mainly post oak (*Quercus stellata*) and blackjack oak (*Q. marilandica*). Fire exclusion has increased woody species presence and allowed eastern redcedar (*Juniper virginiana*), a native, evergreen conifer, to encroach the prairie, and infill the oak-dominated savannas and forests (DeSantis et al. 2010b; DeSantis et al. 2011; Hoff et al. 2018). Encroachment of redcedar into grasslands increases ecosystem-level water use, resulting in a reduction of runoff and groundwater recharge potential (Zou et al. 2014; Acharya 2018). The effect of redcedar encroachment and infilling into the oak forest on water use and ecosystem level water budgets remains unknown.

Transpiration is usually the dominant component of the water budget in forest ecosystems, especially in semiarid and subhumid regions (Huxman et al. 2005). Redcedar is an evergreen conifer with a strong tolerance for water stress (Bahari et al. 1985; Maherali et al. 2006). Physiologically, redcedar is known for having a strong anisohydric tendency and can extract water from soil with very low water potential (Maherali et al. 2006). Also, redcedar has a flexible water use strategy and can extract water from deeper soil layers when water in the shallow soil is not available (Eggemeyer et al. 2009), exploiting and depleting soil water at deeper layers to meet high transpiration during drought (Zou et al. 2014; Liu et al. 2017). Caterina et al. (2014) found that redcedar is capable of transpiring almost all water reaching the mineral soil during a year with average precipitation under the high atmospheric demand in the south-central Great Plains, USA. As a result, strong interspecific competition for soil moisture is expected during drought episodes in the post oak and redcedar mixed forest.

The water use of planted redcedar stand was estimated using sap flow technique in the Sandhills of Nebraska (Awada et al. 2013) and in encroached grasslands in central Oklahoma (Caterina et al. 2014; Starks et al. 2014). Redcedar maintains active transpiration when the air temperature is above -3 °C (Caterina et al. 2014). As a result, redcedar trees can transpire throughout much of the year including during winter in the south-central Great Plains climate. In contrast, post oaks start to produce leaves in late March and senescence starts around late November in the south-central Great Plains. The rate of transpiration of redcedar increases with tree size, atmospheric vapor pressure deficit, and availability of soil water. The daily average water use was approximately 24 L per tree for a redcedar woodland in north-central Oklahoma but varied between 1.7 and 46.6 (Caterina et al. 2014). A redcedar tree in a low-density stand uses more water than a redcedar tree of similar diameter but growing in a dense stand (Caterina et al. 2014; Starks et al. 2014), however there was no significant difference in stand-level water use when expressed on a tree crown area basis (Caterina et al. 2014). The stand level transpiration of redcedar woodland averaged 413 mm year^{-1} in Nebraska in a year with above-average precipitation (Awada et al. 2013). A later study conducted in a hot and below average precipitation year in south-central Oklahoma reported a similar value of stand-level transpiration (431 mm).

There is no documented information of stand-level transpiration of the post oak in the Cross Timbers forest. However, a recent study showed that a stand of post oaks in the Lost Pines ecoregion of Texas could transpire up to 0.44 mm day^{-1} during the growing season (Cooper et al. 2018). Also in Texas, Owens (1996) found that the total daily water use of Ashe juniper (*J. ashei*) was 58% higher than that of southern live oak (*Q. virginiana*). Heilman et al. (2014) reported that in five years the largest difference in evapotranspiration between Ashe juniper savanna and a southern live oak and Ashe juniper mixed woodland was 62 mm year^{-1}, where Ashe juniper savanna evapotranspired 649 mm of 697 mm in rainfall. This evidence suggests that ecosystem water use changes after species change or re-assemblage of tree species in savanna and woodland systems.

Water use by a tree is influenced by soil water availability and atmospheric conditions (Thorburn et al. 1993; Awada et al. 2013; Caterina et al. 2014). Most studies indicate that sap flow in the tree is strongly influenced by solar radiation, vapor pressure deficit, air temperature, and soil water content (Granier and Loustau 1994; Phillips and Oren 2001; Liu et al. 2017). For example, in a Mediterranean oak stand, daily transpiration of oak species was highly correlated with solar radiation, and vapor pressure deficit (Hernández-Santana et al. 2008). The sap flux technique estimates the transpiration of a tree by continuously tracking the sap flow density from the xylem tissue (Granier and Loustau 1994; Wilson et al. 2001) providing opportunities to establish empirical models to simulate water use from environmental variables at different time scales. The Cross Timbers ecoregion is located at the grassland and forest transition zone, and its climate is highly variable, with the temperature and the vapor pressure deficit (VPD) both being projected to increase in future (Collins et al. 2013). Therefore, the establishment of an empirical relationship among tree water use and environmental variables at the daily scale will assist stand level estimation of water use under the projected climate change in this ecoregion at the margin of the eastern deciduous forest.

Our overall aim was to understand the change of ecosystem-level transpiration after redcedar encroachment into the oak forest in the Cross Timbers. Our specific objectives were 1. To understand how environmental variables affect the sap flow density of post oak and redcedar; 2. To compare sap flow density of individual trees under intra and inter-specific competition; and 3. To estimate and compare stand-level transpiration for post oak only, redcedar only, and post oak and redcedar mixed stands. I employed three sap flow systems to quantify the sap flow of individual post oak and redcedar trees of different sizes growing in single species or mixed stands. I used a multiple/ partial regression approach to construct a model to explain sap flow density based on environmental factors.

Material and methods

Study Site

The research site was located at the Cross Timbers Experimental Range, a research and outreach facility owned by Oklahoma State University, 15 km southwest of Stillwater in Payne County, Oklahoma, USA (36°04'05.1"N, 97°11'25.7"W). The average annual precipitation is 887.9 mm, with 66% falling during the growing season (April-October). The annual mean temperature is 15 ºC, with a monthly temperature reaching a minimum of -4.3 ºC in January and a maximum of 34 ºC in August. The elevation is 331 m above the sea level, and the soil type is Stephenville series with the upper 20 cm mostly sandy loam, and loam and clay loam in deeper layers (Soil Survey Staff, 2018). The vegetation at the site is characterized by a mosaic of tallgrass prairie, oak savanna, and oak-dominated forests. Many stands have been heavily encroached by redcedar.

Experimental Design

I selected three stands representative of different woody species compositions. The first stand had 85% of the basal area composed of post oak (OAK), with a mean canopy height of 11.4 m and a basal area of 20.4 m^2 ha^{-1}. The second stand was a mixed stand with 44% of the basal area composed of redcedar and 46% of the basal area of post oak (MIX), the mean canopy height was 7.6 m for redcedar and 8.4 m for post oaks, and the basal area was 20.1 m^2 ha^{-1}. The third stand had 81% of the basal area composed of redcedar trees, with a mean canopy height of 8.6 m and a basal area of 19.5 m^2 ha^{-1} (ERC) (Table 3.1). This basal area is representative of the current stands in Cross Timbers (DeSantis et al. 2010a; Hoff et al. 2018). I selected seven post oaks in OAK, seven redcedar trees in ERC, and five of each species in the MIX to install sap flow sensors. The distribution of diameters at breast height (DBH) of selected trees was intended to cover the range of tree size in the Cross Timbers. In this study, I did not select trees with DBH less than 5 cm due to its limited contribution to the stand level water use.

Environmental Variables

Daily data for net solar radiation (R_s), precipitation, air temperature (T), relative humidity, wind speed, and VPD from Oklahoma Mesonet Marena Station (Oklahoma Climatological Survey, 2018) located 2.1 km from the study site were used for this study. I calculated potential evapotranspiration (ETo) using these meteorological variables based on the Food and Agriculture Organization of the United Nations Penman-Monteith equation (Allen et al. 1998). I determined volumetric soil water contents (θ) (cm^3 cm^{-3}) at four depths (5, 20, 45, and 80 cm) from the soil surface using soil moisture array consisting of four probes (EC-5; Meter Environment, Pullman, WA). There were three soil moisture arrays installed near the study site within 100 m distance from the selected stands. Soil water content was continuously measured at 15-minute intervals and daily averages of each sensor were calculated. The θ for a given depth used in this study was the daily mean value of three probes at the same depth.

