ABSTRACT

The Growth Patterns of Woody Vegetation in Central Texas Woodlands
in Response to Industrial Atmospheric Carbon Dioxide

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Anthropogenic greenhouse gas emissions contribute to climate change. Climate change influences plants within ecosystems; however, plant growth may mitigate climate change consequences. In southern and central Texas, recent woody plant abundance increased within ecosystems historically dominated by herbaceous species. This study investigates carbon budgets of aggrading woodlands in context of climate change and industrial carbon dioxide levels. Carbon storage was estimated for tree foliage, stem, litter, fine and coarse roots. Vine and shrub carbon were estimated. Photosynthesis and litter decomposition measurements estimated carbon flux into and out of woodland ecosystems, respectively. Soil moisture was measured to evaluate water availability as a controlling mechanism of carbon storage between upland and riparian woodlands. A process model, Biome-BGC, assessed potential consequences of carbon dioxide and climate on carbon sequestration. Modeling showed carbon dioxide concentrations and climate influenced carbon sequestered in vegetation; these factors were not consistent across ecosystems and plant components.

The Carbon Budgets of Central Texas Woodlands in the Context of Climate Change and Industrial Atmospheric Carbon Dioxide Concentrations

by

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CHAPTER ONE

Introduction

1.1 History of Climate Change Research

The biological consequences of climate change are thoroughly discussed in scientific literature (Parmesan 2006). Shifts in geographic range for both plant and animal species in connection with climate change were observed as early as the 1700s. Since the 1800s, increasing atmospheric carbon dioxide concentrations were correlated with warming temperatures (Ramanathan and Feng 2009). In the 1890s, scientific observations revealed the influences of extreme weather on wildlife species (Parmesan 2006). In the early 1900s, scientists observed the influence of climate thresholds of species on the boundaries of species geographic ranges. The climate change consequences on population evolution were increasingly studied in the 1940s. Before the 1970s, climate change was considered to be a warming issue solely caused by increasing atmospheric carbon dioxide concentrations (Ramanathan and Feng 2009). In the 1980s, scientists addressed the climate change consequences on the size of the wildlife populations (Ehrlich et al. 1980). Climate factors, including precipitation, affect populations, which may decrease in numbers under climatic stress.

1.2 Causes of Climate Change

The increase in Earth's temperature over the past hundred years is unprecedented in comparison with the past thousand years (Crowley 2000). Temperatures on the surface of Earth increase by roughly 0.6 °C during the past century (Levitus et al. 2001). The

occurrence of some natural processes alter Earth's climate (Crowley 2000). Natural processes that alter climate include volcanic eruptions and solar variations. In addition, Earth's climate is affected by the release of carbon dioxide and methane from vegetation and soil (Heimann and Reichstein 2008). The natural consequences on Earth's climate contribute to the increasing temperatures (Crowley 2000). However, the natural climate variability has a small role in the climate change of the 20th century. Climate observations and computer models indicate anthropogenic factors are responsible for climate change. The increase in the global average temperature is likely due to the increase in anthropogenic greenhouse gases and the warming of the atmosphere is not due to natural causes alone (IPCC, 2007).

Anthropogenic emissions of carbon dioxide and other greenhouse gases contribute to climate change (Cox 2000). The annual carbon dioxide emissions increased between 1970 and 2004 by roughly 80% (IPCC, 2007). Human activities result in the emissions of carbon dioxide, methane, and nitrous oxide. The increase in greenhouse gases and aerosols of Earth's atmosphere indicate the rising Earth's surface temperatures are anthropogenic in origin (Levitus et al. 2001). Modern industry fossil fuel emissions increase atmospheric carbon dioxide concentrations. Carbon dioxide emissions through fossil fuel combustion increased during the twentieth century (Lal 2004). Land use changes, including deforestation and agricultural land-use conversion, also release greenhouse gases.

Atmospheric carbon dioxide concentrations fluctuate over short time scales (Zachos et al. 2008). The concentrations of carbon dioxide and other greenhouse gases increased since the industrial revolution in 1750. Carbon dioxide concentrations increased from 280

ppm in 1750 to 367 ppm in 1999. Half of the 3.67 billion tonnes of anthropogenic carbon dioxide emissions occurred since the industrial revolution (Allen et al. 2009). Carbon dioxide concentrations continue to increase at the current rate of 1.5 ppm/year (Lal 2004). Mitigation strategies for greenhouse gas emissions are based on projections of future emissions and temperatures (Allen et al. 2009). By 2400, industrialization is predicted to release 5,000 gigatonnes of carbon dioxide to the atmosphere (Zachos et al. 2008).

Shortwave radiation is intercepted by the Earth's atmosphere, which retains heat and influences temperatures (Arrhenius and Holden 1897). The radiation budget of the atmosphere includes solar shortwave radiation absorption by the Earth's atmosphere (Hartmann et al. 2013). Solar shortwave radiation absorption is based on the difference between the incoming shortwave radiation and outgoing long-wave radiation.

Radiative forcing is the net change in the energy balance of the Earth system and the change in net flux of radiant energy per unit area in the tropopause (Myhre et al. 2013). Climate change occurs as the system counteracts the flux changes (Hartmann et al. 2013). Fossil fuel emissions and biomass burning increase the ozone concentrations (Sitch 2007). The increase in ozone leads to direct radiative forcing (W/m^2) of climate change. High ozone concentration in Earth's atmosphere damages plants, limits plant primary productivity, increases stomata closure, and reduces photosynthetic rates. Increased anthropogenic CO_2 emissions accumulate in the atmosphere and cause indirect radiative forcing (W/m^2), which occurs through feedbacks on the global carbon cycle. The rate of increase of radiative forcing since the industrial revolution has been unprecedented in the past 10,000 years (IPCC, 2007) with the carbon dioxide radiative forcing having increased between 1995 and 2005 by 20%.

Increasing concentrations of carbon dioxide and other gases, including methane, nitrous oxide, and ozone, enhance the greenhouse effect (Hartmann et al. 2013). The greenhouse effect occurs as gases prevent long-wave radiation from being released from the Earth's atmosphere (Ramanathan and Feng 2009). Outgoing long-wave radiation is reduced as the atmospheric greenhouse gas concentration increases, preventing the release of heat from Earth's atmosphere to balance incoming solar radiation. As gas concentrations increase, the greenhouse effect leads to the accumulation of the excess energy within the atmosphere. The increased energy within the atmosphere due to the greenhouse effect influences temperatures on the surface of Earth (Hartmann et al. 2013).

1.3 Carbon Dioxide and Plant Growth

Terrestrial ecosystems assimilate carbon dioxide; however, the absorption of greenhouse gases is sensitive to climate change (Cox 2000). The difference between carbon gain and loss determines the carbon balance of an ecosystem (Heimann and Reichstein 2008). An ecosystem gains carbon though photosynthesis and loses carbon through autotrophic and heterotrophic respiration. In addition, carbon is released through death and decomposition of organic material (Arrhenius and Holden 1897). Vegetation releases carbon into the atmosphere as carbon dioxide (Heimann and Reichstein 2008).

Carbon is sequestered in living biomass after absorption during the process of photosynthesis (Pan et al. 2011). Plant growth occurs due to the uptake of carbon dioxide during photosynthesis and the conversion of carbon to biomass. Plant growth increases as carbon is converted into biomass (Heimann and Reichstein, 2008). Carbon is sequestered in biomass, including leaves, branches, and stems. The diversity and abundance of plant species determine the aboveground biomass. The largest carbon pools in forest

ecosystems are the aboveground biomass and mineral soil organic matter, with smaller carbon pools in belowground biomass and surface detritus (Fahey et al. 2010). The changes in carbon pools dictate the net primary productivity, which is the rate of carbon accumulation into an ecosystem.

The carbon sequestration capacity of an ecosystem depends on the plant species composition and alterations in the species composition (Bunker et al. 2005). The capacity of an ecosystem for carbon sequestration is determined by the aboveground biomass (Bunker et al. 2005). A long-term shift in plant community composition affects the transfer of photosynthetic carbon to belowground biomass and the ecosystem carbon dynamics (Bardgett 2011). Plant and microbial community composition is a control on carbon mineralization rate based on litter quality and decomposition (De Deyn 2008).

1.4 Effects of Climate Change on Vegetation

Climate change alters species geographical distribution and species composition of ecosystems. Climate change allows the invasion of new species into an ecosystem. Invasive species affect the species, community, and ecosystem levels (Vila et al. 2011). Invasive plant species decrease the plant species diversity of the invaded ecosystem. Invasive species influence plant community structure and ecosystem functioning. Invasive species may alter nutrient cycling of the invaded ecosystem. However, invaded ecosystems experience increased plant productivity.

Climate change shifts species geographical ranges, which changes ecosystem plant composition based on temperature and precipitation tolerances of species (Walther et al. 2002). Climate change alters temperatures and precipitation, which shifts species composition of plant communities on both local and regional scales (Bardgett 2011).

Vegetation growth and carbon dioxide fluxes are altered by climate change influences on temperature (Peng et al. 2013). Warming temperatures increase vegetation productivity through extended growing season (Wang et al. 2011). Plant species at mid to high latitudes of North America are sensitive to temperature changes (Wang et al. 2011). Plant species shift towards poles or higher latitudes as temperatures increase (Walther et al. 2002). Climate change modifies seasonal biogeochemical processes, especially those controlled by temperature (Walther et al. 2002). Plant carbon sequestration occurs at increasing rates in parallel with warmer temperatures (Yao et al. 2012).

Climate change directly alters ecosystem dynamics by influencing the amount, intensity, and seasonal patterns of precipitation (Heimann and Reichstein 2008). In over half of the world's ecosystems, primary productivity is limited by the availability of water. High temperatures increase the evaporation and negative water balances in vegetation (Brown 2002). A carbon dioxide rich environment decreases the severity of stomata water loss (Heimann and Reichstein 2008).

Flooding affects the carbon sequestration for plant species growth. The tolerance of flooding varies between plant species (Kreuzwieser et al. 2004). Climate change increases flooding risk and waterlogging of clay-rich soils. The oxygen deprivation associated with flooding controls carbon metabolism of roots. Plants slow root growth and energy consuming processes under flooded conditions and decrease the demand for carbon. Flooding influences stomatal closure signals that potentially occur in the root system. Decreased stomatal conductance may be caused by changes to water conductance between the plant and soil. The influence of flooding on stomata closure alters photosynthetic rate and leaf gas exchange, which reduces carbon dioxide assimilation.

The carbon allocation and flux within an ecosystem depends on the balance between respiration and photosynthesis, which is changes due to climate change (Ryan 1991). Rising temperatures and ozone concentrations increase the photosynthetic rate. Temperatures control plant respiration process throughout the day (Peng et al. 2013). Plants respire half the carbon available from photosynthesis (Yao et al. 2012). The remaining of the absorbed carbon is allotted for growth, propagation, nutrient acquisition, and litter production.

Greenhouse gases are released or absorbed from terrestrial ecosystems (Heimann and Reichstein 2008). Terrestrial ecosystems play a major role in mitigating climate change by absorbing greenhouse gases from the atmosphere. Carbon sequestration moderates the consequences of climate change (Bardgett 2011). Carbon dioxide fertilization of photosynthesis, climate, historical land use, erosion, and sedimentation contribute to the increasing carbon sequestration (Schimel et al. 2000). Vegetation responds to increasing carbon dioxide by growing more vigorously (Bardgett 2011).

Plants both sequester and release carbon; however, an ecosystem is a carbon sink when carbon gains are higher than carbon losses (Bardgett 2011). Forests sequester carbon from the atmosphere and act as a sink for carbon dioxide. Forests shift from sinks to sources of carbon dioxide as plant and soil respiration exceed primary productivity (Brown 2002). Forests sequester roughly forty-five percent of terrestrial carbon (Bonan et al. 2008). The current estimation of the carbon stock in forests is roughly 861 Pg of carbon (Pan et al. 2011). The carbon sequestered in the forests changes between years due to the flux of available carbon dioxide.

Forests grow faster, mature earlier, and die quickly on an ecosystem scale due to the consequences of climate change (Ryan 1991). Forests cover changes due to naturally occurring shifts in the forest ecosystem (Brown 2002). However, anthropogenic factors, including wood harvesting and land-use change, also alter forest cover. Alterations to forest cover release carbon dioxide to the atmosphere. Forest ecosystems also influence climate through exchanges of energy, water, and carbon dioxide (Bonan et al. 2008).

The rise in atmospheric carbon dioxide concentration increases sequestered carbon in the vegetation biomass and increases the fluxes of carbon to the roots (Bardgett 2011). Carbon and other elements, including nitrogen, hydrogen, and oxygen, flow through the root system into the soil and react with microbial life (Pan et al. 2011). The activity of soil microbes causes a net increase in atmospheric carbon dioxide released into the atmosphere from soil (Bardgett 2011). Climate change enhances the decomposition of soil-bound carbon, which shifts soil from sink to source of carbon dioxide.

The climate-ecosystem feedbacks, including between the carbon cycle and climate, amplify or dampen climate change (Heimann and Reichstein 2008). The sequestration of carbon in forest ecosystems is a strategy for mitigation of climate change due to the role of forests in the carbon cycle (Brown 2002). Forest management is a strategy for climate change mitigation that maximizes carbon sequestration (Naudts et al. 2016). Forest management mitigates climate change by controlling the forest structure and the ability to act as a carbon dioxide sink.

Forest management decreases the rate of atmospheric carbon dioxide concentration increase (Fahey et al. 2010). Management determines the net carbon exchange with the atmosphere by altering sequestration in carbon pools. The influence of management on

greenhouse gas emissions depends on forest type. Protected forest ecosystems prevent release of carbon and sequesters carbon into plant biomass. Without management, the maximum carbon sequestration depends on forest characteristics and species composition. Forest management slows climate change and decreases atmospheric carbon dioxide concentration (Yao et al. 2012). Prescribed fire is a management strategy to reduce carbon emissions by utilizes low-intensity burns to remove fuel to avoid intense wildfires. Fire affects carbon sequestration and biogeochemical cycling. Fires shift vegetation composition by increasing fire sensitive species.

Savanna ecosystems are characterized by both woody and herbaceous plant species (Archer 1990). The balance between herbaceous and woody species is determined by alterations to climate, soil, and anthropogenic disturbance. Grasslands established in past climates are only marginally supported by current climate (Brown and Archer 1989).

Anthropogenic factors contribute to shifts in vegetation composition (Asner et al. 2003). Terrestrial sequestration of carbon is largest in the Northern Hemisphere (Schimel et al. 2000). Woody plant abundance increased within the past three hundred years in many parts of the world, including North American grasslands (Archer 1989). Texan and Mexican ecosystems were classified as savanna ecosystems; however, current ecosystems are dominated by woodland. The plant species composition of grasslands has shifted to favor woody tree and shrub species in place of herbaceous species (Asner et al. 2003). Woody vegetation spread at the expense of herbaceous species as climate change increases the susceptibility of savannas and grasslands to the invasion of woody plant species (Archer 1990). Climate change, over-grazing by herbivores, and reductions in fire frequency have been proposed as causes for the invasion of woody plants into

grasslands (Archer 1989). The invasion of woody species negatively influences the primary productivity of herbaceous species (Asner et al. 2003).

There is a reduction in the growth of oak species in woodland of North America (Murray et al. 2013). For example, Plateau live oak (*Quercus fusiformis*) has not been recruited in South Texas ecosystems (Russell and Fowler 1999). The limitation of adult oaks is potentially due to high mortality rates. The introduction of livestock, reduced fire frequency, and increases in herbivore populations appear to affect oak populations. However, disturbance of oak woodlands affects oak recruitment and growth (Murray et al. 2013). Climate influences the growth of oak species due to constraints on carbon assimilation. In addition, prolonged climate events can influence tree growth by changing competition between woody tree species. *Q. fusiformis* appears to have a role in converting savanna ecosystems to Ashe's juniper (*Juniperus ashei*) stands (Russell and Fowler 1999).

The invasion of mesquite (*Prosopis* sp.) coincides with the introduction of livestock, which disperses woody plant species (Brown and Archer 1989). The spread of mesquite facilitates the invasion of other woody plant species (Archer 1989). Woodlands were previously restricted to riparian areas but spread to other ecosystems. Mesquite and other woody species spread from riparian zones towards upland prairies (Brown and Archer 1989).