Thermal Dissipation Probes System Installation and Sapwood Estimation

Sap flow of each selected tree was continuously monitored from May 2017 to December 2018 using thermal dissipation probes (TDPs) (Model TDP-10 and TPD-30, Dynamax Inc., Houston, TX, USA). For trees with DBH larger than 10 cm, I installed 30 mm TDPs, and I used 10 mm TDPs for trees with DBH less than 10 cm. Two holes, 5 cm from each other at approximately 1 m above the ground were drilled on the north side of the tree trunk to insert the TDP following the instructions recommended by the manufacturer. Putty was applied carefully to seal around the base of each probe, and then the entire TDP was covered with an aluminized thermal bubble foil to insulate the trunk from excessive thermal fluctuation. Two sets of TDP probes were used for trees larger than 15 cm DBH, and three sets for trees larger than 30 cm DBH. The temperature differential from each probe was sampled at a 10-minute interval, averaged every 60 minutes, and then recorded using three customized FLOW32A-K systems (Dynamax Inc., Houston, TX, USA), one on each stand. Sapwood area (SA, cm_{sw}^2) was estimated based on the tree radius and sapwood width at the height where the probe was installed. For post oaks which has symmetrical sapwood width, sapwood width was determined using increment cores taken from each tree during July 2018. For redcedar with relatively asymmetrical sapwood, the sapwood width was estimated based on color differentiation between the light colored sapwood and the reddish heartwood by carefully drilling into the trunk and analyzing residuals left on drill bits. I drilled one to four different locations, depending on the tree size and shape.

Sap Flow Density to Whole-tree and Whole-stand Water Use

I calculated sap flow densities ($S_{d\ \mathrm{Granier}}$, $cm^3\ cm_{sw}^{-2}\ hr^{-1}$) for both species from measured temperature differential using original equation developed by Granier (1985), [$S_{d\ \mathrm{Granier}}$ = $0.0119*[(\Delta Tmax-\Delta T)/\Delta T]1.231$ ($cm^3\ cm^{-2}\ h^{-1}$)], where ΔT is the temperature differential between the upper probe which is heated and the lower probe (control temperature), and ΔTmax is the temperature difference at zero flow. $S_{d\ \mathrm{Granier}}$ was converted to actual sap flow density (S_d) based on species-specific calibration equations. For redcedars, S_d was re-calculated based on the calibration equation reported by Caterina et al. (2014) ($S_d = 2.3* S_{d\ \mathrm{Granier}}$). For post oaks, S_d was re-calculated based on the calibration equation for *Quercus alba* developed by Sun et al. (2012) ($S_d = S_{d\ \mathrm{Granier}} / 0.892$).

To determine the diurnal variation in S_d in response to drought, I re-calculated the mean value of S_d for the entire growing season and also during the two different drought episodes in 2017 and 2018 on an hourly basis. I calculated daily sap flow density (Sd, L cm_{sw}^{-2} day^{-1}) by summing the hourly sap flow density of each day. Hourly water use (WU_{hr}, L hr^{-1}) for each tree was calculated from S_d ($WU_{hr} = SA\times S_d$). Daily water use (WU, L day^{-1}) for each tree was calculated by summing the hourly water use for each day.

I estimated the daily water use for species without probes using linear regressions equations developed from DBH, sapwood area, S_d, and water use (for nonmeasured redcedar trees) and post oak (for nonmeasured post oak and other angiosperm species) (Moore et al. 2004). The daily water use for the stand was determined by summing the daily water use for all individual trees in each stand and then converted to water use per hectare.

Data Analysis

Analyses were performed using SAS (9.4; SAS Inc., Carey, NC, USA). I tested the following comparisons, 1) post oak growing at the oak only stand (OAK) vs post oak growing in the mixed stand (MIX) to determine the effects of intra- vs interspecific competition on post oak S_d, 2) redcedar growing at the redcedar single stand (ERC) vs redcedar growing in the mixed stand to determine the effects of intra- vs interspecific competition on redcedar S_d, 3) post oak vs redcedar at the MIX stand to determine how the two species compete when growing together.

Comparisons involving post oak (1 and 3) were only for spring, summer and fall seasons, while the comparison among redcedar included winter data. Seasons were defined as spring from April to June, summer from July to September, fall from October to December, and winter from January to March. As our data collection started in May 2017, the spring of 2017 included only May and June. The growing season was defined from spring to fall. I tested for differences in S_d and WU using a PROC MIXED with general linear model and repeated measurements with autoregressive covariance structure. Seasons, species, and stand were considered fixed effects and individual trees were considered a random effect. The θ measurements were analyzed using PROC MIXED with a similar model, testing for differences in seasons and depths as well as their interaction. The PDIFF option was used in both analyses to compare pairs of LS-means of different treatment groups.

Simple linear regressions between sapwood area and DBH, S_d and DBH, water use and sapwood area, and water use and DBH for post oaks and redcedars were conducted. Analysis of covariance (ANCOVA) was performed for each set of the relationship to identify whether the linear regression differed between the two species.

Multiple regression between S_d and environmental variables were performed, and stepwise regression was used to select the best model for each species. Selection of environmental variables was initially based on Flick's law where sap flow density by trees is a diffusion gradient between canopy and atmosphere. In our multiple regression, I used average daily VPD, total daily Rs, average daily temperature (T), daily ETo, and average daily θ to explain the diffusion gradient that drives conductance of water from canopy to the atmosphere (Lloyd et al. 1995). All tests were conducted using $p < 0.05$.

For clarity, the post oaks at the OAK stand were abbreviated as "Oak" and the post oaks at the MIX stand was abbreviated as "Moak". Redcedar trees at the ERC stand were abbreviated as "erc" and the redcedar trees at the MIX stand was abbreviated as "Merc".

Results

Environmental Conditions

The total precipitation for the 20 months from May 2017 to December 2018 was 1541 mm, with 919 mm from January to December 2018 (Figure 3.1a). There were 147 days with rain events, of them 77 days with precipitation less than 5 mm and 14 days greater than 25 mm, with the largest daily precipitation of 125 mm on April 29. The longest period with no precipitation was 36 days between January 11 and February 15, 2018. From July 4 to September 25, 2017, the study area experienced an abnormally dry period (United States Drought Monitor, 2019). Generally, θ peaked in the spring, gradually decreased and usually reached a minimum in the fall with inter-seasonal fluctuation which was usually greater for shallower soil depths (Figure 3.1b). Except for the spring and the summer of 2018, the seasonal mean θ at 5 cm was significantly lower than θ at 20 cm ($p < 0.05$) which was then lower than θ at 45 cm ($p < 0.05$) except for the fall of 2018. In contrast, seasonal mean θ at 45 cm was significantly higher than θ at 80 cm ($p < 0.05$), except for the spring of 2017.

The daily solar radiation (R_s), average air temperature (T), average vapor pressure deficit (VPD), and potential evapotranspiration (ETo) varied seasonally (Figure 3.1c,d,e,f). Mean daily solar radiation (±SD) was 21.2 ±6.8, and 19.6 ±7.7 MJ m^{-2} during the growing season of 2017 and 2018, respectively, and 10.3 ±5.3MJ m^{-2} during winter of 2017 (Figure 3.1c). Mean daily T (±SD) was 22.5 ±5.1 and 23.1 ±5.0 °C for the growing seasons of 2017 and 2018, respectively, and 6.2 ±6.4°C during the winter of 2017 (Figure 3.1d). The mean daily ETo (±SD) and mean daily VPD (±SD) was 5.0 ±2.2 mm day^{-1} and 0.9 ±0.4 kPa during the growing seasons of 2017 and 2018, respectively, and 2.3 ±1.6 mm day^{-1} and 0.4 ±0.3 kPa for the winter (Figure 3.1e, f).

Sap Flow Densities

The sap flow of most post oaks started around May 15 and ended about November 3 in 2017, then started about April 30, and ended about November 8 in 2018. There was measurable sap flow from redcedar year round, but the sap flow density was relatively low from December 16, 2017 to March 10, 2018 and from December 3 to Dec 31st 2018 when this study was concluded. The missing data accounted for 0.3%, 3.3% and 2.1% of the total data for the OAK, MIX and ERC stand, respectively. No gap filling was attempted since the missing data occurred mostly during winter 2018 when sap flow densities were very low or negligible.