1.5 Computer Modeling

Climate models indicate that periods of greenhouse gas emissions cause abrupt warming occurring over brief time intervals, even less than tens of thousands of years (Zachos et al. 2008). Computer models examine water and carbon cycles under current

and historical climates (White et al. 2000). The theoretical basis for model processes is typically based on laboratory or field observations. However, computer models are used to understand ecosystem functions that cannot be practically studied in the field and to understand management needs for an ecosystem in response to climate change.

Biome-BGC is a model used to estimate the fluxes of carbon, nitrogen, and water into and out of ecosystems (Golinkoff 2010). Biome-BGC replicates plant carbon pools in ecosystems based on set parameters. Biome-BGC allocates carbon from photosynthesis into a carbon pool used during the growing season. The fluxes and storage of carbon is scaled to per meter squared. The Biome-BGC model represents fluxes of carbon for an ecosystem by using site conditions, meteorology, and parameter values.

Biome-BGC uses a daily and annual time-step. A daily timescales is used due to the availability of daily temperature and precipitation data, which allows the model to represent short-term variation in carbon fluxes. The physiological processes modeled by Biome-BGC include photosynthesis, evapotranspiration, autotrophic and heterotrophic respiration, decomposition, allocation of photosynthetic assimilate, and mortality of vegetation. Biogeochemical processes are represented based on plant functional type.

1.6 Study Purpose

Earth's climate is continuously changing; however, anthropogenic factors alter climate with serious consequences. Climate change influences terrestrial ecosystems and species within these ecosystems. Increasing carbon dioxide concentrations in Earth's atmosphere is a leading cause of climate change. Fluctuating carbon dioxide concentrations influence vegetation within ecosystems. This study examined the changing carbon budgets of upland and riparian woodland ecosystems in Central Texas in

the context of ongoing climate change and increasing atmospheric carbon dioxide concentrations. An investigation of the carbon balance revealed the response of vegetation in woodland ecosystems to climate change caused by increasing level of atmospheric carbon dioxide. The Biome-BGC model was incorporated for the investigation of the consequences of climate and increasing atmospheric carbon dioxide concentrations on plant growth.

1.7 Research Questions

For this study, I propose to investigate processes and the amount of carbon sequestered in trees species within Central Texas woodlands. As part of this study, I anticipate that carbon budgets are associated with habitat differences particularly in the upland and riparian woodlands due to soil moisture differences. Using the Biome-BGC, the model will represent accurately predicted differences in the carbon allocation of carbon between the woodlands. In addition, there were likely differences in the amount of carbon in live and dead plant biomass. Also, woodland systems carbon dynamics was evaluated based on different tree species. Soil moisture was examined to determine the water budgets of the woodlands as a possible control on carbon dynamics. In addition, I will be investigating the consequences of increased atmospheric carbon dioxide and climate on the growth of the upland and riparian woodlands over the span of ten years, using data previously gathered and computer modeling to determine the effects on woodland growth.

CHAPTER TWO

Materials and Methods

Field data was gathered to estimate the biomass of tree canopy, stem, and the fine root system. As a standard, the amount of carbon was half the estimated biomass (Liski et al. 2006). The amount of carbon gained and/or lost from the system as evaluated from photosynthesis and litter decomposition measurements. In addition, soil moisture was measured to evaluate the water balance of the woodland ecosystems.

2.1 Study Site

The carbon budgets were examined in two woodlands at the Waco Wetlands located in the North Bosque River watershed, a floodplain system within the Brazos River Basin located in the Prairie Parkland Province and the West Gulf Coastal Plain (Bailey 1995). Upland and riparian woodlands are located at the wetlands. The upland woodland is above the wetland cells and the river system. The upland woodland is above the water table. The riparian woodland system is between the wetland cells and the river. The water table is very close to surface in this ecosystem. Study plots were 15 meters by 15 meters. Three plots were located in the upland woodland and three were located in the riparian woodland.

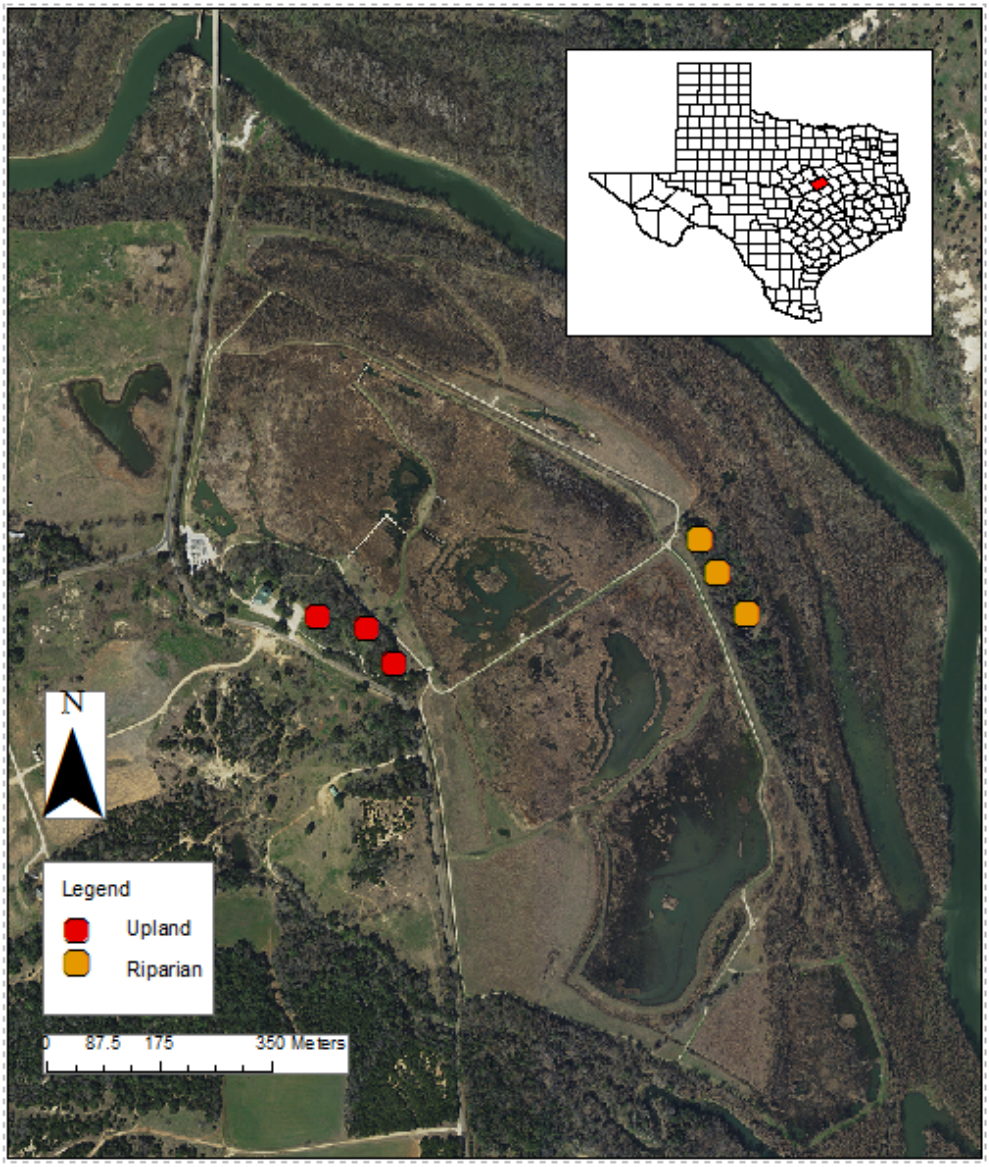

Figure 2.1 Upland and riparian woodland plots: Six woodland plots were set up at the Lake Waco Wetlands. Three were within the upland woodland and three within the riparian woodland. The upland woodland is located above the wetland. The riparian woodland is located between the North Bosque River and the wetland. The upland plots are indicated with red and the riparian plots are indicated with gold. Location with the State of Texas is indicated in Red on the Texas State Map (http://www.countymapsoftexas.com/mclennan.shtml).

The soil is clay loam for both the upland woodland and the riparian woodland (United States Department of Agriculture 2016). The soil is shallow and the bedrock is at the depth of roughly 40 cm. Tree species within the study sites include Ashe's juniper (*J. ashei)*, Cedar Elm (*Ulmus crassifolia*), Hackberry (*Celtis laevigata*), Mesquite (*Prosopis*

sp.), Buckthorn (*Rhamnus caroliniana)*, Osage Orange (*Maclura pomifera*), *Q. fusiformis*, and Chinaberry (*Melia azedarach).* Vine species include Sevenleaf Creeper (*Parthenocissus heptaphylla),* Greenbrier *(Smilax bona-nox),* Mustang Grape *(Vitis mustangensis),* and Poison Ivy*(Toxicodendron radicans)*. Shrub species include Deciduous Holly (*Ilex deciduous)*, American Beautyberry (*Callicarpa americana*), and Elbow Bush (*Forestiera pubescens*). In the Prairie Parkland Province, summers are hot and winters are cold (Bailey 1995). Summer temperatures range between 21 and 27 °C. The winters are relatively short and mild in southern parts of the province. Winters temperatures range between 10 and 16 °C. Average annual precipitation ranges between 890-1410 mm. Grasslands have historically dominated the region and more recent expansion of woodlands has been associated with climate change and CO_2 fertilization influence (Archer 1989).

2.2 Canopy Carbon

Canopy carbon was based on the canopy biomass, which was estimated by leaf area index (LAI). LAI was used to estimate of the foliage biomass and canopy carbon (Burton et al. 1991). The LAI was measured with a LAI-2000 (LI-COR Inc., Lincoln, NB), which derived canopy LAI from a single viewpoint by using five sensors that measure light intensities through the canopy (Nackaerts et al. 2000). The LAI-2000 measured the total plant area index, which includes branches, stems, and leaves. The raw LAI data was post-processed to correct the results (White et al.1997). The relationship between measured LAI (Le) and actual LAI was described by $L = (1 - \alpha)L_e \gamma_E \Omega_E$. In this equation α was the fraction of woody total area, γE was the needle-to shoot area ratio, and ΩE was a factor that describes clumping at scales larger than shoots. The average clumping value was

1.58 in the upland woodland and 1.39 in the riparian woodland. The woody portion was an average of 0.3.

The LAI-2000 measurements were taken for above the canopy and below the canopy. Above- canopy measurements were taken in an open area and below canopy measurements were taken below the canopy of the plot (Deblonde et al. 1994). The difference between above and below-canopy measurement was used to calculate the canopy gap fraction, which represents the probability of light penetration through the canopy (Nackaerts et al. 2000). This was represented by T (□, Ø)=exp (-G (□, Ø) μ S (□, Ø)), where T (□, Ø) is the probability of non-interception of light by the canopy, G (□, Ø) was the fraction of foliage projected toward (□, Ø), μ was the foliage density (m^2 foliage/m^3 canopy), and S (□, Ø) was the path length through the canopy. The open areas selected were roughly the same size as study plots; however, under no canopy cover without any vegetation shading the LAI-2000 (Deblonde et al. 1994). Above-canopy measurements were taken once before below-canopy measurements and once after below canopy measurements. The number of below canopy measurements depended on the size of the plot and if the canopy-cover was homogenous or heterogeneous. The plot size was small with homogenous canopy cover, so below canopy measurements were taken eight times within each plot. LAI measurements were measured between 14:00-15:00 for every sampling. The sample time was chosen based on the angle of the sun because the LAI-2000 was not used under direct sunlight and measurements were better suited at near sunrise or sunset.

The LAI-2000 instrument does not partition LAI quantities among different tree species within a mixed-species canopy (Eriksson et al. 2005). However, percentages of

live foliage were measured during the winter visually estimate canopy cover from below. The foliage cover was estimated solely for *J. ashei* in the upland woodland and *Q. fusiformis* in the riparian woodland. Percentage values were taken at the four corners of the plot at roughly two to three meters from the center. The percentages were averaged for an estimation of foliage cover for each plot.

The percentage of live *J. ashei* or *Q. fusiformis* canopy was multiplied by LAI to calculate an estimation of the LAI for *J. ashei* or *Q. fusiformis*. The LAI was converted to the amount of canopy biomass with the leaf mass per area (LMA). The canopy biomass of evergreen species was calculated by multiplying evergreen LAI by evergreen LMA. The fraction of LAI for *J. ashei* or *Q. fusiformis* was multiplied by the appropriate LMA of 257.1 (g/m^2) for *J. ashei* or 141.1 (g/m^2) for *Q. fusiformis* to calculate canopy biomass for the species (Thomas et al. 2016). An average LMA for *U. crassifolia* and *C. laevigata* of 64.75 (g/m^2) was used to determine canopy biomass for the deciduous species. The portion of LAI not covered by *J. ashei* or *Q. fusiformis* was multiplied by the average LMA to obtain biomass for the deciduous tree species. For example, to convert LAI into canopy mass in the upland woodland, biomass =((*J. ashei* canopy cover portion*LAI)*257.1) + ((Deciduous canopy cover portion*LAI) *64.75). To convert LAI into canopy mass in the riparian woodland, biomass =((*Q. fusiformis* canopy cover portion*LAI)* 141.1) + ((Deciduous canopy cover portion*LAI) *64.75). The LAI was measured every two months during the year to determine if canopy biomass changes seasonally.

2.3 Stem Carbon

The amount of carbon sequestered in the stem of the tree was estimated based on stem biomass. The stem circumference was measured for all trees within each plot in 2005 (Sides, unpublished data), and again in 2015 to estimate change in stem biomass. Also in 2015, the circumferences were measured for mature trees over the height of 2 m, which were not present in 2005. The heights of saplings and seedlings individuals were measured during late summer. Saplings and seedlings were distinguished from each other based on height; seedlings were 10 cm or smaller and saplings were divided into three categories of < 0.5 m, 0.5 - 1.0 m, and 1.0 - 2.0m.

The circumference at breast height was converted to diameter at breast height by dividing the circumference by 3.14. Allometric equations were used to convert the diameter to biomass (Yao et al. 2012) (Table 2.1). The circumference of individual trees were originally measured in 2005 and then re-measured in 2015. At the time of the death of the tree, these individuals were assumed to maintain roughly the same circumference as the original 2005 measurement. Tree death over the course of the ten years was assumed to constitute a separate carbon pool. The same allometric equations were used to estimate the amount of carbon within the dead stem carbon pool.

The allometric equations used to estimate biomass were based on the tree species but general equations were used when a specific species allometric equation cannot be accessed (Yao et al. 2012) (Table 2.2).

Table 2.1 Species Specific Allometric Equations: Stem biomass was estimated for all trees within the upland and riparian woodlands using allometric equations. Allometric equations were divided based on species of tree. The circumference was taken for all trees within the woodland plots and converted to diameter. X was the diameter a breast height. Y was the resulting biomass in kilograms. (Yao et al. 2012).

Species	Equation
Juniperius ashei (14cm < X < 43cm)	$Y=0.1632 * X^{2.2454}$
Ulmus crassifolia (X < 28 cm)	$Y= 2.17565 * (X/2.54)^{2*1.2481} * 0.45$
Quercus fusiformis (2.5cm <X < 73cm)	$Y=\exp(-0.20127+2.4342 \ln X)$

Table 2.2 General Allometric Equations: Allometric equations were divided based on species of tree; however, general equations were used when species-specific equations were not found. dbh was the diameter a breast height. Log_{10} Biomass was the resulting biomass in kilograms. (Yao et al. 2012).

Species	Equation
Small junipers	$\log_{10}$ Biomass= 1.2727 + 1.4039* $Log_{10}(dbh^2)$
Oaks and broad-leaf	$\log_{10}$ Biomass=1.1843 + 1.5327 * $Log_{10}(dbh^2)$

2.4 Litter Carbon

The measurement of litter biomass provided an estimation of the amount of carbon that fell from plants in the form of litter, including leaves, branches, and seeds. Four litter traps were placed in each plot constructed from a wooden frame with a close-knit, wire mesh base to allow water movement through the base. The four traps were each placed at different corners of the plot at roughly two to three meters away from the center of the plot.

The litter was collected every two to three months and placed in paper bags. The litter was divided into categories based on the specific litter trap and the type of litter (Yang et al. 2007), which included: leaf, branches with a diameter smaller than 2mm, branches with a diameter between 2 and 5 mm, branches with a diameter larger than 5 mm, and seeds. The litter was oven dried in paper bags at 60 °C for forty-eight hours and weighed. The final biomass estimated the amount of carbon in the litter.