The highest seasonal mean values of S_d occurred during the spring independent of the species or stand (Figure 3.2). Comparison of S_d among the post oaks growing in different stands (Oak vs Moak) differed between season ($p < 0.0001$) and stand type ($p < 0.0001$), with significant date and stand interaction ($p = 0.0006$). The S_d of Moak was significantly higher than that of Oak in the spring and the summer of 2017 and 2018 ($p < 0.05$) (Figure 3.2). Comparing S_d of redcedar growing in different stands was affected by season ($p < 0.0001$) and by stand ($p = 0.003$), with S_d of redcedar was higher in the MIX stand (Merc) than in the ERC stand (Erc). However eastern redcedar had no significant season and stand interaction ($p = 0.71$). S_d in the MIX stand was affected by date ($p < 0.0001$) and species ($p < 0.0001$) with significant date and species interaction ($p < 0.0001$). Overall, in the mixed stand, S_d of redcedar was 40.3% higher than that of post oak. S_d of Merc was significantly higher than Moak ($p < 0.05$) except for the summer of 2018 (Figure 3.2).

During the growing season, sap flow of post oak and redcedar started approximately at 7:00 and the sap flow density increased throughout the first part of the day reaching a peak at approximately 14:00 for both species (Figure 3.3a). However, the sap flow density of redcedar raised quickly during the morning and was generally higher than post oak after 10:00. During a moderate drought of 2018, the diurnal pattern of post oak was not greatly affected, and the S_d dropped by 17% compared to the growing season average, but the diurnal pattern of S_d of redcedar skewed towards the afternoon and peaked at 16:00, and decreased by 51% compared with its growing season average (Figure 3.3b). However, during the abnormal drought of 2017, the reduction in S_d was similar with 58% for post oak and 63% for redcedar compared with the mean value in the growing season (Figure 3.3c). The S_d of post oak peaked earlier at 12:00 and gradually declined since.

The relationship between averaged S_d and VPD of both post oak and redcedar was characterized by a bell shape and the S_d peaked around 1.0 – 1.2 kPa and substantially decreased (< 0.25 L cm^{-2}_{SA} day^{-1}) when VPD was below 0.2 kPa or over 2.4 kPa (Figure 3.4).

Water Use and its Relationship with DBH, Sapwood Area, S_d

The mean sapwood area (±SD) was 102.4 ±56.0, 129.6 ±108.1, 78.4 ±35.9, and 78.0 ±43.4 cm^2 for the Oak, Moak, Merc, and Erc, respectively (Table 3.1). The mean daily average (±SD) water use per tree was 13.3 ±18.1 and 8.0 ±7.5 L day^{-1} with a maximum of 27.9 ±33.0 and 28.0 ±25.9 L day^{-1} for post oaks and redcedar, respectively (Table 3.2). On per tree basis, the water use of post oaks in the MIX stand had its highest seasonal average (19.5 ±24.3 L per tree day^{-1}) for the summer of 2017 while the highest seasonal average for post oaks in the OAK stand was 8.4 ±13.3 (L per tree day^{-1}) for the spring of 2018 (Figure 3.5a). The highest seasonal water use of redcedar was 18.5 ±11.19 and 23.5 ±22.2 (L per tree day^{-1}) for Erc and Merc, respectively, in the spring of 2017 when soil moisture at multiple depths was generally high (Figure 3.1b and Figure 3.5c). For the growing season, the average daily water use was 6.92 L day^{-1} for redcedar and 10.85 L day^{-1} for post oaks across all trees.

Seasonal average WU of post oak differed significantly by season ($p < 0.0001$), by stand ($p < 0.0001$), with significant season and stand interaction ($p = 0.002$). The WU of post oaks at the mixed stand (Moak) was 32%, 64%, and 49% higher than that in the single stand (Oak) during spring and summer 2017 and spring 2018, respectively (Figure 3.5a). Seasonal average WU of redcedar differed significantly by season ($p < 0.0001$), by stand ($p < 0.0001$), but without season and stand interaction ($p = 0.31$). Overall, redcedar in MIX exhibited 47% higher WU than redcedar in ERC for the entire study period (Figure 3.5c). When WU of post oak and redcedar in MIX was compared, seasonal WU was affected by season ($p < 0.0001$), by species ($p = 0.02$), with significant season and species interaction ($p = 0.006$). Seasonal average water use of Moak was 37% and 53% higher than that of Merc ($p < 0.05$) for the summer of 2017 and the summer of 2018, respectively (Figure 3.5b).

Sapwood area (SA) increased with DBH for both species, with different slopes ($p = 0.009$), but similar intercept ($p = 0.26$) (Figure 3.6a). The relationship between S_d and DBH differed by species (Figure 3.6b). The S_d of post oaks increased with DBH, while S_d of redcedar had no significant slope with DBH (Figure 3.6b). Daily water use of post oak and redcedar increased linearly with SA but the slopes and the intercept of the regression lines for oak and redcedar did not differ significantly ($p > 0.05$) (Figure 3.6c). The daily water use of post oak increased linearly with DBH, but there was no significant relationship between water use of redcedar and DBH (Figure 3.6d).

Stand-level Water Use

Stand-level water use was calculated for the calendar year of 2018 using the relationships from Figure 3.6. The cumulative water use was the highest for ERC stand until June when it was overtaken by the MIX stand and the OAK stand (Figure 3.7). In 2018, the total stand-level water use was 635 mm, 557 mm, and 498 mm for MIX, OAK and ERC stand, respectively.

Sap Flow Density Response to Environmental Variables

The S_d of post oak and redcedar had positive correlations with average daily VPD, total daily R_s, average daily temperature (T), daily ETo, and average daily θ ($p < 0.05$) (Figure 3.8). Using the stepwise regression, the variability of S_d in post oak was explained by R_s (11.3%), T (11.0%), ETo (9.0%) with limited impact from θ. In comparison, the variability of S_d in redcedar was described by R_s (16.5%), ETo (14.0%), T (8.2%), θ_{80cm} (8.1%), and θ_{20cm} (1.1%). Post oaks S_d could be expressed as $S_d = - 0.02 + 0.003\ T + 0.003\ R_s - 0.34\ VPD$ (R2 = 0.16, $p < 0.0001$). Redcedar S_d could be expressed as $S_d = -0.14 + 0.004\ T + 0.004\ R_s - 0.22\ VPD + 0.79\ \theta_{80cm}$ (R2 = 0.23, $p < 0.0001$).

Discussion

Sap Flow Density

The mean S_d of redcedar was usually higher than post oaks for any given season except for summer in 2018. The rainfall from November 2017 to May 2018 was 40% lower than the long term average for this period, which was insufficient to replenish the soil profile to the level observed in May 2017. A low soil water content during the summer of 2018 (Figure 3.1b) likely affected the S_d of redcedar more than the post oaks due to its higher sensitivity to soil moisture (Figure 3.8d,e). In our study, the post oaks exhibited 40.3% lower S_d than that of redcedar in the mixed stand with a density of 914 tree/ha. In comparison, a study in Texas reported mature post oak to have 31% lower S_d than mature loblolly pine (*Pinus taeda*) when growing in a density of 764 tree/ha density (Cooper et al. 2018). This difference in S_d between species may be related to redcedar having lower leaf water potential than post oaks when growing together (Torquato et al. 2019), consequently pulling water faster.

The S_d and its diurnal pattern change under water stress (Fernández et al. 2001; Nadezhdina et al. 2007). In our study, under moderate drought in 2018, the S_d of redcedar was greatly reduced, however, under abnormal drying condition in 2017, S_d of post oak was reduced by more than half. The differences of S_d behavior to drought might reflect the species-specific limitation of stomatal conductance and gas exchange in response to decrease in θ (Fisher et al. 2006). In addition, because the S_d of redcedar was more affected by θ than the post oaks (Figure 3.8d,e), species might be taking up water at different soil depth, where redcedar relies more in shallower soils and post oaks more in deeper soils. In an Aleppo pine (*P. halepensis*) and holm oak (*Q. ilex*) mixed forest, isotope composition in the water uptake revealed that oaks and pines rely heavily on shallow soil water in single species stand. However, when in mixed stands, oak shift water extraction to deeper soil layers as shallow soil moisture is mostly extracted by the pines (del Castillo et al. 2016). Our study period did not encounter extremely drying soil condition. Therefore, future study to encompass a protracted, severe drought episode will help better define in situ hydraulic behavior of post oak and redcedar.