The traps were collected every two to three months to estimate litter fall over time. Seasonal litter values were estimated based on the total amount of litter fall during winter, spring, summer, and autumn. A total annual litter fall (g/m^2) was estimated for both upland and riparian woodlands through the summation of the amount of litter biomass gathered over the year. The amount of carbon in the litter traps was used to estimate the amount of carbon in litter-fall for the entire plot. Each litter traps covered 0.25 m^2, with a total of 1 m^2 per plot. Litter carbon was scaled up for each plot by multiplying the representative sample by the area of the plot, which is equal to 225 m^2.

2.5 Litter Decomposition

The measurement of biomass loss through decomposition provided an estimation of the amount of carbon released into the soil. The litterbag method was used to estimate the litter biomass loss through decomposition (Cotrufo et al. 2010). The litterbags enclosed plant material of a known mass into a flexible fabric mesh bag (Wider and Lang 1982). The litterbags were made out of mesh with the same amount of litter material in each bag (Wardle et al. 1997).

Before being placed into litterbags, the litter was oven- dried in paper bags for forty-eight hours at 60 °C (Harner et al. 2009). Litter decomposition was assessed for different

types of litter material including: the evergreen leaf of *Q. fusiformis* and *J. ashei*, deciduous leaf, branches, and seeds. *J. ashei* foliage was double bagged to prevent the material from falling through the mesh due the foliage breaking apart as it decomposes. Five grams of litter material was placed into decomposition bags for evergreen leaf, deciduous leaf, and branches. Four grams of litter material was placed into decomposition bags for seeds. The litterbags were secured to the soil within the plots. The litterbags were retrieved to determine the changes in mass (Wider and Lang 1982). The litter was dried for twenty-four hours at 40 °C before being weighted. The change in litterbag mass was measured every month for six months.

The litter mass loss was calculated by subtracting the remaining dried weight from the dry weight of the litter that was placed into the litterbags. The proportion of carbon to biomass did not change; however, the rate of decomposition changed over time. The difference between the initial and final dry mass was used to calculate of the amount of carbon that was lost through decomposition. The litter biomass lost after decomposition was calculated by subtracting the dry mass of litter after decomposition from the original dry mass, which was divided by the original dry mass. This was used to determine the percentage nutrient remaining by multiplying this value by 100. This calculation was used to determine the amount of carbon that remained in the litter after decomposition. The data collected from the litterbags was scaled to a flux by dividing mass lost by unit time.

The data was also scaled up to the plot scale based on the amount of litter biomass per unit area. The data was scaled up based on the amount of litter that fell into the litter traps over the year. The amount of biomass lost due to decomposition was equal to the amount

of fallen litter over the plot multiplied by the portion of biomass lost as the litter decomposes. For example, plot biomass released through decomposition= ((initial mass-final mass)/initial mass)* biomass of litter for plot (g/m^2)* 225 m^2. When scaled to plot, decomposition was considered for combined litter biomass loss instead of biomass lost in specific categories.

2.6 Root Carbon

Initial root mass was taken with root cores and root growth was measured by installing ingrowth cores in the top 40 cm of soil in the plots. The root cores were taken by driving a soil auger, roughly 3.5 cm across and 40 cm tall, with a surface area of 9.62 cm^2. The depth of the cores was based on the average maximum depth of the soil and deeper depths reached bedrock. Eight root cores were taken and eight ingrowth cores were placed in each plot. Four root cores were placed randomly near mature trees. Four cores were placed in the central areas at an equal distance from surrounding trees.

Annual fine root production of the plot was derived from root growth into root-free soil of the ingrowth cores (Nadelhoffer and Raich 1992). Before the soil was returned, the site was marked and the ingrowth cores were placed to measure changes in growth over time (Brassard et al. 2011). Roots were removed from the soil because the soil placed into the ingrowth cores needed to be root free (Yuan and Chen 2012). The ingrowth cores were made out of plastic mesh. Each core was labeled with the plot and numbered.

The roots were placed into paper bags and transported back to the lab. The roots were oven dried at 60 °C in paper bags for twenty-four hours. The roots were separated into two categories; roots were considered coarse roots or fine roots determined by diameter

(Kiley and Schneider 2005). Fine roots were less than 2mm in diameter and coarse roots were 2mm or larger in diameter. The roots were separated to estimate the fine root system and the coarse root system biomass. The roots were weighted separately as coarse roots and fine roots. The production of fine roots was determined by the dry weight values of the roots that grew in the ingrowth cores (Brassard et al. 2011).

The amount of carbon in the root cores was used to estimate the entire belowground carbon for each plot. The carbon in the fine root system was based on the amount of carbon that is in the cores. The root sample carbon was scaled up to plot value based on the surface area covered by removed cores. The scaled up value was equal to the amount of biomass per unit of surface area (g/m^2) multiplied by the area of the plot of 225 m^2. This measurement was taken in December of 2015 and January 2017 to estimate of the growth rate of the fine root system.

2.7 Vine and Shrub Carbon

The diameters at breast height (dbh) of all vines within the plots were measured with calipers. Rangefinders were equipment used to measure the distances of an object. The vine heights estimated with a rangefinder. Allometric equations were used to convert diameter and height to vine biomass (Elliot and Clinton 1993) (Table 2.3).

Table 2.3 Vine Species Allometric Equations: Allometric equations were based on vine species. Where B is vine biomass, d is diameter, and h is height. (Elliot and Clinton 1993).

Species	Equation
Parthenocissus heptaphylla	B=-0.9289+(0.8012*d)+(0.0953*h)
Smilax bonanox	B=-2.7891+(6.2733*d)+(0.106*h)
Vitis mustangensis	B=-0.9289+(0.8012*d)+(0.0953*h)
Toxicodendron radicans	B=-0.9289+(0.8012*d)+(0.0953*h)

The biomass of shrub species was estimated for shrub species. For all shrubs, the number of basal stems was counted. The shrub height and width were measured with a measuring stick. Allometric equations were used to convert data to an estimation of biomass (Sah et al. 2004). A general equation for a mixed species ecosystem determined biomass: $B= 0.446*CA^{0.869} * HT^{1.112}$, where CA was the canopy area in square meters and HT was the height in meters.

2.8 Photosynthesis

Photosynthesis was measured with an infrared gas analyzer (IRGA) to estimate the amount of carbon assimilation measured in summer and fall. Spring samples were not taken because of variable photosynthetic activity of newly formed leaves. Samples were taken in autumn and summer to estimate photosynthesis at high and low temperatures while deciduous plants retained leaves (Yamori et al. 2014). Multiple samples per plot, four samples during the summer and two samples during the autumn, were taken to determine an average photosynthesis rate for the plot and tree type. Only one sample was taken per plant. Photosynthesis was measured with an TPS-1 Photosynthesis System (PP

System, Amesbury, MA), which was a closed system where amount of CO_2 assimilated by the plant material was calculated from the volume of the total system as air was pumped through the sample cell tube (Van et al. 1976; Haszpra et al. 2001). The plant material samples filled the chamber for each measurement to obtain accurate readings due to a high surface area for photosynthesis (Rodgers et al. 2012).

The leaves chosen for analysis were whole and healthy from mature trees in each plot. Analyzed species were representative of the species composition by choosing evergreen and deciduous species found within the plot. The leaf samples used for photosynthesis values were collected using a pole pruner extended 10 m into the canopy. Leaf samples were scanned into the computer and ImageJ (National Institute of Health, Bethesda, MD, https://imagej.nih.gov/ij/) was used to estimate the surface area of each leaf. New surface area values were used to recalculate photosynthetic rate per unit area.

Photosynthesis values were scaled from individual leaf values to the canopy value to make a comparison to the foliage canopy values. An average photosynthesis value was calculated for each plot and the average leaf photosynthesis ($\mu mol/m^2/s$) was scaled up to the average canopy photosynthesis. Photosynthesis was scaled up to canopy photosynthesis using LAI estimations. To estimate the amount of carbon per unit area, the photosynthesis was multiplied by LAI to adjust the value based on the amount of canopy coverage. The average leaf photosynthesis ($\mu mol/m^2/s$) was multiplied by measured LAI (m^2/m^2) values corresponding by plot. The photosynthesis rate is converted from $micromoles/m^2/s$ to $moles/m^2/s$. The photosynthesis rate was then multiplied by the molecular mass of carbon dioxide (44.01 g/mol). The photosynthesis rate was multiplied by the carbon portion of carbon dioxide mass (0.273). The

photosynthesis rate is then converted from amount per second to amount per day. The LAI was measured over several months during the year, which allowed for the estimation of photosynthesis during months of winter, spring, summer, and fall. Annual photosynthesis values were estimated by estimating canopy photosynthesis for each leaf area index measurement.

2.9 Soil Moisture

Soil moisture was measured for both the upland and riparian woodlands Estimations of soil moisture were taken using a Delta-T Devices HH2 soil moisture meter with a PR2 Profile Probe (Delta-T Devices, London), which estimates soil moisture comparing applied current to return signals. The profile probe provided raw measurements in millivolts at the depths of 100 mm, 200 mm, 300 mm, and 400 mm. These values were converted to soil moisture (m^3/m^3). Millivolts measured by the PR2 Profile Probe were converted to soil moisture using:

$$\mathrm{Y} = -0.113 + (1.62 * \mathrm{X}) - (3.56 * (\mathrm{X2})) + (8.63 * (\mathrm{X3}))$$

for mineral soils, where *X* is a millivolts value. Clay loam was present in the upland woodland and the riparian woodland (United States Department of Agriculture, 2016). Soil texture with small grain size was assumed to have better water retention capacity (Saxton and Rawls 2006). Two soil fiberglass moisture tubes were placed in each of the six plots to protect the profile probe from moisture exposure; two measurements were taken for each tube.

2.10 Biome-BGC Model

The Biome-BGC model was used to estimate carbon and climate change in the study plots. The model was used to determine if climate and atmospheric carbon dioxide affected carbon sequestration. The amount of carbon in vegetation biomass was hypothesized to change with climate and the increase in atmospheric carbon dioxide.

To model photosynthesis, Biome-BGC converted leaf carbon to leaf area based on the specific leaf area (SLA) specified within the model (Golinkoff 2010). Photosynthesis and respiration were modeled under high and low light. The ratio of shaded specific leaf area to sunlit shaded specific leaf area is a user-defined parameter, which was maintained at the initial ratio value of 2. The total assimilate is the sum of the sun and shade leaf assimilation. The carbon assimilated through photosynthesis is placed into a storage pool that is portioned to future growth storage current growth. The demand for nitrogen is calculated to determine if nitrogen limits the allocation of assimilated carbon. The rate of photosynthesis depends on the nitrogen content of leaves, the portion of N in Rubisco, and the temperature. Photosynthesis depends on the amount of absorbed PAR, the calculated maintenance respiration, and the difference between the internal and external partial pressure of CO_2. Stomatal conductance was converted to water vapor, which was converted to a conductance for CO_2. The conductance for CO_2 was converted to units used by the photosynthesis (m/s to umol/m^2/s/Pa):

$$g_{mTc} = 1*10^6 * g_{Tv} / (1.6 * R(Tday+273.15)$$

where R is the universal gas constant, g_{TV} is the leaf scale conductance to transpired water, tday is the daytime temperature, and 1.6 is the ratio of the molecular weights of water vapor to CO_2.

The CO_2 diffusion constraints of photosynthetic rate, which indicates the rate that CO_2 can enter the leaf and is function of stomatal opening and the difference between the atmospheric CO_2 pressure and the leaf internal CO_2 pressure. Photosynthesis was calculated by:

$$A= g_{mTc} * (C_a-C_i),$$

where Ca is the atmospheric concentration of CO_2 (Pa) and C_i is the intercellular concentration of CO_2 (Pa). The equation is solved for C_i, which was substituted into the following equations to estimate the rate of carbon assimilation:

$A_v= V_{cmax} (C_i- \Gamma)/ ((C_i +K_c) +(1+O_2/K_o)) –MR_{leaf\ day}$ represents the carboxylation rate that controls the photosynthesis reaction.

$Aj=(J*(Ci- \Gamma))/ (4.5 *Ci +10.5 * \Gamma) –MR_{leaf\ day}$ represents the electron transport limitation of RuBP regeneration.

Where C_a the atmospheric concentration of CO_2 (Pa) and C_i is the intercellular concentration of CO_2 (Pa), Γ^* (Pa) is the CO_2 compensation point in the absence of leaf MR, K_c and K_o are the kinetic constants for rubisco carboxylation and oxygenation scaled by the temperature using a Q_{10} relationship, O_2 is the atmospheric concentration of O_2 (Pa), $MR_{leafday}$ is the daytime leaf maintenance respiration on a Projected LAI (PLAI) basis, and J is the maximum rate of electron transport.

Photosynthesis provided an input of carbon into the system and all carbon in the modeled system came from the carbon assimilated during photosynthesis. The maintenance respiration value was the respiration required for the maintenance of living tissue and was the first to be calculated by:

Day maintence respiration (mr)

$$= \text{leaf day mr} + \text{leaf night mr} + \text{root daily mr} + \text{live stem mr} + \text{live coarse root mr}$$

as the sum of leaf daily maintenance respiration, leaf night maintenance respiration, fine root maintenance respiration, live stem maintenance respiration, and coarse root maintenance respiration.

The amount of carbon that needed to go into growth respiration storage to satisfy all of the storage growth demands was represented by:

growth respiration storage

$$= (\text{Carbon pool to leaf carbon storage} + \text{Carbon pool to fine root carbon storage} + \text{Carbon pool to live stem carbon storage} + \text{Carbon pool to dead stem carbon storage} + \text{Carbon pool to live coarse root carbon storage} + \text{Carbon pool to dead coarse root carbon storage}) * g1 * (1.0 - g2).$$

where g1 is the ratio of C respired for growth to C grown and g2 is the proportion of growth respiration to release at fixation.

The Biome-BGC simulated fluxes were differentiated between fluxes in storage and in the growth of the plant. There was a series of equations used to determine the daily carbon fluxes out of the carbon pool into new growth or storage:

$$\text{Carbon pool to leaf carbon} = nlc * pnow$$

$$\text{Carbon pool to leaf carbon storage} = nlc * (1.0 - pnow)$$

$$\text{Carbon pool to fine root carbon} = \text{nlc} * \text{f1} * \text{pnow}$$

$$\text{Carbon pool to fine root carbon storage} = \text{nlc} * \text{f1} * (1.0 - \text{pnow})$$

$$\text{Carbon pool to live stem carbon} = \text{nlc} * \text{f3} * \text{f4} * \text{pnow}$$

$$\text{Carbon pool to live stem carbon storage} = \text{nlc} * \text{f3} * \text{f4} * (1.0 - \text{pnow})$$

$$\text{Carbon pool to dead stem carbon} = \text{nlc} * \text{f3} * (1.0 - \text{f4}) * \text{pnow}$$

$$\text{Carbon pool to dead stem carbon storage} = \text{nlc} * \text{f3} * (1.0 - \text{f4}) * (1.0 - \text{pnow})$$

$$\text{Carbon pool to live coarse root carbon} = \text{nlc} * \text{f2} * \text{f3} * \text{f4} * \text{pnow}$$

$$\text{Carbon pool to live coarse root carbon storage} = \text{nlc} * \text{f2} * \text{f3} * \text{f4} * (1.0 - \text{pnow})$$

$$\text{Carbon pool to dead coarse root carbon} = \text{nlc} * \text{f2} * \text{f3} * (1.0 - \text{f4}) * \text{pnow}$$

$$\text{Carbon pool to dead coarse root carbon storage} = \text{nlc} * \text{f2} * \text{f3} * (1.0 - \text{f4}) * (1.0 - \text{pnow})$$

where f1 was the ratio of new fine root C : new leaf C, f2 was the ratio of new coarse root C : new stem C , f3 was the ratio of new stem C : new leaf C, f4 was the ratio of new live wood C : new wood C, g1 was the ratio of C respired for growth : C grown, g2 was the ratio of proportion of growth resp to release at fixation, cnl was the ratio of leaf C:N , cnfr was the ratio of fine root C:N, cnlw was the ratio of live wood C:N, cndw was the ratio of dead wood C:N, nlc was actual new leaf C, minimum of C and N limits, and pnow was the proportion of growth displayed on current day.