Water Use

On an annual basis, the stand-level water use by the mixed stand was the highest (Figure 3.8). This high stand-level water use was mainly attributed to the higher sapwood area in comparison to redcedar species, and to the high water use of post oaks species. Deciduous *Quercus spp.* are reported to have low water use efficiency compared to juniper (Bendevis et al. 2010). Also, Torquato et al. (2019) found that post oak has up to seven times greater stomatal conductance than redcedar for the same leaf area. As a result, oaks usually have higher transpiration than juniper of the same size growing in the same conditions (Bendevis et al. 2010). Although post oak was reported to have lower S_d than pines in a region with 820 mm of rainfall in Texas, the water use of post oaks averaged at 0.44 mm day^{-1} during a growing season (Cooper et al. 2018), which is similar to 0.43 mm day^{-1} for the growing season from our study.

Species growing in the mixed stand had higher water use than when growing in single-species stands, perhaps indicating less intense competition for water in mixed-species stands. Stratification in soil water extraction under interspecific competition was reported in both temperate and subtropical forest (Grossiord et al. 2014; del Castillo et al. 2016). When coexisting with conifers, beech was able to extract water from progressively deeper soil layers in temperate mixed species plantation (Grossiord et al. 2014). Even though redcedar exhibits plasticity in sourcing soil water among different seasons, it mostly uses water from the upper 0.5 m when soil moisture is high during the spring (Eggemeyer et al. 2009). Post oak has deeper rooting systems that help to sustain water extraction from deep soil layer when shallow soil is abnormally dry (Abrams 1990; Abrams 1996). The water use of post oak and blackjack oak was not affected by the change of soil moisture in the upper 150 cm, and it did not respond to VPD in a study conducted in Texas (Cooper et al. 2018). These results suggest that the two oak species in the Cross Timbers have the capacity to reach deep soil water to sustain water use which is critical for a generally drier and highly variable climate. The insensitivity of S_d of post oaks to the soil water content in the upper 80 cm in this study also suggests that post oak may be capable of extracting water from soil layers much deeper than 80 cm to sustain transpiration at our site. Post oaks and redcedar when they co-exist would be able to explore soil moisture from a greater soil profile and maximize the overall water extraction from the entire soil profile. Consequently, the stand-level water use of the mixed stand can be higher than either oak or redcedar stand on an annual scale.

Empirical Model

R_s, T, VPD, ETo, and θ are among the main environmental variables to control tree transpiration (Lloyd et al. 1995; Caterina et al. 2014; Elliott et al. 2015; Mayoral et al. 2015; Tanaka 2015). Among these factors, VPD is the primary driver of water transport through the soil-plant-atmospheric-continuum (SPAC) (Monteith 1981), influencing the rate of water flow in plants (Will et al. 2013). Redcedar water use declines at high VPD because of the decrease of leaf conductance (Caterina et al. 2014). Post oaks also present similar behavior, with decreasing leaf conductance when VPD is higher than 2.5 kPa (Hull and Wood 1984; Will et al. 2013). However, when post oaks are not under water stress, VPD does not influence water use (Cooper et al. 2018). In our study, I found that the relationship between S_d and VPD is substantially lower when VPD was below 0.2 kPa or over 2.4 kPa (Figure 3.4).

It is surprising that I did not find stronger correlations between water use and environmental variables. In this study, the soil moisture arrays were randomly distributed to capture the overall soil moisture conditions for the site, not specifically for each type of stand. As a result, a weak correlation between S_d and soil moisture was anticipated. However, the significant correlation between S_d and soil moisture for redcedar but not for oak suggests a general stratification in water extraction of these two species. Given the poor correlation I found, the S_d of post oaks and redcedar also may be influenced by some other variable I did not cover in this study.

Our study showed that replacement of post oak by redcedar of a similar basal area would result in an increase in total transpiration on an annual scale. Naturally, the encroachment and infilling of redcedar into the oak savanna or woodland entail a net increase in basal area and LAI in most cases. The increase of total LAI through the inclusion of a midstory canopy and the expansion of leaf out period through the addition of an evergreen component in the canopy will increase water loss to canopy interception (Zou et al. 2015) which decreases the net precipitation to replenish the soil. Also, the stratification in water extraction of the soil profile by post oak and redcedar in the mixed forest will increase the total transpiration. From a water budget perspective, the increase in evapotranspiration, therefore, has to be balanced by the reduction of either runoff or deep drainage or likely both. Hydrologically, a general dry soil profile lowers the potential to produce both surface runoff, subsurface lateral flow, and groundwater recharge leading to the reduction of total streamflow in general.

Conclusion

Fire exclusion and suppression have resulted in a rapid increase of redcedar into the oak savanna and forest of the Cross Timbers in the south-central Great Plains. Change in the species composition and canopy structure after redcedar establishment into the midstory affects specific water use and increases the stand-level water use on an annual scale. The overall increase in canopy water use primarily results from the stratification in soil water uptake depth under interspecific interaction and the improvement of water use of post oak in the mixed stand than in post oak only stand with the same total basal area.

From a water balance perspective, the increase in the annual transpiration due to redcedar encroachment into the oak savanna will be balanced by reduction of either runoff or groundwater recharge assuming other components remain unchanged for a given water year. The Cross Timbers are important water conservation forests for many water supply reservoirs in the south-central Great Plains. Reduction in streamflow accounts for the loss of a major ecosystem service. Information on water use of post oaks and redcedar under intra- or interspecific competition can assist in assessing the stand-level water use and guiding effective silvicultural practices for sustainable management of Cross Timbers for optimizing water resources.

Further study should quantity the ecosystem level evapotranspiration or direct measurement of runoff using paired watershed to further improve our understanding of alteration of the water budget and its potential impact on water resources in the Cross Timbers in the south-central Great Plains.

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Table 3.1. DBH, height and sapwood area of all trees instrumented with TDP probes. DBH is the diameter at breast height (~1.3 m). Sapwood area was calculated individually for each tree based on sapwood width. Sapwood width of each tree was estimated using one core for each oak tree (symmetric sapwood), and different number of cores for each redcedar tree (somewhat asymmetric sapwood) depending on its size and shape.

Tree ID	Stand	Species	DBH (cm)	Height (m)	Sapwood area (cm^2)
1	OAK	Post oak	31	16	215
2	OAK	Post oak	22	14	137
3	OAK	Post oak	12	10	50
4	OAK	Post oak	19	9	123
5	OAK	Post oak	12	9	48
6	OAK	Post oak	21	12	80
7	OAK	Post oak	15	9	64
8	MIX	Post oak	11	7	51
9	MIX	Redcedar	17	9	132
10	MIX	Post oak	25	12	253
11	MIX	Post oak	7	5	19
12	MIX	Redcedar	14	8	68
13	MIX	Redcedar	8	5	21
14	MIX	Redcedar	17	8	92
15	MIX	Post oak	14	5	56
16	MIX	Redcedar	22	8	79
17	MIX	Post oak	33	13	269
18	ERC	Redcedar	18	7	85
19	ERC	Redcedar	33	12	168
20	ERC	Redcedar	10	8	55
21	ERC	Redcedar	9	8	31
22	ERC	Redcedar	19	9	100
23	ERC	Redcedar	15	8	71
24	ERC	Redcedar	8	9	36

Table 3.2. Daily average (± SD), maximum and minimum water use (liter per day) of all trees equipped with the thermal dissipation probes (TDPs) during the study period. The minimum value reported was from the day when there was active transpiration.