Daily temperature and precipitation data for the city of Waco was downloaded from NOAA (https://www.ncdc.noaa.gov/data-access/land-based-station-data). In addition to

temperature and precipitation inputs, Biome-BGC requires average daytime vapor pressure deficit, the average shortwave radiant flux density, day-length that were simulated using the MTCLIM model (Hungerford et al. 1989) based on the site elevation and latitude.

The eco-physiological constants file (.epc file) was chosen for the broadleaf deciduous forest for both the upland and the riparian woodlands. The .epc file for the evergreen needle-leaf forest was chosen for the upland woodland and the evergreen broadleaf forest was chosen for the riparian forest. The user-defined parameters were adjusted for species composition of the upland and riparian woodlands. The .epc constants files were altered to account for the specific leaf area (SLA) of each species. An average SLA for species was based on samples chosen for photosynthesis measurements (Table 2.4). For deciduous forests, the SLA value was an average between *C. laevigata* and *U. crassifolia*.

Table 2.4 Specific Leaf Area Based on Species: The specific leaf area (SLA) measures the area of a leaf per gram of leaf. Measured in meters squared per gram. Different woody species have different specific leaf area values (Wright et al, 2001). SLA values used in the modeling process were determined through samples of the tree species present within the sampled woodlands. Different SLA values were taken into consideration during computer modeling of the ecosystem processes.

Species	SLA (m^2/g)
Celtis laevigata	26.126
Juniperus ashei	5.096
Quercus fusiformis	12.542
Ulmus crassifolia	20.273

Simulations with the Biome-BGC model included modeling different species in both woodlands, with species differences represented by changing SLA values.

This model was used to compare the growth of the system with different climate conditions, as well as pre-industrial and industrial atmospheric CO_2. Four conditions were

examined with the Biome-BGC model: a) industrial carbon dioxide and current climate, b) industrial carbon dioxide and past climate, c) pre-industrial carbon dioxide and current climate, and d) pre-industrial carbon dioxide and past climate.

Industrial carbon dioxide is set at 400 ppm and pre-industrial carbon dioxide was set at 280 ppm. Past climate encompassed 1950-1990 meteorological data. Current climate data encompassed 1991-2015 meteorological data.

The climate of central Texas during 1950-1990 and 1991-2015 resulted similar mean daily temperatures (Figure 2.2). The average temperature was 19.46°C during 1950-1990 and 19.64 °C during 1991-2015.

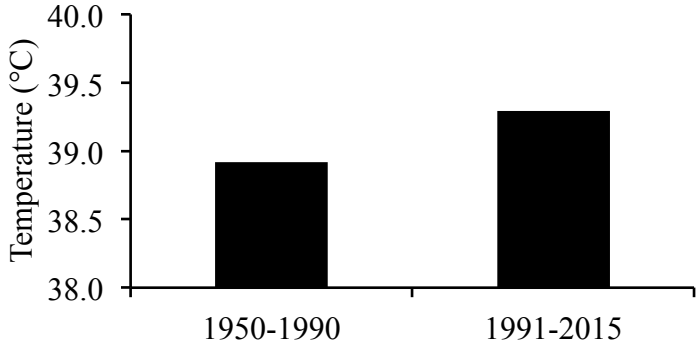

Figure 2.2 Mean Temperature: The mean daily temperature increased over time. The daily temperature was higher in 1991-2015 compared to 1950-1990.

The climate of central Texas during 1950-1990 and 1991-2015 resulted similar mean daily precipitation (Figure 2.3). The average precipitation was 2.19 cm during 1950-1990 and 2.49 during 1991-2015.

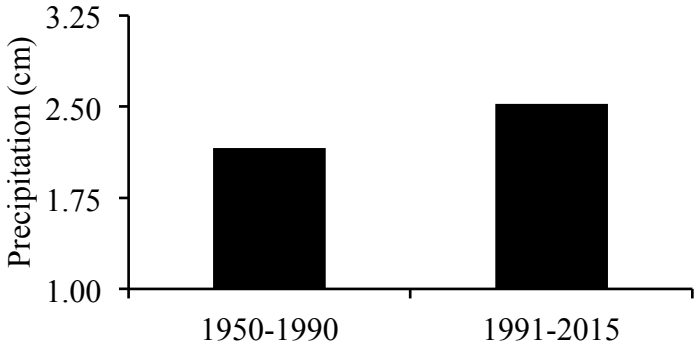

Figure 2.3 Mean Precipitation: The mean daily precipitation is higher for 1991-2015 compared to 1950-1990. In addition to higher daily precipitation, the annual total precipitation was higher in 1991-2015 compared to 1950-1990.

The dates chosen for the meteorological records were based on the IPCC (1995) designation where the atmospheric CO_2 level to pre-1991 level is considered the target for greenhouse gas stabilization. However, it is recognized the CO_2 levels have been increasing for both time periods, although at different levels and rates. .

The data collected from the Lake Waco Wetlands were compared with model simulation results to determine the consequences increasing atmospheric carbon dioxide and climate on carbon sequestration. The t-distribution test was used to statistically determine which of the model simulations produced results most similar to the observed outcomes. The modeled simulations were evaluated by either year or month based on the frequency of observed data collection. The modeled values were average by month for leaf area index (LAI), litter, and photosynthesis. The modeled tree stem and root were averaged by year. The average is calculated as: Average= sum/(number of months or years). The t-distribution test was used for hypothesis testing due to the small size of sample data sets. A t-distribution was used with an alpha value of 0.05. If the observed data was the same as results of the current climate data and industrial atmospheric carbon dioxide simulation, woody vegetation was considered climate and carbon sensitive. If the

observed data was the same as results of the past climate and industrial atmospheric carbon dioxide simulation, woody vegetation was considered climate insensitive and carbon sensitive. If the observed data was the same as results of the current climate data and pre-industrial atmospheric carbon dioxide simulation, woody vegetation was considered climate sensitive and carbon insensitive. If the observed data was the same as results of the past climate and pre industrial atmospheric carbon dioxide simulation, woody vegetation was considered climate insensitive and carbon insensitive.

CHAPTER THREE

Results

3.1 Canopy Carbon

Canopy carbon estimated for the upland and the riparian woodlands during 2015-2016 is shown in Figure 3.1. Canopy carbon differed between the upland and riparian woodlands ($p= 0.031$). The upland woodland contained a higher amount of canopy carbon than the riparian woodland. The upland woodland contained an average of 0.35 kg C/m^2 with an estimated total of 234.02 kg C in the sampled areas. The riparian woodland canopy contained an average of 0.31 kg C/m^2 with an estimated total of 209.48 kg C in the sampled areas. Although, canopy carbon fluctuated seasonally and canopy carbon was not significantly different between woodlands on a seasonal basis.

Canopy carbon estimated for 2005-2007 and 2015-2016 is shown in Figure 3.2. Canopy carbon has increased over time ($p= 4.98 *10^{-7}$). Canopy carbon was higher in 2015-2016 than 2005-2007 on an annual basis. During 2005-2007, the canopy contained an average 0.23 kg C/m^2 with an estimated total of 304.38 kg C in the sampled area. During 2015-2016, the canopy contained an average 0.33 kg C/m^2 with an estimated total of 443.50 kg C in the sampled area. Canopy carbon fluctuated seasonally in 2005-2007 and 2015-2016. The canopy carbon was significantly higher in 2015-2016 compared to 2005-2007 on a seasonal basis.

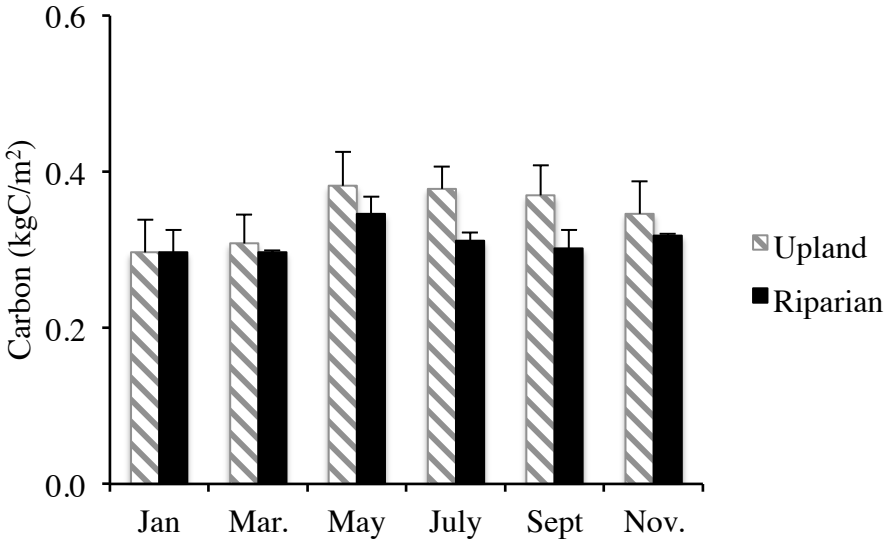

Figure 3.1 Canopy Carbon Based on Habitat: Canopy carbon was estimated in the upland and the riparian woodlands during 2015-2016. The upland woodland had a higher annual canopy carbon compared to the riparian woodland. On a seasonal basis, the woodlands were not different. Error bars indicate one standard error.

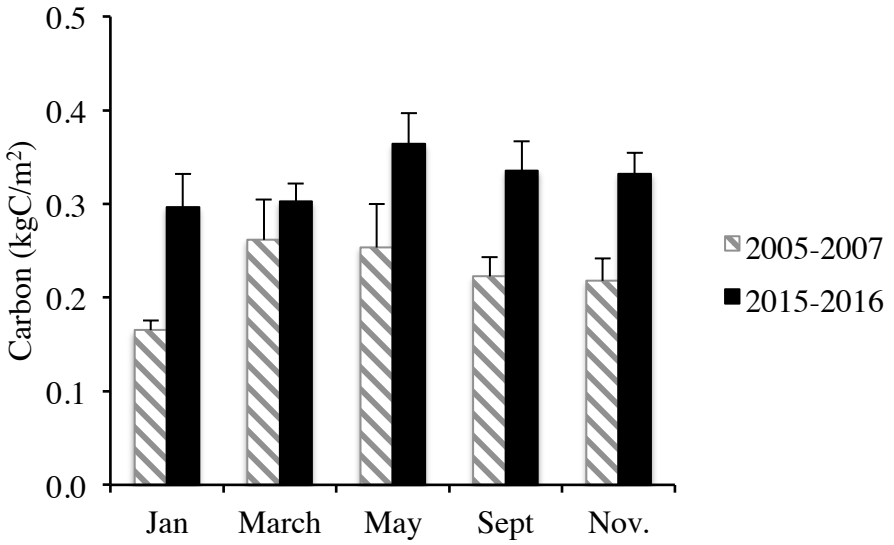

Figure 3.2 Canopy Carbon Over Time: Canopy carbon was estimated for the upland and the riparian woodlands during 2005-2007 and 2015-2016. The amount of carbon in the woodland canopy was different between 2005-2007 and 2015-2016. Canopy carbon was higher during 2015-2016 compared to 2005-2007. The 2015-2016 canopy carbon was higher on an annual and seasonal basis. Error bars indicate standard error.

3.2 Stem Carbon

The amount of carbon sequestered into stem biomass was estimated during 2005 and 2015 in the upland and riparian woodlands (Figure 3.3). The tree stem carbon increased between 2005 and 2015 ($p= 2.81*10^{-6}$ Upland, 0.004 Riparian). The tree stem carbon in sampled woodland equaled 35,157.4 kg C in 2005 and 53,885.05 kg C in 2015.

In both 2005 and 2015, stem carbon was different between the upland and riparian woodlands. In 2005, the stem carbon was higher in the riparian woodland than the upland woodland ($p= 0.02$). Tree stem carbon totaled 4,305.48 kg C in sampled upland woodland and 30,851.92 kg C in sampled riparian woodland. In 2015, stem carbon was higher in the riparian woodland than the upland woodland ($p= 0.006$). Tree stem carbon totaled 4,492.3 kg C in sampled upland woodland and 49,392.7 kg C in sampled riparian woodland.

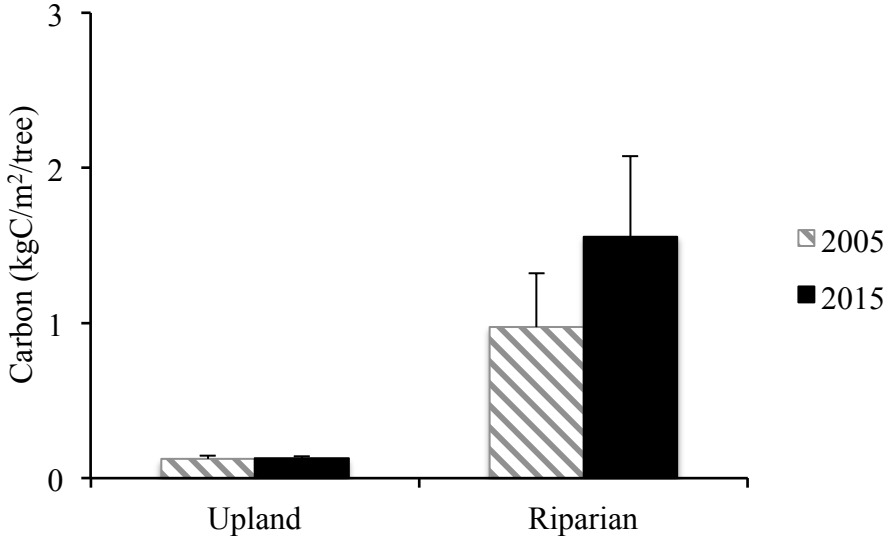

Figure 3.3 Live Stem Carbon Pool: The carbon sequestered in tree stems was estimated in 2005 and 2015 for all trees within the sampled upland and riparian woodland. Stem carbon increased between 2005 and 2015. Stem carbon was different between the woodlands when scaled to the individual tree level. Stem carbon was higher in the riparian woodland than the upland woodland. Error bars indicate one standard error.

The dead stem carbon pool was estimated for both the upland and the riparian woodland in Figure 3.4 with upland and riparian woodlands containing equivalent amounts (p= 0.88).

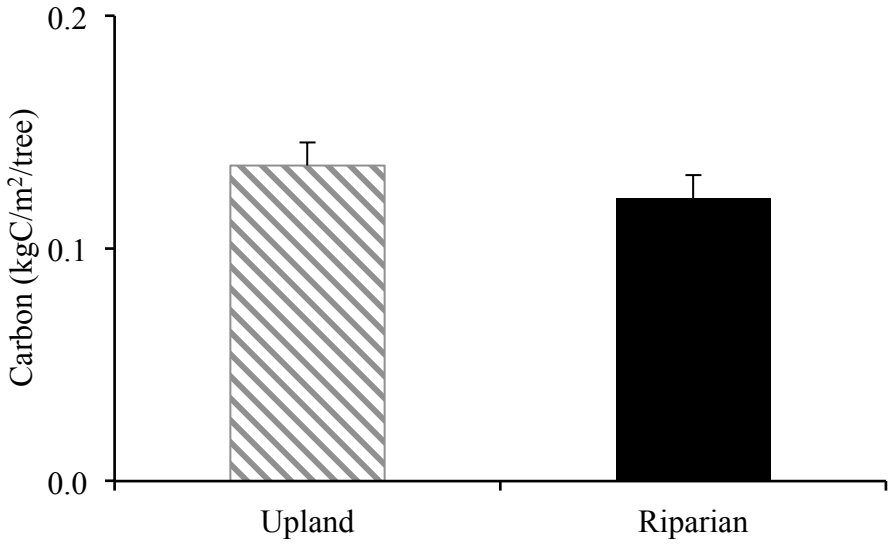

Figure 3.4 Dead Stem Carbon Pool: The dead stem carbon pool was equal between the upland and the riparian woodlands when scaled to the individual tree level. The error bars indicate one standard error.

Saplings and seedlings in the upland and riparian woodlands matured and added equivalent amounts of carbon to the upland and riparian woodlands (p= 0.493) (Figure 3.5). Young trees biomass consisted of 63.69 kg C in the sampled upland woodland and 28.94 kg C in the sampled riparian woodland.

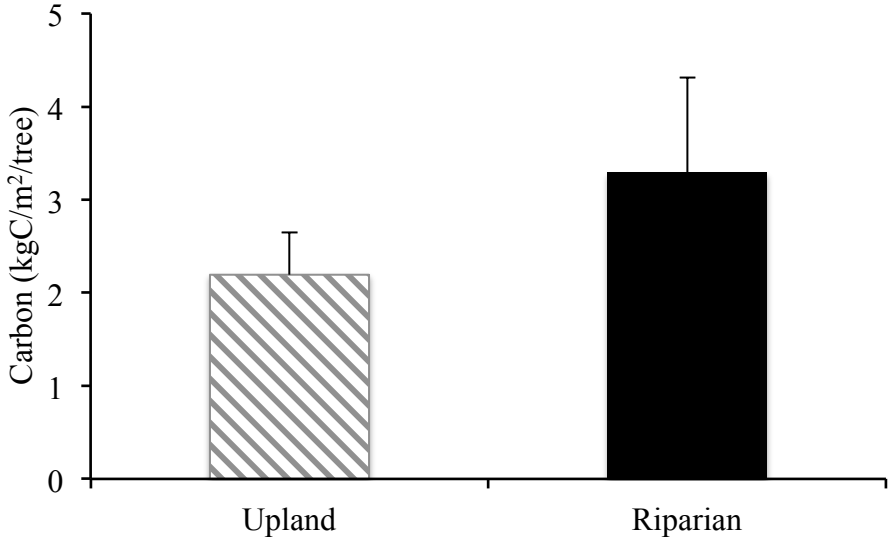

Figure 3.5 Young Tree Carbon Sequestration: Trees matured between measurements in 2005 and 2015. The growth of immature trees required the sequestration of carbon and conversion into biomass. There was no significant difference between woodlands in the amount of carbon that was sequestered into young trees when scaled to the individual tree level. Error bars indicate one standard error.

3.3 Litter Carbon

The annual litter fall was estimated for both upland and riparian woodlands during 2005-2007 and 2015-2016 for leaf, branch and seed litter (Figure 3.6). The total annual litter carbon remained constant between 2005-2007 and 2015-2016 ($p= 0.56$). During 2005-2007, an estimated annual total of 640.49 kg C fell as litter in the sampled woodlands. During 2015-2016, an estimated annual total of 826.4 kg C fell as litter in the sampled woodlands.

During 2005-2007, litter carbon was not different between the upland and riparian woodlands ($p= 0.94$). In 2005-2007, 0.48 kgC/m^2 fell in the upland woodland and 0.47 kgC/m^2 fell in the riparian woodland. However, during 2015-2016, the total litter carbon was different between upland and riparian woodlands ($p= 1.38 *10^{-6}$). In 2015-2016, 0.37 kgC/m^2 fell in the upland woodland and 0.85 kgC/m^2 fell in the riparian woodland. Litter carbon was higher in the riparian compared to the upland woodland.

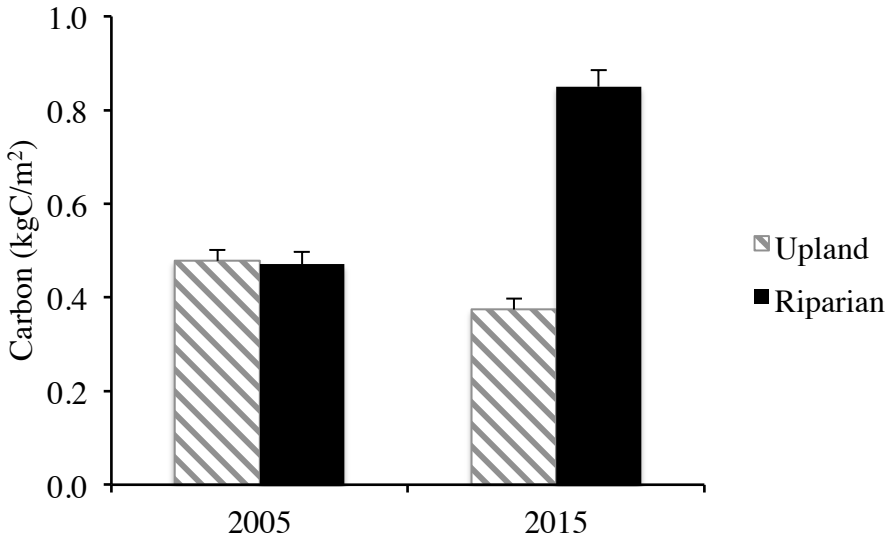

Figure 3.6 Annual Litter Fall: Carbon sequestration was estimated for the upland and riparian woodlands during the 2005-2007 and 2015-2016. There was no difference in the amount of carbon sequestered in the annual litter fall. Litter carbon remained constant over time. Error bars indicate one standard error.

Carbon in the litter types was estimated during 2005-2007 and 2015-2016 (Figures 3.7). Leaf litter was the dominant litter type during 2005-2007 ($p= 3.5 *10^{-14}$) and 2015-2016 ($p= 2.1 *10^{-21}$). The leaf litter carbon did not differ between 2005-2007 and 2015-2016 ($p= 0.15$). The woody litter carbon increased between 2005-2007 and 2015-2016 ($p= 0.0001$ (<2mm), 0.0006 (2-5mm), 0.001 (>5 mm)). The seed litter carbon decreased between 2005-2007 and 2015-2016 ($p= 0.013$).

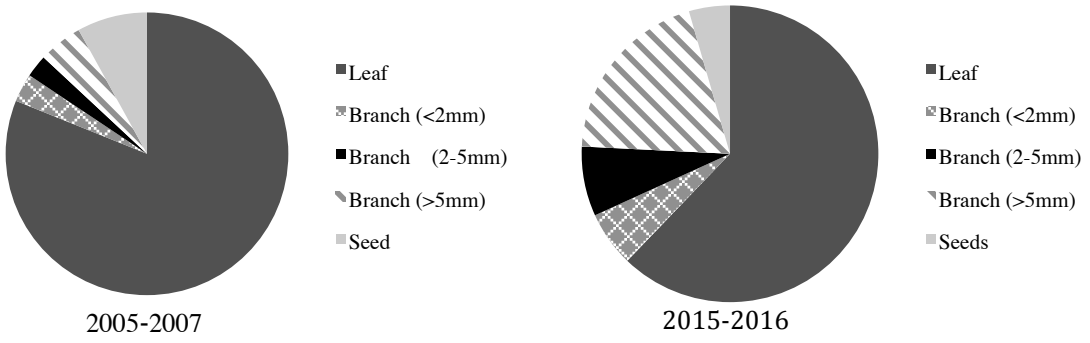

Figure 3.7 Litter Composition: Litter carbon was estimated in different types of litter including leaves, branches, and seeds. The branches were divided based on circumference. Carbon in woody litter material has increased over time and decreased in seed litter material over time.

3.4 Litter Decomposition

The decomposition rate of litter material was estimated in the upland and riparian woodlands (Figures 3.8). Litter material decomposed at different rates in the upland and riparian woodlands ($p=6.19*10^{-8}$). Litter material decomposed at a higher rate in the upland woodland compared to the riparian woodland.

The decomposition was estimated for different the litter types including deciduous leaf (D), woody (W), *Q*. *fusiformis* leaf (LO), seed (S), and *J*. *ashei* leaf (J) (Figure 3.9). The decomposition rate was the different across different litter types ($p= 0.016$ (D), 0.01(LO), $3.18*10^{-11}$ (S), $1.42*10^{-7}$ (J)). In comparison to the overall mean rate, deciduous leaf and seed litter material decomposed relatively quickly; *Q*. *fusiformis* leaf and *J*. *ashei* leaf litter material decomposed relatively slowly. Woody litter material decomposed at the same rate as overall mean litter decomposition rate ($p=0.34$).

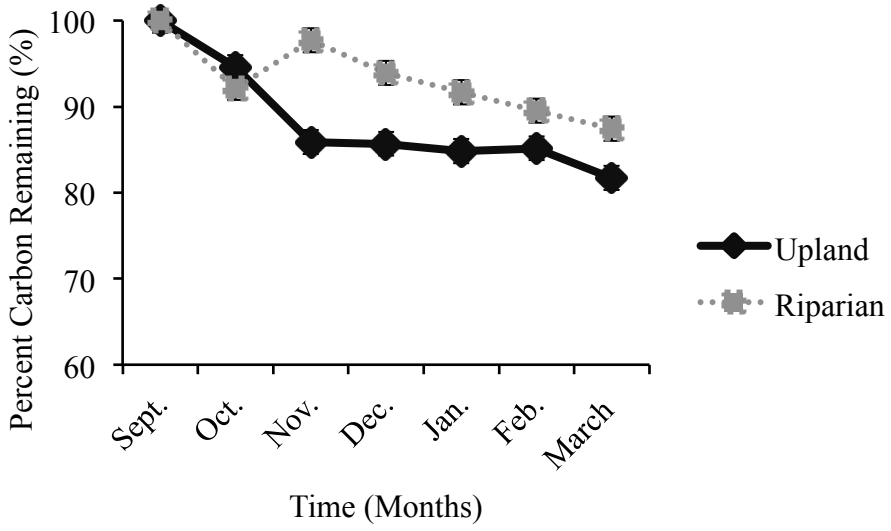

Figure 3.8 Decomposition Based on Habitat: Decomposition was estimated for deciduous leaves, woody material, Live Oak leaves, seed material, and Juniper leaves. The decomposition of material slowed over time. There was no difference between the woodlands in decomposition rate of litter material. Error bars indicate one standard error.

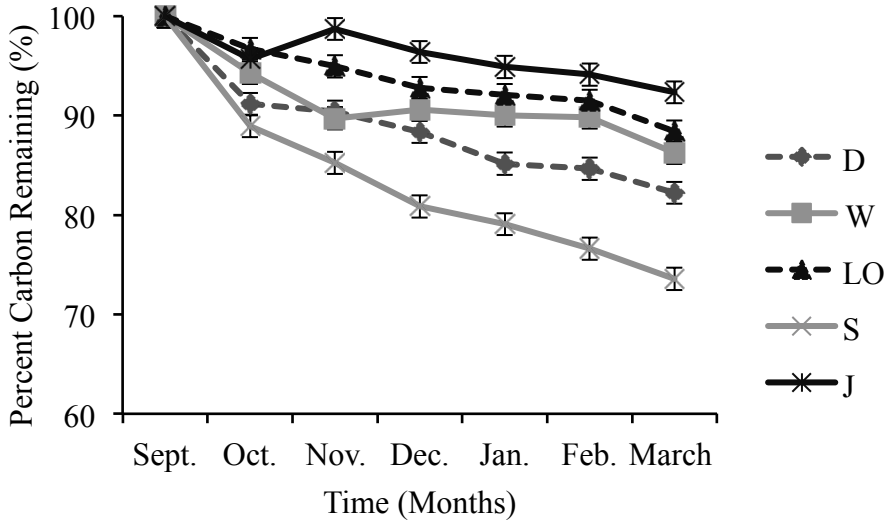

Figure 3.9 Decomposition Based on Litter Type: Decomposition was estimated for deciduous leaves (D), woody material (W), *Q. fusiformis* leaves (LO), seed material (S), and *J. ashei* leaves (J). The decomposition of material slowed over time. Error bars indicate one standard error.

3.5 Root Carbon

The fine root (<2mm) carbon and coarse root (>2mm) carbon were estimated in the upland and riparian woodlands (Figure 3.10). The fine root carbon was not different between the upland and riparian woodlands (p= 0.39). In the sampled upland woodland, the fine root system contained 0.32 kg C/m^2 with an estimated total of 215.59 kg C. In the sampled riparian woodland, the fine root system contained 0.35 kg C/m^2 with an estimated total of 238.54 kg C. The coarse root carbon was equal between the upland and riparian woodlands (p= 0.55). In the sampled upland woodland, the coarse root system contained 0.63 kg C/m^2 with an estimated total of 423.14 kg C. In the sampled riparian woodland, the coarse root system contained 0.79 kg C/m^2 with an estimated total of 529.99 kg C.

The fine root carbon pool was estimated at individual trees and centered between trees in the upland and riparian woodlands (Figure 3.11). Equivalent root carbon was estimated near individual trees and center areas in upland and riparian woodlands (p=0.59).

The flux of carbon into the fine root system was estimated for the upland and riparian woodlands (Figure 3.12). The carbon flux into the fine root system was higher in the upland woodland than the riparian woodland ($p=1.197* 10^{-6}$). The carbon flux occurred at the rate of 5.09 g C/m^2/yr in the sampled upland woodland and 0.58 g C/m^2/yr in the sampled riparian woodland.

The carbon flux into the fine root system was estimated near individual trees and centered between trees (Figure 3.13). The carbon flux was equivalent between the individual trees and center areas in the upland and riparian woodlands (p=0.59).

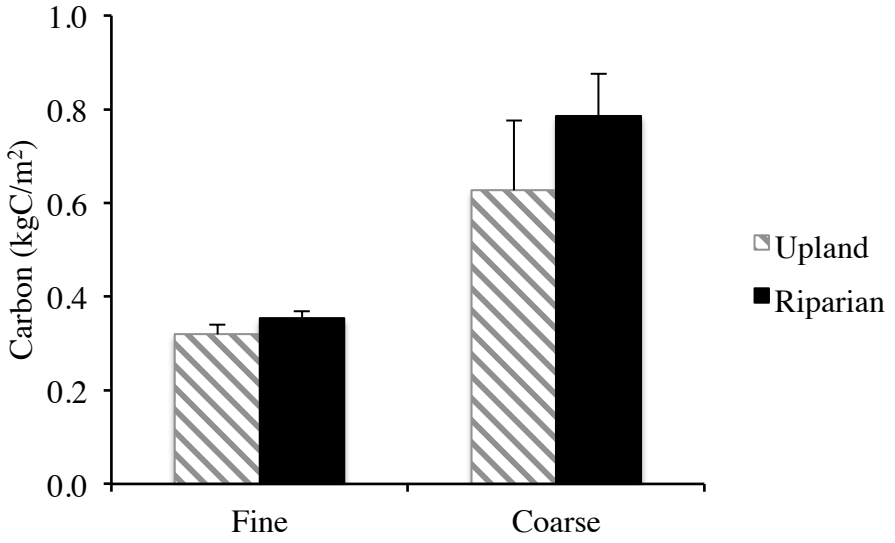

Figure 3.10 Fine and Coarse Root Carbon Based on Habitat: The carbon sequestration of the fine and the coarse root system was estimated for the upland and the riparian system. Carbon sequestration did not differ between the upland and riparian woodlands. Error bars indicate one standard error.

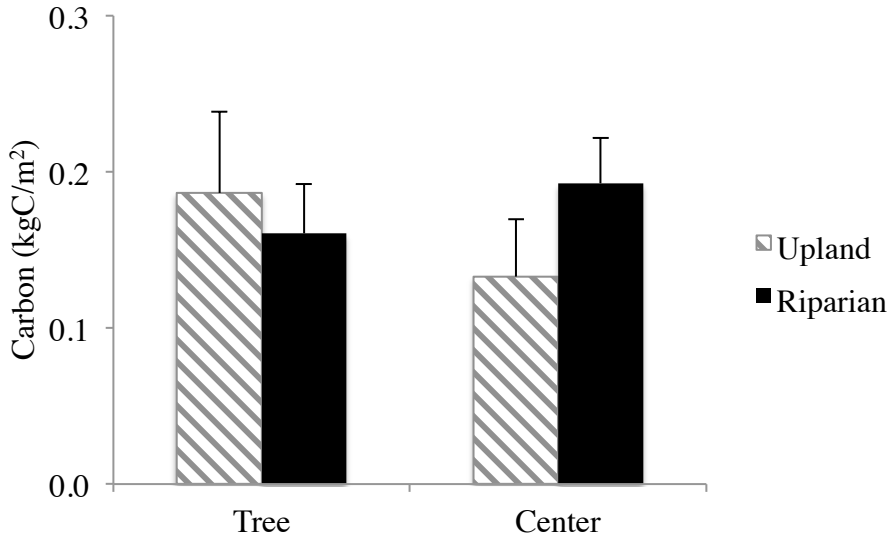

Figure 3.11 Fine Root Carbon Pool Based on Location: The fine root carbon was estimated in the upland and riparian woodland. The carbon in the fine root system was estimated in areas close to individual trees and center areas. Carbon was not different between areas close to individual trees and in the center areas. Error bars indicate one standard error.