Tree ID	Stand	Species	Average (± SD, L day^{-1})	Maximum (L day^{-1})	Minimum (L day^{-1})
1	OAK	Post oak	26.4 (±13.6)	66.6	1.0
2	OAK	Post oak	18.3 (±7.8)	39.5	0.8
3	OAK	Post oak	0.6 (±0.5)	2.2	0.1
4	OAK	Post oak	7.4 (±3.0)	16.2	0.3
5	OAK	Post oak	1.0 (±0.7)	3.8	0.1
6	OAK	Post oak	4.6 (±1.4)	6.7	0.2
7	OAK	Post oak	1.4 (±0.7)	2.8	0.1
8	MIX	Post oak	2.3 (±0.8)	5.3	0.1
9	MIX	Redcedar	29.8 (±20.3)	96.1	1.8
10	MIX	Post oak	37.4 (±13.8)	73.1	3.8
11	MIX	Post oak	1.8 (±0.6)	2.8	0.1
12	MIX	Redcedar	5.3 (±4.2)	20.4	0.2
13	MIX	Redcedar	4.4 (±2.9)	14.1	0.1
14	MIX	Redcedar	5.9 (±5.6)	27.5	0.2
15	MIX	Post oak	2.1 (±0.6)	4.4	0.2
16	MIX	Redcedar	2.2 (±1.4)	7.2	0.2
17	MIX	Post oak	56.5 (±19.1)	99.3	1.8
18	ERC	Redcedar	4.2 (±3.6)	17.9	0.3
19	ERC	Redcedar	14 (±11.0)	49.1	1.5
20	ERC	Redcedar	4.4 (±2.8)	11.9	0.4
21	ERC	Redcedar	6.9 (±4.9)	29.9	0.6
22	ERC	Redcedar	9.0 (±8.5)	38.4	1.0
23	ERC	Redcedar	3.6 (±2.8)	13.9	0.2
24	ERC	Redcedar	6.1 (±4.4)	22.5	0.5

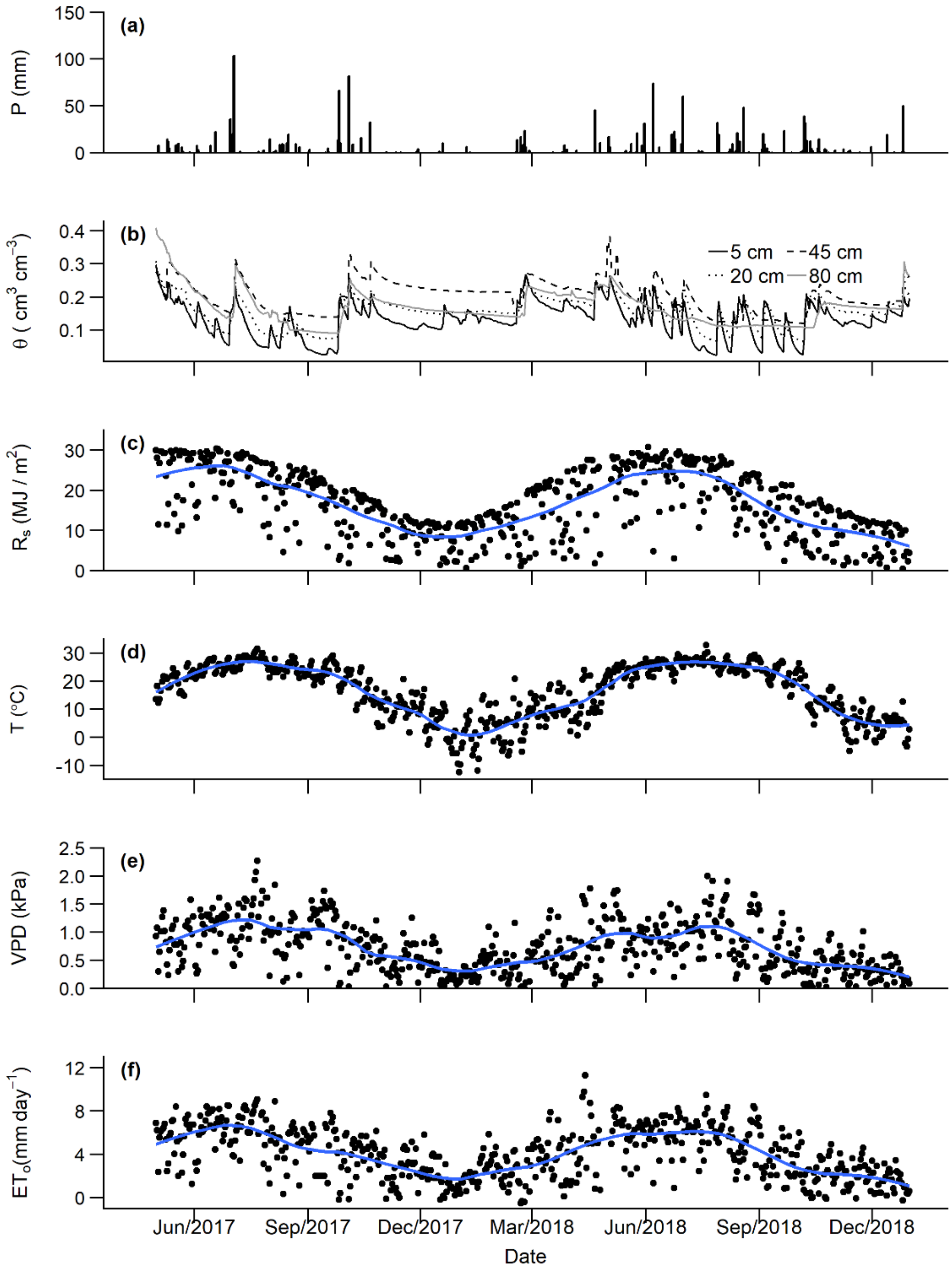

Figure 3.1. Daily precipitation (P) (a), soil water content (θ) from 5, 20, 45, 80 cm (b), solar radiation (R_s) (c), temperature (T) (d), potential evapotranspiration (ETo) (e), and vapor pressure deficit (VPD) (f) from May 2017 to December 2018. The blue line is the locally weighted regression.

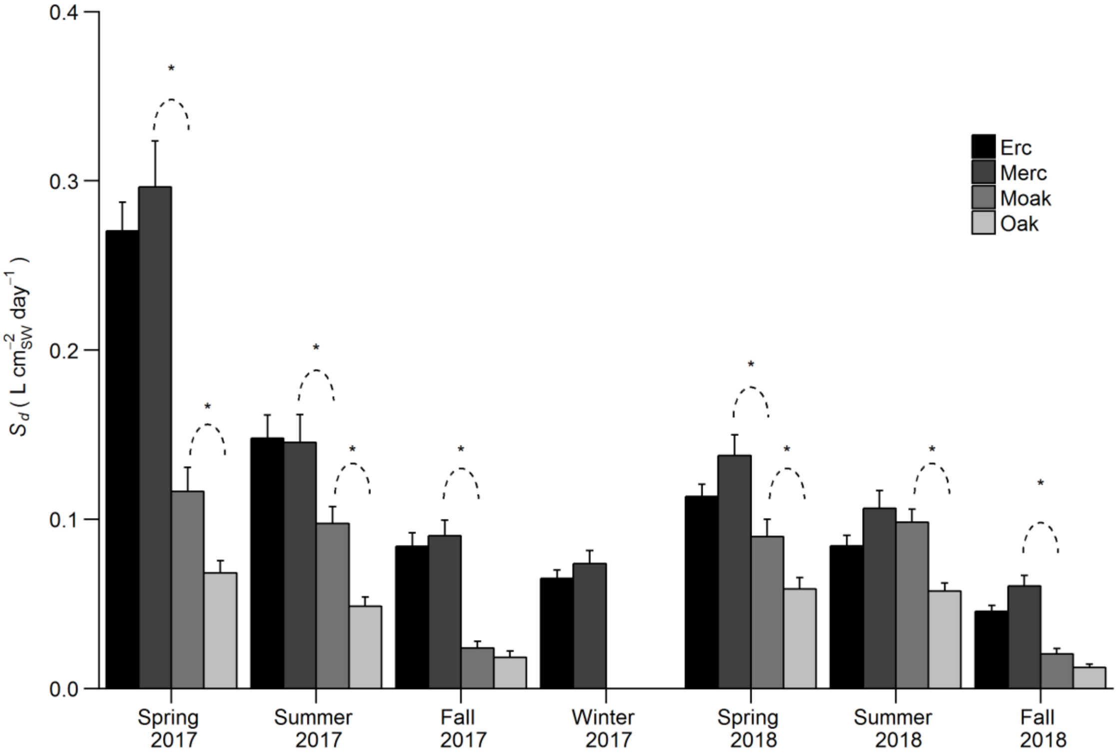

Figure 3.2. Seasonal averages of sap flow density (S_d) for Erc, Merc, Moak, and Oak. The S_d data for the Spring of 2017 cover only from May 15 to May 31st. The fall season for Oak covers from September 1 to November 5 for both years. An asterisk (*) indicates significant differences ($p < 0.05$). Vertical bars denote standard errors.