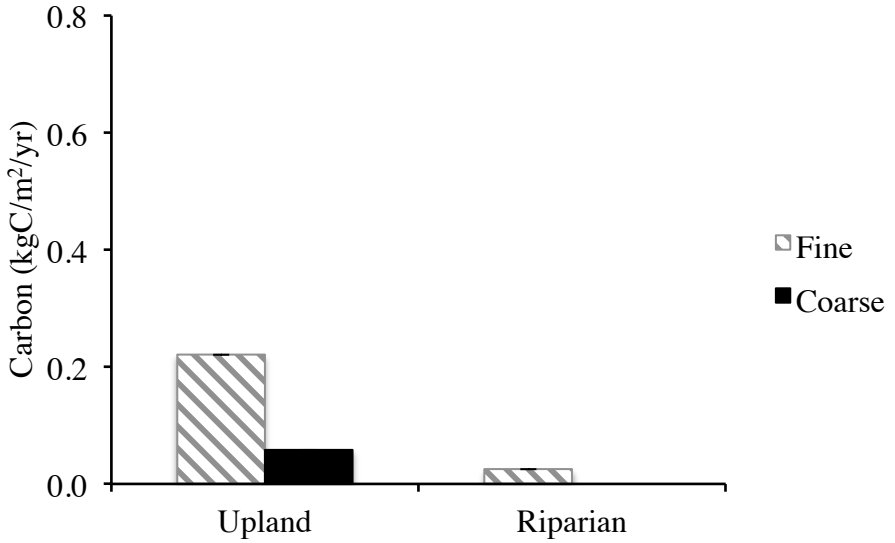

Figure 3.12 Root Carbon Flux: The flux of carbon into the fine root system over a year was measured for the upland and the riparian system. The carbon flux differed between the upland and riparian woodlands, with the upland woodland having a higher carbon flux to the fine root system. Error Bars indicate standard error.

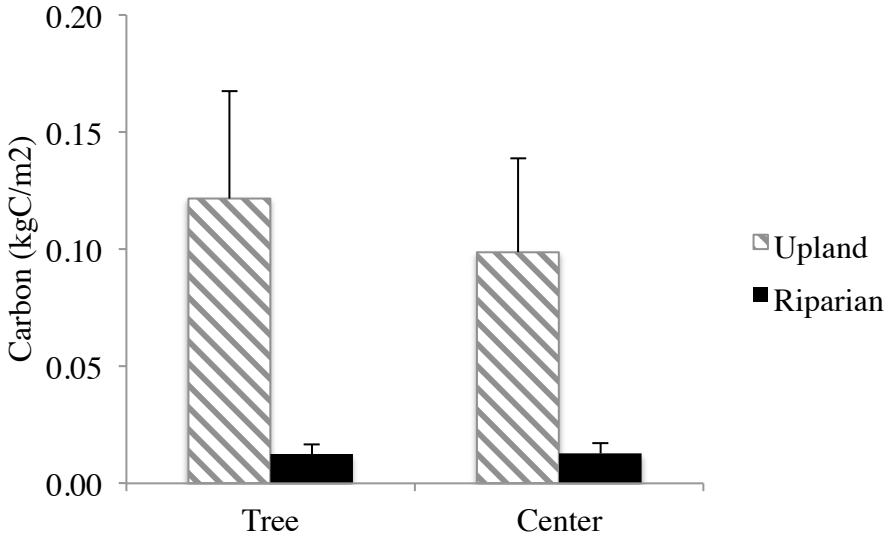

Figure 3.13 Fine Root Carbon Flux Based on Location: The flux of sequestered carbon into the fine root system was different between the upland and the riparian woodland. The flux of carbon in the fine root system was estimated near individual trees and the center areas. The carbon flux was not different between areas close to individual trees and the center areas. Error bars indicate one standard error.

3.6 Vine and Shrub Carbon

Vine biomass was estimated in the upland and riparian woodlands (Figure 3.14). Vine carbon differed between the upland and riparian woodlands ($p<0.001$). The riparian woodland had higher vine carbon compared to the upland woodland. Vine species contributed of 9.11 kg C/m^2 with a total of 6,147.63 g C in the sampled upland woodland and 68.69 kg C/m^2 with a total of 46,363.48 g C in the sampled riparian woodland.

The relationship between vine carbon and the rate of carbon sequestration into tree stems was estimated in the upland and riparian woodlands (Figure 3.15). A strong inverse relationship existed between vine carbon and tree stem carbon sequestration in the sampled riparian woodland. However, vine carbon had a weak inverse relationship tree stem carbon sequestration in the sampled upland woodland.

The carbon in woody shrub species was estimated in the upland and riparian woodlands (Figure 3.16). Shrub species grew in the upland sample area and shrub biomass contained a total of 89.206 kg C. However, no shrub species grew in the riparian sample area.

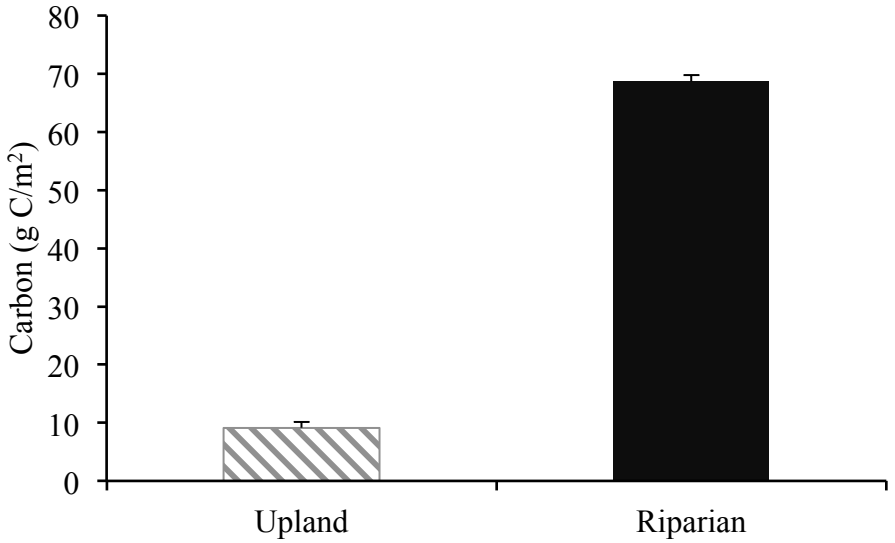

Figure 3.14 Vine Species Carbon Pool: Vine carbon was estimated in both the upland and the riparian woodlands. The riparian woodland contained more vine carbon compared to the upland woodland. Error bars indicate the standard error.

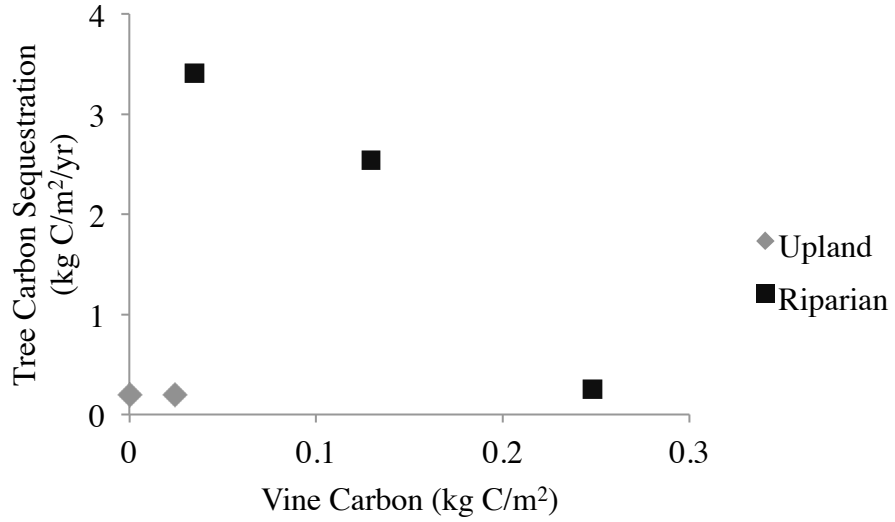

Figure 3.15 Vine Species Influence on Stem Carbon Sequestration: There was an inverse relationship between the amount of biomass of vine species and the carbon sequestration of tree species. High amounts of vine biomass limited the amount of carbon sequestration in the tree species.

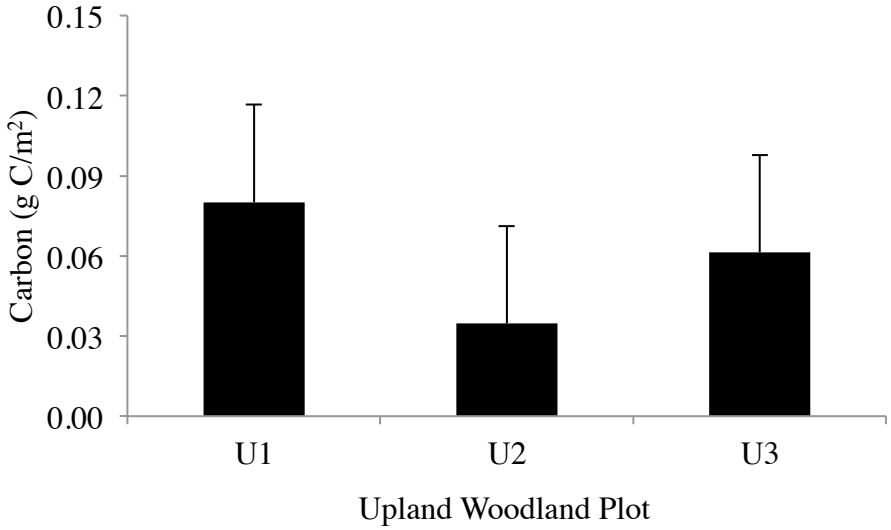

Figure 3.16 Shrub Species Carbon Pool: Shrub species were present in upland woodlands plots (U1, U2, U3). No shrub species were present in the riparian woodland. Error bars indicate one standard error.

3.7 Photosynthesis

The photosynthesis rate was estimated for upland and riparian woodlands under high and low light (Figure 3.17). Under high light, equal carbon absorption occurred during photosynthesis in the upland and riparian woodlands ($p= 0.76$). In the sampled upland woodland, an average of 20.98 g C/m^2/day with an estimated total of 14,162.51 g C/day was absorbed during photosynthesis. In sampled riparian woodland, an average of 24.13 g C/m^2/day with an estimated total of 16,287.51 g C/day was absorbed during photosynthesis. Under low light, carbon absorption during photosynthesis differed between the upland and riparian woodlands ($p=0.0003$). In the sampled upland woodland, an average 1.93 g C/m^2/day with an estimated total of 1,302.41 g C/day was absorbed during photosynthesis. In the sampled riparian woodland, the carbon dioxide absorbed during photosynthesis under low light was lower than the carbon dioxide released during autotrophic respiration. In riparian woodland, the net balance between respiration and

photosynthesis resulted in carbon release into the atmosphere at the rate of 3.36 g C/m^2/day with an estimated total of 2,266.09 g C/day.

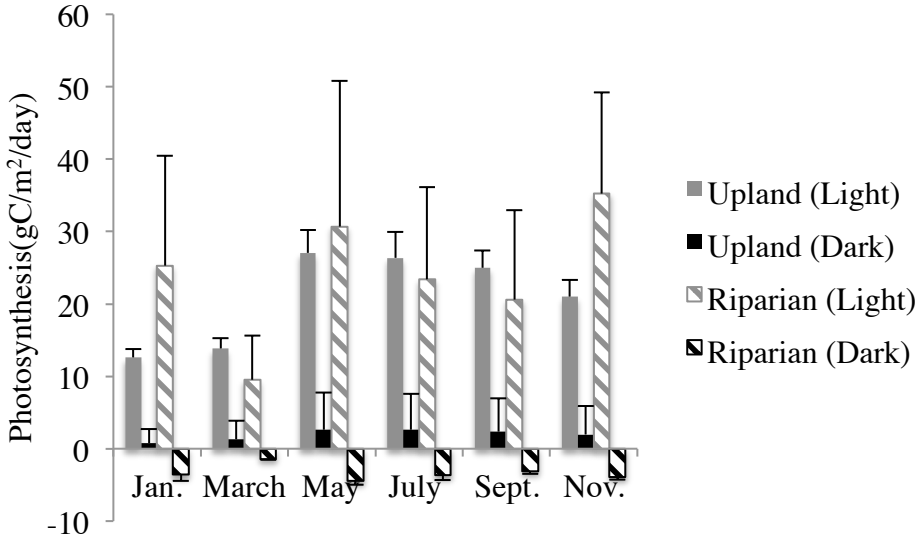

Figure 3.17 Photosynthesis, High and Low Light: Photosynthesis was estimated in the upland and riparian woodlands. The photosynthesis rates under high light were higher than those under low light. The photosynthesis rate under high light conditions was not different between the woodlands. The woodlands had different photosynthesis rates under low light. Error bars indicate one standard error.

3.8 Soil Moisture

Soil moisture was estimated for the upland and riparian woodlands during 2005-2007 and 2015-2016 (Figure 3.18). The average soil moisture decreased between 2005-2007 and 2015-2016 ($p= 0.005$).

Soil moisture decreased between 2005-2007 and 2015-2016 ($p= 0.005$) (Figure 3.19). However, soil moisture fluctuated on a seasonal basis during both time periods.

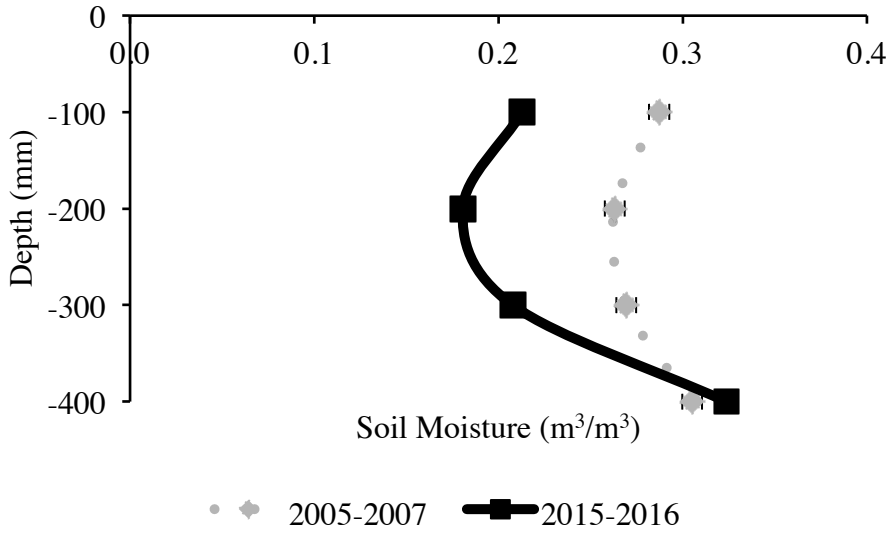

Figure 3.18 Soil Moisture Change Over Time: Soil moisture was estimated during 2005-2007 and 2015-2016. The soil moisture decreased over time. Error bars indicate one standard error.

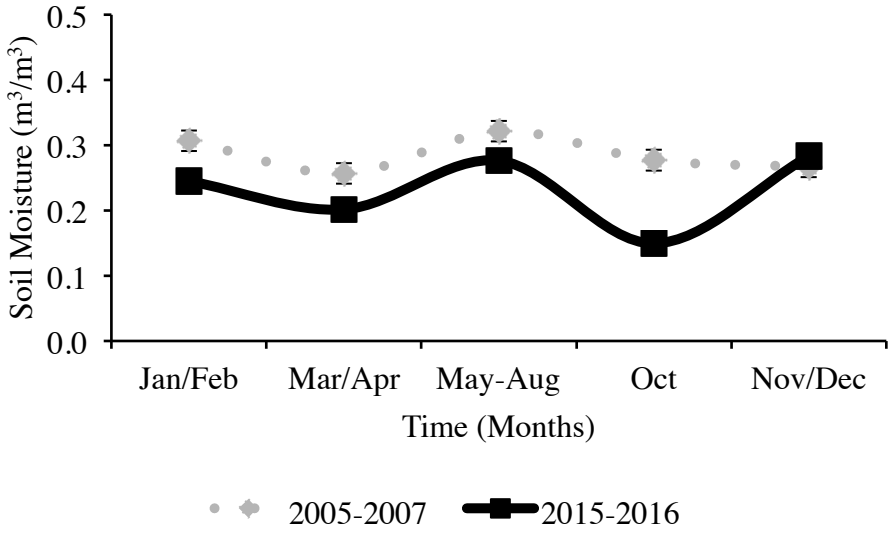

Figure 3.19 Soil Moisture Based on Season and Time: Fluctuations occurred in soil moisture during 2005-2007 and 2015-2016. The average 2005-2007 soil moisture was higher than the average 2015-2016 soil moisture. Error bars were based on standard error.

Soil moisture was estimated in the upland and riparian woodlands (Figure 3.20). The soil moisture was different between the upland and the riparian woodlands ($p= 0.0002$). Despite the proximity of the riparian woodland to the North Bosque River, the upland

woodland had higher soil moisture compared to the riparian woodland. The soil moisture fluctuated on a seasonal basis in the upland and riparian woodland (Figure 3.21); however, was consistently higher in the upland compared to the riparian woodland (p= 0.0002).

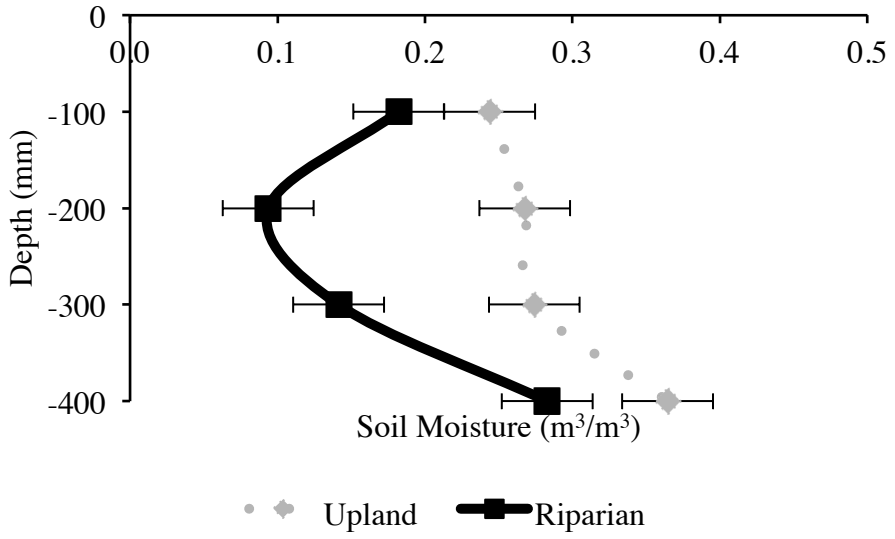

Figure 3.20 Soil Moisture Based on Habitat: The soil moisture was different between the two woodlands. Both woodlands had the same soil type. In addition, the riparian woodland was closer to the Bosque River system. However, the upland woodland has higher soil moisture than the riparian woodland. Error bars indicate one standard error.

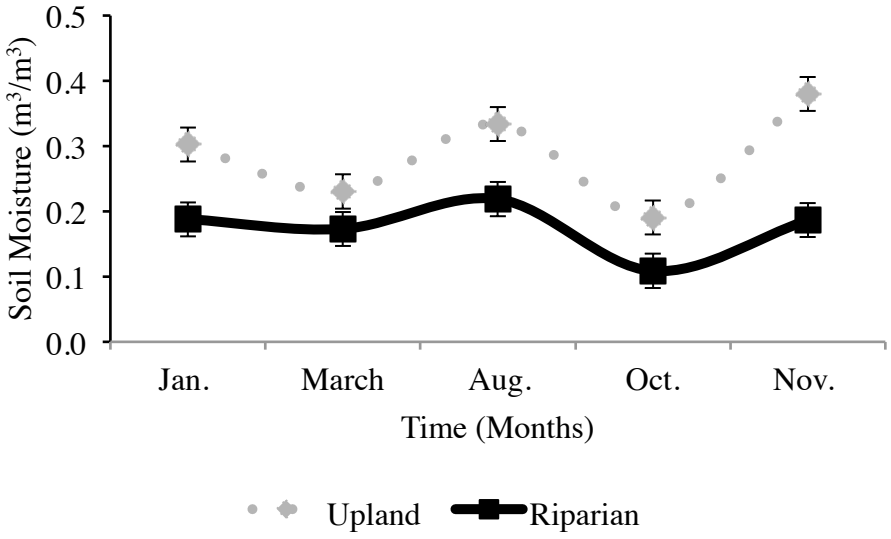

Figure 3.21 Soil Moisture Based on Season and Habitat: Fluctuations occurred in soil moisture of the upland and riparian woodlands. The average upland soil moisture was higher than the average riparian soil moisture. Error bars indicate one standard error.

3.9 Biome-BGC Model

The concentration of carbon in canopy biomass was based on the leaf area index (LAI). LAI was sensitive to atmospheric carbon dioxide concentrations (Figure 3.22). The comparison of observed LAI to modeled LAI under industrial carbon dioxide concentrations resulted in higher p-values than the comparison to modeled LAI under pre-industrial carbon dioxide concentration.

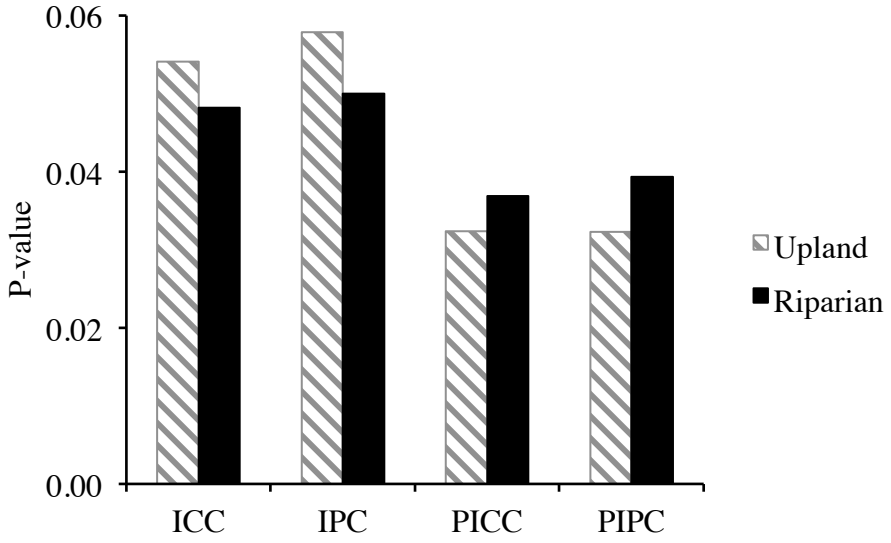

Figure 3.22 Observed and Modeled Leaf Area Index: Leaf area index was measured in the upland and riparian woodlands to estimate canopy carbon. Bars represent the p-value of modeled upland and riparian woodlands under industrial CO_2 and current climate (ICC), industrial CO_2 and past climate (IPC), pre-industrial CO_2 and current climate (PICC), and pre-industrial CO_2 and past climate (PIPC).

Stem carbon in the upland and riparian woodlands was not sensitive to atmospheric carbon dioxide or climate (Figure 3.23). The increase in atmospheric carbon dioxide and differences in climate did not have a significant influence on the carbon sequestration of tree stems. The comparison of observed stem carbon with modeled stem carbon under all carbon dioxide concentrations and climates resulted in equal p-values in the upland and riparian woodlands. The equivalent p-values indicated the stem carbon was equal under all modeled conditions.

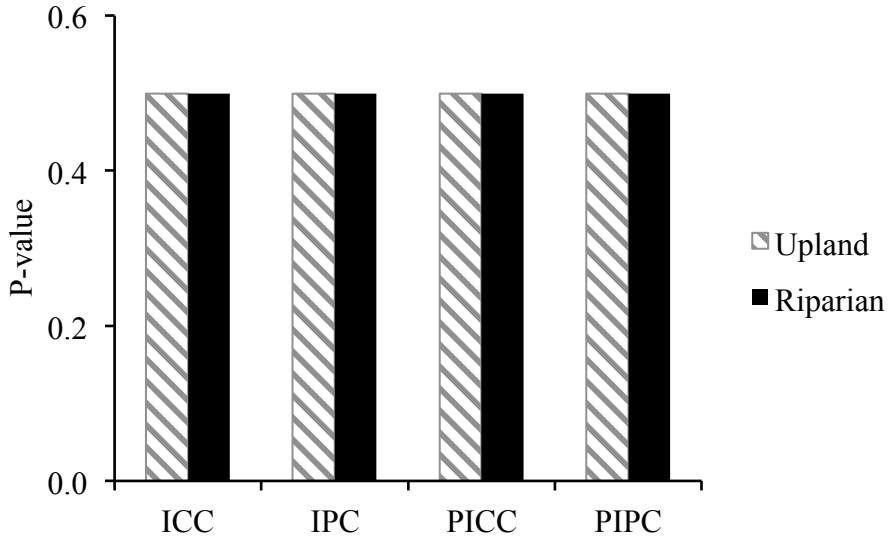

Figure 3.23 Observed and Modeled Live Stem: Live stem carbon was measured in 2005 and 2015. Bars represent the p-value of modeled upland and riparian woodlands under industrial CO_2 and current climate (ICC), industrial CO_2 and past climate (IPC), pre-industrial CO_2 and current climate (PICC), and pre-industrial CO_2 and past climate (PIPC).

Litter carbon was not sensitive to atmospheric carbon dioxide concentrations or climate in the upland and riparian woodlands (Figure 3.24). Litter carbon was consistent across woodland ecosystems and all modeled carbon dioxide concentrations and climates. The p-values indicated observed litter carbon was different from modeled litter carbon under all carbon dioxide concentrations and climates.

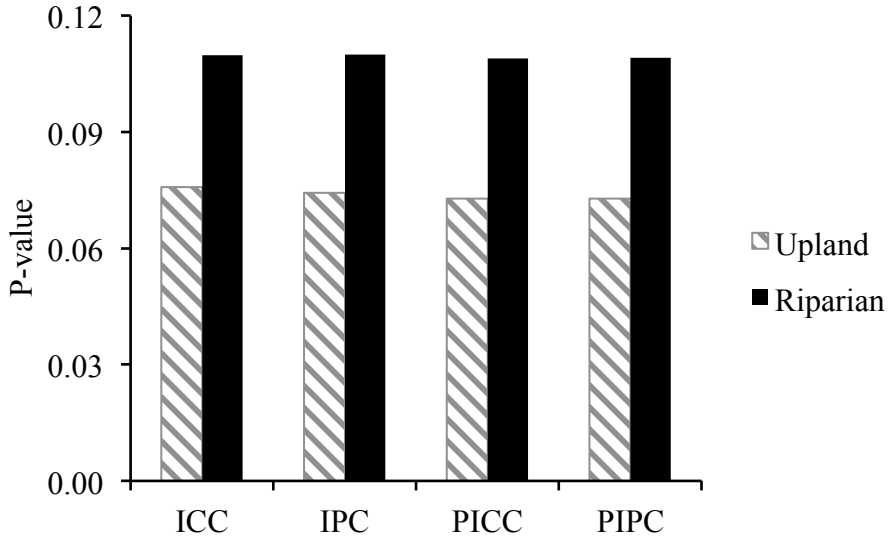

Figure 3.24 Observed and Modeled Litter: Litter fall was estimated for the upland and riparian woodlands. Bars represent the p-value of modeled upland and riparian woodlands under industrial CO_2 and current climate (ICC), industrial CO_2 and past climate (IPC), pre-industrial CO_2 and current climate (PICC), and pre-industrial CO_2 and past climate (PIPC). An average CO_2 concentration was compared between the observed data and the four simulations.

Carbon sequestration into fine root system was sensitive to atmospheric carbon dioxide in the upland woodland (Figure 3.25). The comparison of observed fine root carbon to modeled fine root carbon under industrial carbon dioxide concentrations resulted in higher p-values than the comparison to modeled fine root carbon under pre-industrial carbon dioxide concentrations. In the upland woodland, the average p-value was under industrial carbon dioxide 0.0799 and under pre-industrial carbon dioxide 0.0568. In the riparian woodland, the fine root system was not sensitive to atmospheric carbon dioxide or climate. The p-values indicated observed root carbon was different from modeled root carbon under all carbon dioxide concentrations and climates. . In the upland woodland, the average p-value was under industrial carbon dioxide 0.0261 and under pre-industrial carbon dioxide 0.0258.In the riparian woodland, the fine root carbon was not sensitive to atmospheric carbon dioxide or climate.

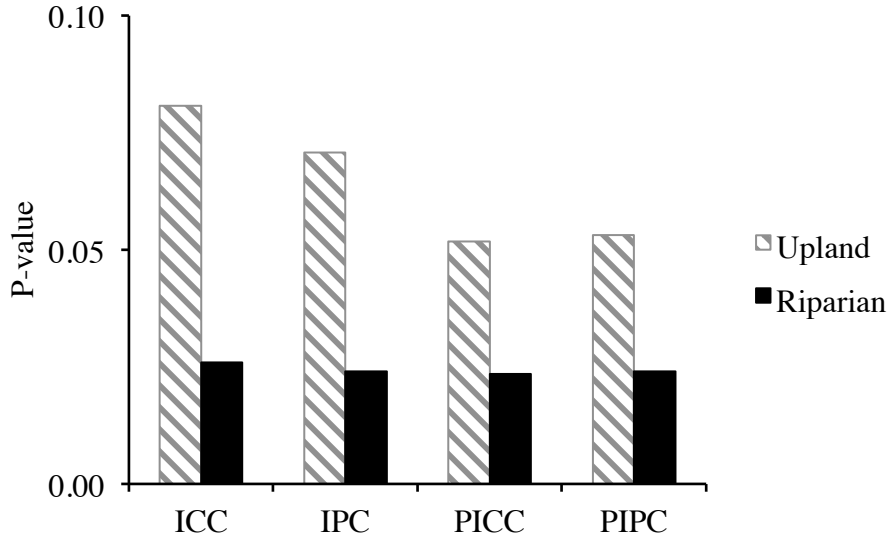

Figure 3.25 Observed and Modeled Fine Root: The amount of carbon was estimated in the fine root system. Bars represent the p-value of modeled upland and riparian woodlands under industrial CO_2 and current climate (ICC), industrial CO_2 and past climate (IPC), pre-industrial CO_2 and current climate (PICC), and pre-industrial CO_2 and past climate (PIPC).

The uptake of carbon dioxide through photosynthesis was sensitive to atmospheric carbon dioxide (Figure 3.26). Modeled photosynthesis under industrial carbon dioxide fit the observed photosynthesis. The comparison of observed photosynthesis to modeled photosynthesis under industrial carbon dioxide concentrations resulted in higher p-values than the comparison to modeled photosynthesis under pre-industrial carbon dioxide concentrations.

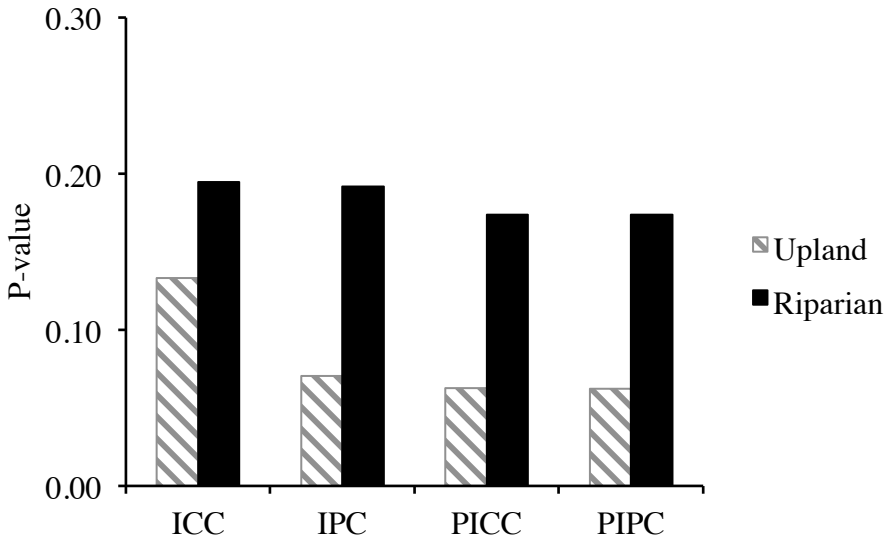

Figure 3.26 Observed and Modeled Photosynthesis: Photosynthesis measurements were used to estimate the carbon entering the ecosystems. Bars represent the p-value of modeled upland and riparian woodlands under industrial CO_2 and current climate (ICC), industrial CO_2 and past climate (IPC), pre-industrial CO_2 and current climate (PICC), and pre-industrial CO_2 and past climate (PIPC).