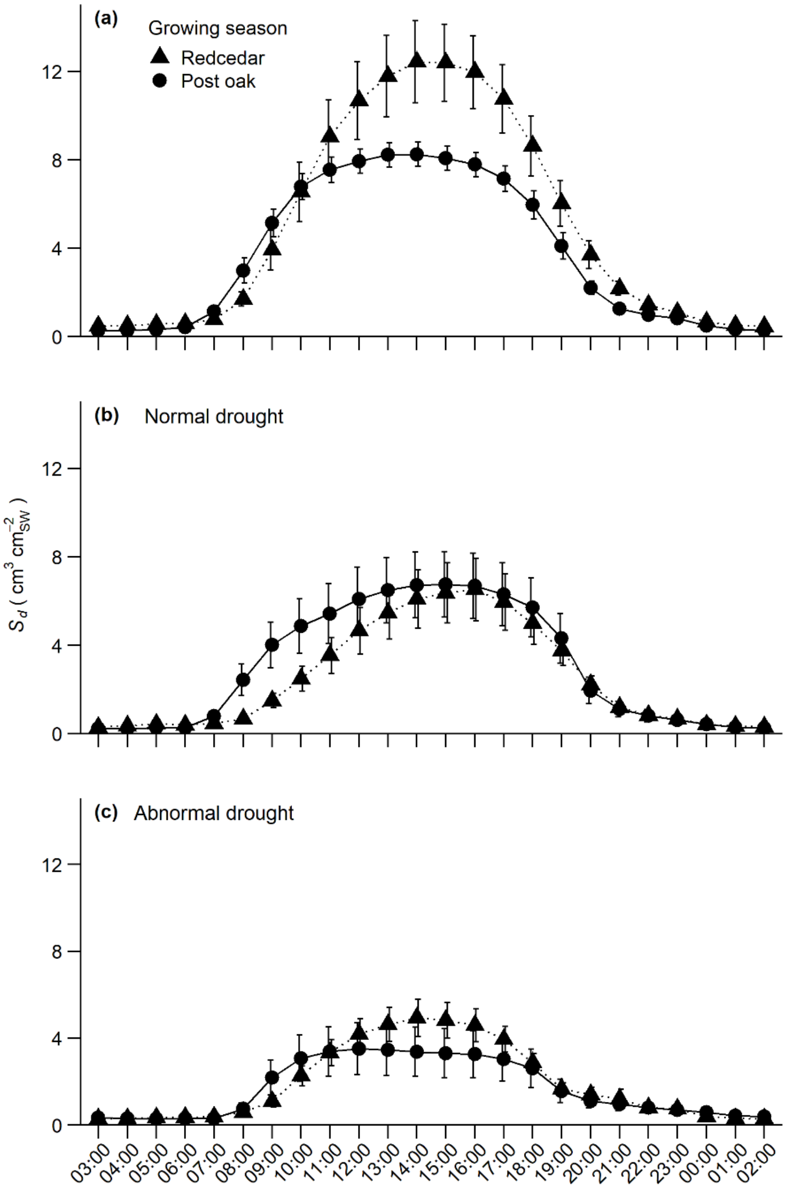

Figure 3.3. The diurnal change of S_d for the post oaks (OAK) and redcedars (ERC). Data were hourly values averaged over the growing season (from May to October) (a), during the normal drought in 2018 (July 14th to 28th) (b), and during the abnormal drought (dry conditions that could turn into drought or are recovering from drought but are not yet back to normal) in 2017 (September 1st to 24th) (c).

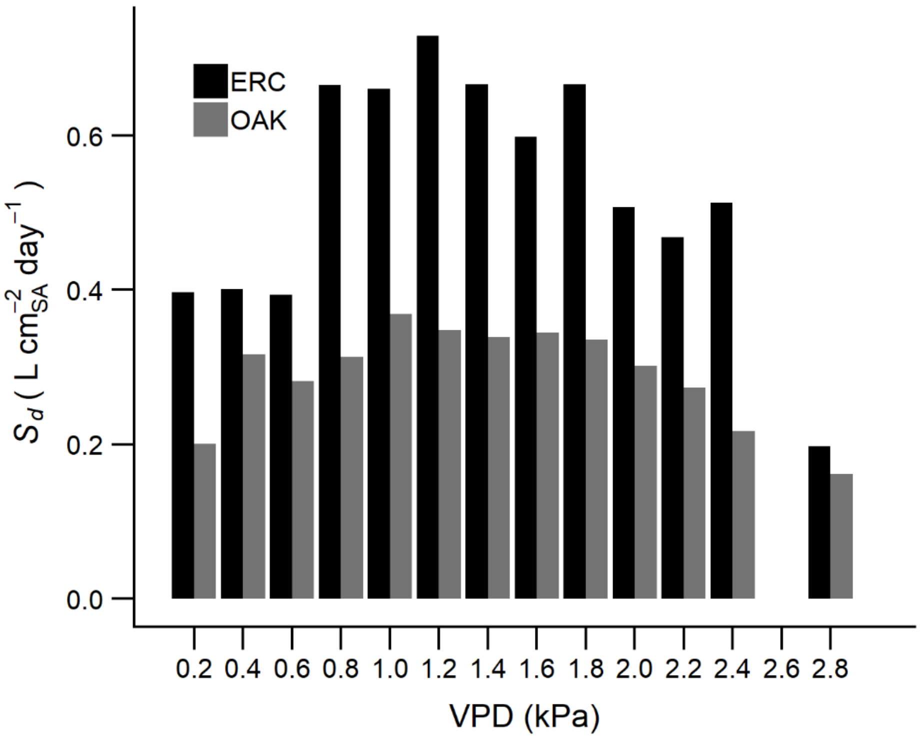

Figure 3.4. Relationship between daily mean sap flow density (S_d) and daily mean VPD (kPa).

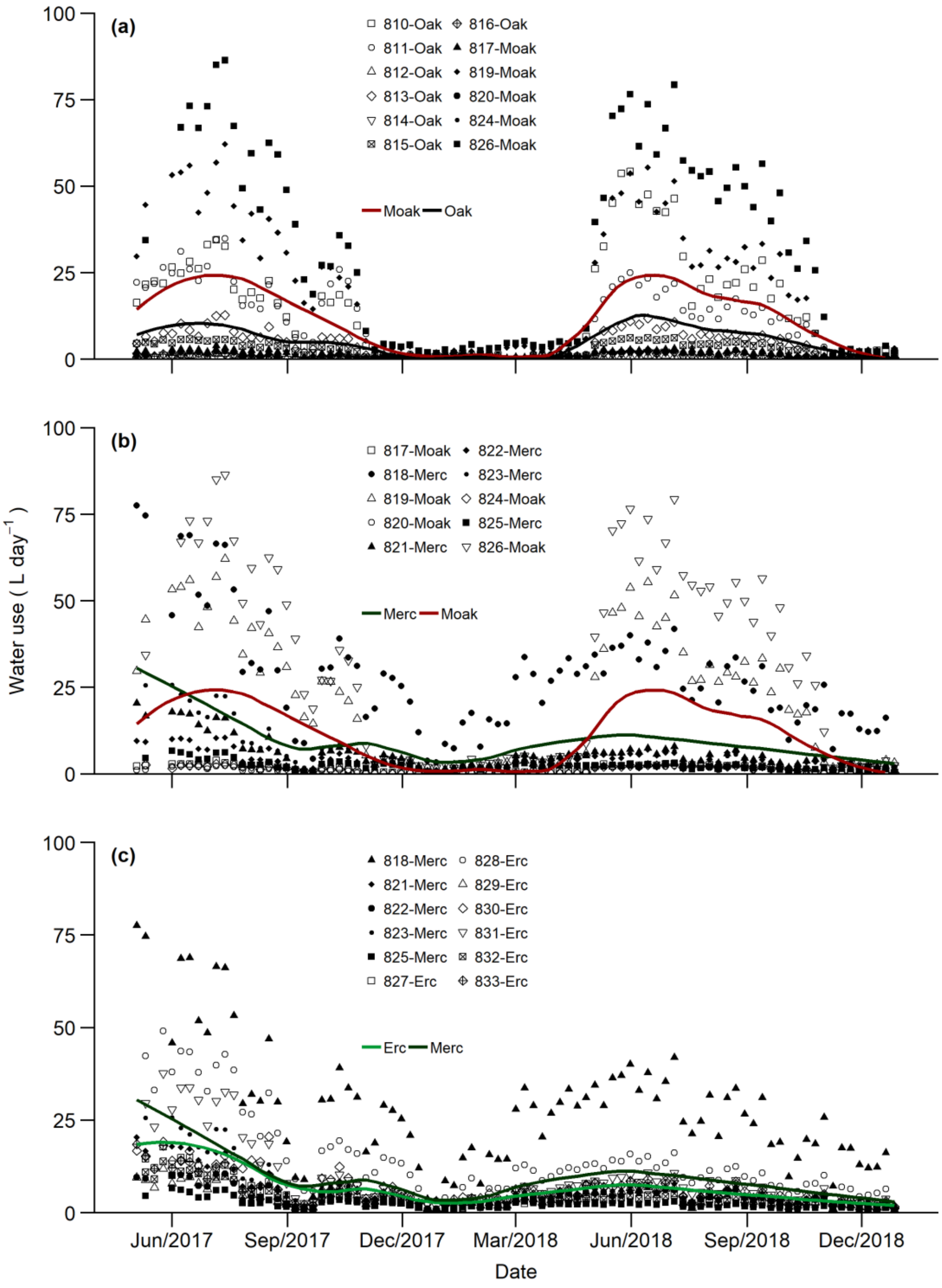

Figure 3.5. Calibrated daily water use for individual post oaks and redcedars from the OAK stand (a), MIX stand (b) and ERC stand (c). Lines are locally weighted regressions for Oak, Moak, Merc, and Erc, respectively.

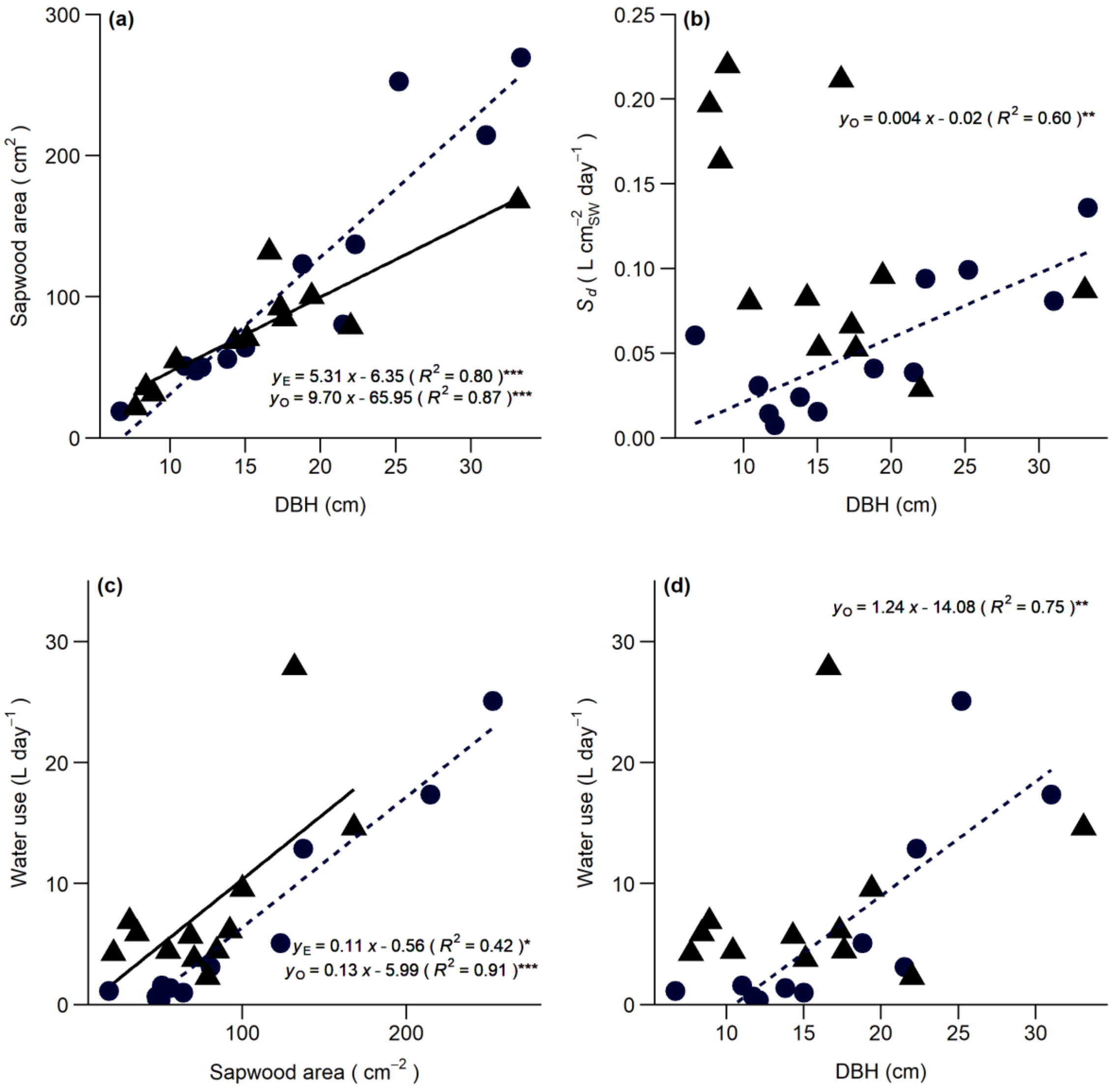

Figure 3.6. The relationships between sapwood area and DBH (a), sap flow density (S_d) and DBH (b), water use and sapwood area (c), and water use and DBH (d) for post oaks (circles) and redcedar (triangles). The linear regression equations (post oak dashed, redcedar solid) are shown when there are statistically significant correlations. Asterisks denote level of significance with * at $p < 0.05$, ** at $p < 0.001$, and *** at $p < 0.0001$.

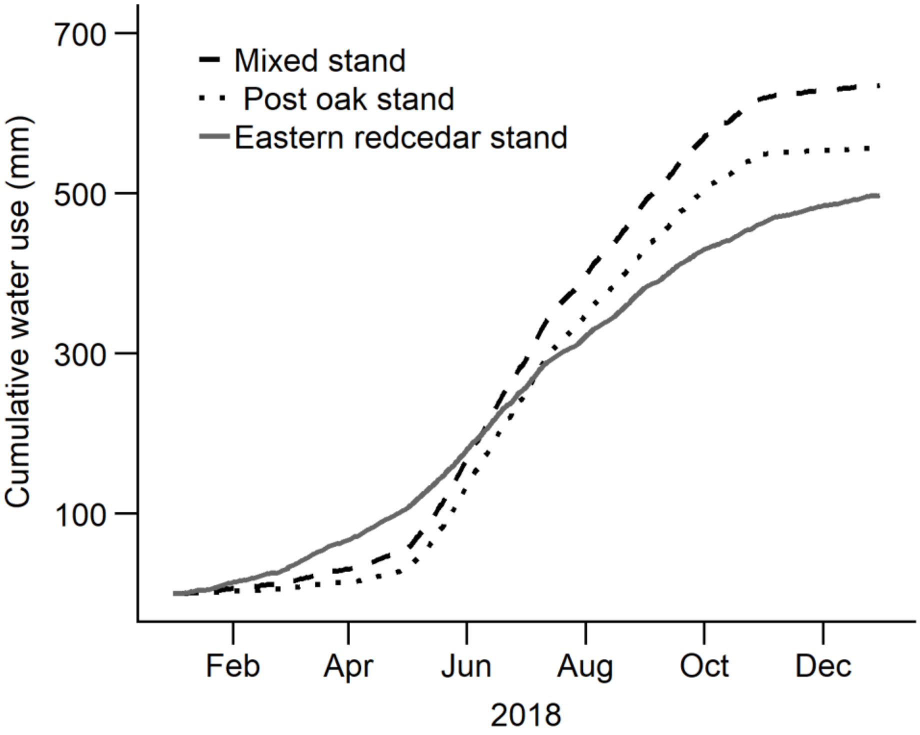

Figure 3.7. Cumulative daily water use of redcedar single stand (498 mm, ERC), post oak single stand (557 mm, OAK), and redcedar and post oak mixed stand (635 mm, MIX).

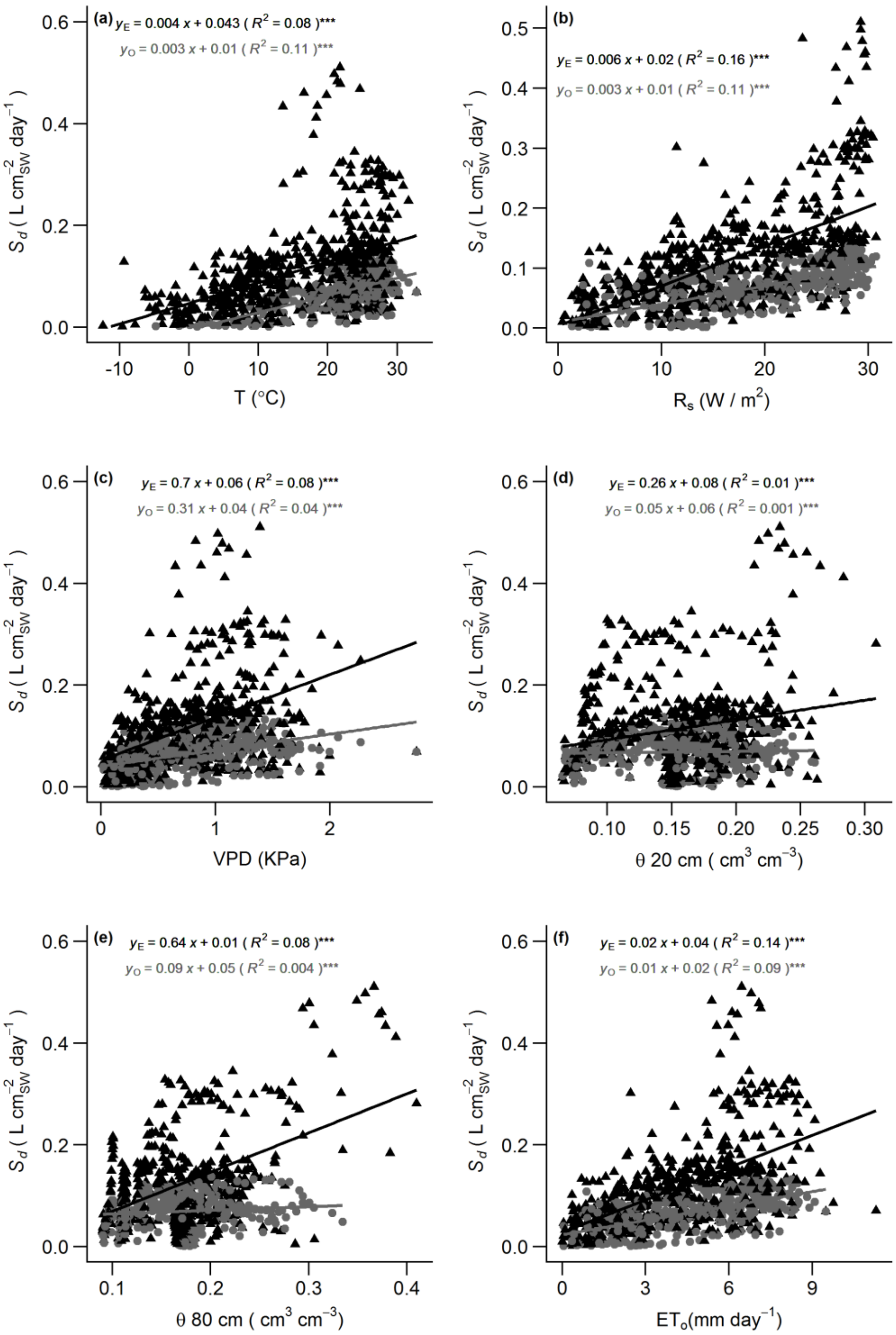

Figure 3.8. Relationships between sap flow density and environmental factors. Asterisks denote level of significance with * at $p < 0.05$, ** at $p < 0.001$, and *** at $p < 0.0001$.

CHAPTER IV

General Conclusions

A two-year field study was conducted to determine if the physiological traits of redcedar provide it a competitive advantage over post oak, which assists its successful encroachment and establishment into the midstory under the oak canopy. Also, whether converting a post oak dominated savanna and forest to redcedar and post oak mixed forest will result in a substantial change of ecosystem-level transpiration in the Cross Timbers.

Our results showed that both redcedar and post oak are equally effective and responsive to moderate water stress through water regulation with similar depression in midday water potentials. The physiological adaptation and competition avoidance rather than the extreme drought tolerance may be the physiological mechanism underlying the establishment of evergreen redcedar into the oak savanna. This information can assist the projection of species composition of the Cross Timbers under predicted higher temperatures and more frequent droughts for this region. The future successional trajectory in species composition is essential for carbon and water dynamics predictions for the Cross Timber ecoregion.

Redcedar establishment into the midstory affects water use and increases the stand-level water use on an annual scale. With the same total basal area, post oak and redcedar under interspecific interaction had higher water use than under intraspecific interaction. The increase in annual transpiration due to redcedar infilling under oaks may lead to the total increase in evapotranspiration at the expense of runoff or groundwater recharge. Large scale conversion of the post oak dominated savanna and forest to the mixed forest may reduce streamflow to water supply reservoirs. This information can assist in silvicultural practices for Cross Timbers management for sustainable water resources.

Further study should explore the potential niche separation between post oak and eastern redcedar in light compensation or soil water extraction. Also, direct quantification of the ecosystem level evapotranspiration or runoff using paired watershed approach will further improve our understanding of alteration of the water budget and its potential impact on water resources in the Cross Timbers in the south-central Great Plains.

VITA

Patricia Rettondini Torquato

Candidate for the Degree of

Master of Science

Thesis: WATER RELATION AND PHOTOSYNTHETIC PERFORMANCE OF EASTERN REDCEDAR (*JUNIPERUS VIRGINIANA*) AND POST OAK (*QUERCUS STELLATA*) IN THE CROSS TIMBERS

Major Field: Natural Resource Ecology and Management

Biographical:

Education:

Completed the requirements for the Master of Science in Natural Resource Ecology and Management (NREM), Oklahoma State University, Stillwater, Oklahoma in May 2019.

Received Bachelor in Forest Engineering, Luiz de Queiroz College of Agriculture, University of Sao Paulo, Piracicaba, Brazil, in January 2015.

Experience:

Graduate Research Assistant – NREM, Oklahoma State University. Fall 2016 – Spring 2019.

Graduate Intern - NREM, Oklahoma State University. Spring 2016.

Graduate Intern – Ecosystem and Forest Sciences, University of Melbourne. 2015.

Undergraduate Intern – Forest Resources Department, University of Sao Paulo. 2012-2015.

Professional Memberships:

Xi Sigma Pi Forestry Honor Society