3.10 Result Summary

Table 3.1 Result Summaries: The carbon of the observed plant components are indicated as significantly different ($P<0.05$) or not significantly different ($P>0.05$) between habitats and over time.

Measurement	Habitat	Time
Canopy	P<0.05	P<0.05
Stem	P<0.05	P<0.05
Litter	P<0.05	P>0.05
Decomposition	P<0.05	
Roots	P>0.05	
Root Growth	P<0.05	
Photosynthesis	P>0.05	
Soil Moisture	P<0.05	P<0.05

CHAPTER FOUR

Discussion

4.1 Canopy Carbon

The canopy carbon was higher in the upland woodland than the riparian woodland. Upland woodland trees invested more carbon resources into the growth of canopy biomass compared to riparian woodland trees. Species composition of the upland and riparian woodlands was a potential explanation for the difference in canopy carbon. Tree species vary in foliage characteristics (Wright et al. 2001). The specific leaf area (m^2/g) varied between tree species, which indicated the difference in species composition affected the woodland canopy carbon.

Canopy carbon increased between 2005-2007 and 2015-2017. The atmospheric carbon dioxide emissions concentrations increased over a short time period due to anthropogenic carbon emissions (Lal 2004). The increase in canopy carbon was potentially due to increased availability of carbon dioxide for photosynthetic uptake and conversion to canopy biomass. Over time, woodland trees devoted an increasing portion of absorbed carbon resources to the growth of canopy biomass. Woodland ecosystems under high carbon dioxide concentrations allocate roughly half the carbon uptake to short-lived tissue, including foliage in the canopy (Schlesinger and Lichter 2001).

4.2 Stem Carbon

The tree stem carbon increased between 2005 and 2015. The upland and riparian woodlands differed in the amount of stem carbon. The riparian woodland supported higher stem carbon compared to the upland woodland, which indicated that trees in the riparian woodland allotted more carbon resources to the growth of tree stems. The riparian woodland is a transition zone between aquatic and terrestrial ecosystems, while the upland woodland is terrestrial ecosystem (Gregory et al. 1991). The upland and riparian woodlands were defined by different habitat characteristics. Habitat differences between upland and riparian woodlands possibly influenced the stem carbon and the rate of carbon sequestration into stem biomass (Gregory et al. 1991). In addition, species composition provided a potential explanation for the difference in stem carbon between the upland and riparian woodland (Yao et al. 2012, Kohyama et al. 2003). In contrast, habitat and species composition did not result different carbon release rates between the upland and the riparian woodlands.

The carbon sequestered in stem biomass in the woodlands was higher than carbon released, which increased the stem carbon over time. The balance between carbon sequestration and release determined the carbon budget in the upland and riparian woodlands (Heimann and Reichstein 2008). The carbon budget based on carbon sequestration and release resulted in a higher net carbon sequestration into tree stems within the riparian woodlands compared to the upland woodland.

The carbon in young trees was not different in the upland and riparian woodlands. There were more young individuals in the upland woodland compared to the riparian

woodland. The species composition possibly explained the similarity in young tree carbon coinciding with difference in the number of individuals (Kohyama et al. 2003).

4.3 Litter Carbon

Increasing atmospheric carbon dioxide typically resulted in higher rates of litter fall (Schlesinger and Lichter 2001). The canopy carbon increased between 2005-2007 and 2015-2016, which did not result in a correlating increase litter fall. The annual litter carbon observed in the upland and riparian woodlands did not change between 2005-2007 and 2015-2016.

Leaf litter carbon was dominant, which suggested trees allotted a large portion of carbon resources into the production of leaves for the purpose of photosynthesis and gas exchange (Yao et al. 2012). However, woody litter carbon increased and seed litter carbon decreased over time. Plants sequestered more carbon into biomass with increasing atmospheric carbon dioxide (Heimann and Reichstein 2008). Tree species increased carbon sequestration into woody material in correlation with the rise in atmospheric carbon dioxide concentrations. However, increased carbon sequestration into woody litter material potentially occurred at the expense of carbon sequestration into seed litter carbon and resulted in the maintenance of the leaf litter carbon.

4.4 Litter Decomposition

Litter decomposition was dependent on climate (Aerts 1997). The climate and soil type were the equivalent in the upland and riparian woodlands, which created similar conditions for litter decomposition between the woodlands. However, the soil moisture was higher in the upland woodland compared to the riparian woodland. The litter material

decomposed at different rates in the upland and the riparian woodland. Litter material decomposed at higher rates in the upland woodland compared to the riparian woodland.

The different types litter decomposed at different rates. Deciduous leaf and seed litter material decomposed at relatively fast decomposition rates in comparison with other litter types. However, *J. ashei* leaf and *Q. fusiformis* leaf litter material decomposed at a relatively slow decomposition rate in comparison with other litter types. The decomposition of litter was also dependent on the chemistry of litter material (Aerts 1997). The chemical composition of litter dictates the decomposer activity (Hattenschwiler et al. 2005). The chemical composition of the evergreen and woody litter material was likely slowed the decomposition rate. In addition, the chemical composition of the deciduous leaf and seed litter material allowed for quick decomposition rate.

Some litter samples increased in biomass, possibly due to an addition to the litterbags during decomposition. Increases in sampled biomass may originate from decomposers (microbes, microorganisms, fungus, etc.) in the litterbags during the decomposition process (Hattenschwiler et al. 2005). In addition, the litter or bagging material was potentially not completely dried of moisture from precipitation.

4.5 Root Carbon

The riparian woodland is a transition zone between aquatic and terrestrial ecosystems, which resulted different ecosystem characteristics from the terrestrial upland woodland (Gregory et al. 1991). The root carbon pool was equal between the upland and riparian woodland. The root carbon pool was not influenced by habitat differences between the upland and riparian woodlands. The location of the riparian woodland in proximity to the North Bosque River did not alter the fine root carbon pool in comparison

to the upland woodland. Woody plant species maintain a similar structure of fine root system (Pregitzer et al. 2002). The different species composition between the upland and riparian woodland did not control the root carbon pool (Kohyama et al. 2003).

The growth rate of the fine root system was higher in the upland woodland than the riparian woodland. The difference in carbon flux between the woodlands indicated trees in the upland woodland allotted more carbon resources for root growth than trees in the riparian woodland. Although the proximity of the North Bosque River did not influence the fine root carbon pool, the river location did potentially affect the flux of carbon into the root system. Flooding possibly limited fine root growth (Kreuzwieser et al. 2004). Flooding of the riparian woodlands occurred during the summer of 2016 and conceivably led to the difference in fine root carbon allocation between the upland and riparian woodlands. The frequency and depth of flooding were higher in the riparian woodland than the upland woodland, which led to a high influence of flooding on the riparian woodland. In contrast, there was no major flooding in the upland woodland, which resulted in little influence of flooded soils on the growth of the fine root system.

The carbon pool and flux were not different between individual trees and centered areas. Plant competition for resources and nutrients within the soil occurs through the belowground root system (Casper and Jackson 1997). Competitive strategies include the growth of a root system below the shallow root system of other species, which resulted in potential overlap in root systems. Many woody plants absorb resources from both shallow and deep soil layers. However, some plant species avoid belowground overlap of the root system to reduce competition. The fine root system extends from individual trees. The similarity in the fine root system next to individual trees and in open areas

possibly occurred due to the extension and overlap in the root systems of individual trees. In a woodland ecosystem, the growth of individual tree decreased with increased tree density (Burkes et al 2003). Under high density, individual tree invest resources in tree stems and lower resources towards foliage and roots. The upland and riparian woodlands have similar tree densities, which likely leads to similar pressure on the fine root system. The upland and riparian woodlands allow for similar growing spaces for the growth of the fine roots.

4.6 Vine and Shrub Carbon

The vine carbon was different between the upland and riparian woodlands. The riparian woodland supported a higher vine carbon. Habitat differences potentially influenced the growth and carbon sequestration of vine species (Gregory et al. 1991). The ecosystem characteristics of the transitional riparian and terrestrial upland woodland conceivably resulted in different amounts of vine carbon.

The vine biomass affected sequestration of carbon in the tree stem. There was a strong inverse relationship in the riparian woodland. High amounts of vine biomass placed strong limitations on carbon sequestration into stem biomass of tree species. In contrast, the vine biomass placed weak limitations on tree carbon sequestration in the upland woodlands. Vine biomass had a weak influence on the carbon sequestration into tree stems in the upland woodland. The low correspondence was potentially due to lower vine biomass in the upland woodland. Habitat characteristics potentially explained the difference in vine and tree relationship (Gregory et al. 1991).

Shrub species only grew in the upland woodland, indicating habitat differences between the woodlands sites Riparian zones typically contain hydric soils, which formed

under flooded conditions (Gregory et al. 1991). The hydrophilic plant community characterizes riparian zones. The hydrophilic plant community of a riparian zone was dependent on the hydrology of the ecosystem. The hydric soils and hydrology of the riparian zone may limit shrub species in the riparian woodland. The characteristics of the riparian woodlands, including the frequency and depth of flooding, potentially limit the shrub biomass in the riparian woodland (Kreuzwieser et al. 2004).

4.7 Photosynthesis

The photosynthesis rate was equal between the upland and riparian woodlands under high light. In contrast, the rate of photosynthesis was different between woodlands under low light. The photosynthetic capacity of tree species depended on characteristics of the species, including nitrogen concentrations and the specific leaf area (SLA) (Reich et al. 1995). The characteristics differ between tree species, which indicated species composition differences between the woodlands conceivably explained the difference in photosynthesis under low light. Habitat differences provide a potential explanation for the difference in the photosynthetic rate. The riparian woodland experienced more flooding compared to the upland woodland. Flooding may limit gas exchange in foliage during photosynthesis (Kreuzwieser et al. 2004). Flooding limits gas exchange through reduced stomatal conductance and high carbohydrate concentrations in the leaves. Stomatal closure signals potentially occur in roots, which may be altered under flooded conditions. In addition, decreased stomatal conductance may be caused by changes to water conductance between the plant and soil, which leads to decreased water potentials. Enhanced starch and sugar accumulation occurs in leaves under flooded conditions due to reduced phloem translocation from shoot to roots. The influence of flooding on gas

exchange possibly explained the release of carbon dioxide under low light in the riparian woodland while the upland woodland foliage absorbed carbon dioxide.

4.8 Soil Moisture

As expected, the soil moisture of the woodlands changed over time. The soil moisture decreased between 2005-2007 and 2015-2017. Climate change alters precipitation possibly affecting soil moisture in the woodlands (Heimann and Reichstein 2008). Climate change increases the frequency of flooding of ecosystem, which increased soil moisture. In contrast, climate change likely increased vegetation growth that increased the demand for moisture by woodland vegetation and decreased soil moisture.

The soil moisture was different between the upland and riparian woodlands with the upland woodland found to have higher soil moisture than the riparian woodland. Alterations to the soil characteristics determined the ability to hold moisture. For example, soil compaction decreases the ability of the soil to become saturated with moisture (Hamza and Anderson 2005). The flooding of the riparian zone possibly altered the soil moisture by changing soil characteristics and the moisture capacity of soil within the riparian zone (Naiman and Decamps 1997). In addition, the riparian woodland supported a higher amount of plant biomass, which plausibly increased the water demand from vegetation. The high demand for water decreased the amount of soil moisture available.

The moisture available to the plants potentially determined the carbon sequestration into plant biomass (Heimann and Reichstein 2008). The high soil moisture was associated with the rate of photosynthesis, canopy carbon, and the carbon flux into the fine root system. In the upland woodland, high soil moisture but lacked the high

frequency of flooding. The high soil moisture of the upland woodland was associated with the higher photosynthetic rate under low light conditions and the high amount of canopy carbon. The upland woodland experienced limited flooding, which was also associate with higher the carbon-flux into the root system. In comparison, the riparian woodland had lower soil moisture, which was associated with the lower photosynthesis under low light and the lower canopy carbon. In addition, the high amount of flooding in the riparian woodland was associated with limited carbon flux into the fine root system. The flooding of the riparian woodland slowed the fine root carbon growth and influenced the amount of canopy carbon and the rate of photosynthesis (Kreuzwieser et al. 2004). However, soil moisture had an inverse relationship with stem carbon and litter carbon. The stem and litter carbon were lower in the upland woodland and higher in the riparian woodland, despite the low soil moisture in the riparian woodland in comparison to the upland woodland.

During 2005-2007 and 2015-2016, the soil moisture fluctuated on a seasonal basis. The changing precipitation throughout the year resulted in the fluctuations in soil moisture in the upland and riparian woodlands. Vegetation growth during the growing seasons possibly explained dips in soil moisture as plants absorbed moisture during growth. In addition, the slowed vegetation growth likely contributed to peaks in soil moistures. Both 2005-2007 and 2015-2016 experienced periods of flooding, which potentially increased soil moisture levels. During both time periods, the flooding occurred in the May-August seasonal period.

The majority of roots were found within the top 30 cm of the soil (Casper and Jackson 1997). Soil moisture decreased at the 30 cm depth. The fine root system absorbs

nutrients and water, which resulted in decreased soil moisture within the zone of the fine root system. In addition, the roots potentially change the soil characteristics, which may alter the reading of the equipment used for soil moisture estimation. Soil with pockets of air or a loose structure decreased the precision of the reading.

4.9 Climate and CO_2 Sensitivity Modeling

From the model simulations, the woodland canopy carbon was sensitive to atmospheric carbon dioxide concentrations. Atmospheric carbon dioxide concentrations likely increased the availability of carbon dioxide during photosynthesis (Yao et al. 2012). Woodland trees allocated a high percentage of absorbed carbon into foliage. More carbon resources were allotted for the growth of the canopy biomass as atmospheric carbon dioxide concentrations increased. However, canopy carbon was less sensitive to differences in climate. Climate factors potentially had a minor effect on carbon sequestered into canopy biomass.

The observed stem carbon in the upland and riparian woodlands increased over time. However, the stem carbon was not sensitive to atmospheric carbon dioxide or climate. The p-values of the t-test indicate stem carbon was equivalent under all conditions, which implied no influence of carbon dioxide or climate. Even as atmospheric carbon dioxide increased, the carbon sequestration into stem biomass was likely enhanced or limited by other environmental factors (Beedlow et al. 2004). The increased atmospheric carbon dioxide concentrations potentially significantly affected young tree growth, while having limited influence on mature trees (Asshoff et al. 2006). The observed growth of tree stems possibly occurred in individuals that had not reached maturity. Climate had no major influence on stem carbon. The difference in climate was possibly too small to

result in a major influence on stem carbon as stem growth has been shown to drastically change in other climate change studies (Ryan et al 1995). Direct carbon dioxide fertilization appears to have a limited impact on the growth of the stem carbon in comparison to temperature and precipitation (Graunlich, 1991). However, trees under low climatic stress may experience a carbon dioxide fertilization effect. The limited response to atmospheric carbon dioxide or climate was potentially due to the slow response of tree stems to changing conditions. The drastic change in growth rate with changing conditions also potentially affects the response of tree stems to climate and atmospheric carbon dioxide (Brubaker 1986). Trees convert more carbon resources to biomass under good climate conditions compared to harsh climate conditions. However, a lag in the effect of climate change on trees exists due to the long lifespans of most tree species.

Litter carbon was not sensitive to atmospheric carbon dioxide concentrations or climate, an interesting result as canopy carbon was found to be sensitive to atmospheric carbon dioxide concentrations. There was no change in the overall litter fall over time. However, there was an increase in woody litter material and a decrease in seed litter material. Stress factors may limit the seed production of plant species (Young et al. 2004). Stress altered the physiological conditions caused by factors that disrupted the equilibrium (Jaleel et al. 2009). Plants were exposed to stress factors, including drought and flooding, high and low temperatures, or oxidative stress. Other factors affected the changing proportion of litter, the amount of litter falling from the canopy, and the amount of biomass carbon within each litter type while carbon dioxide and climate had little effect.

The fine root carbon was sensitive to atmospheric carbon dioxide in the upland woodland likely associated with enhanced the fine root growth such as in the upland woodland (Zachos et al. 2008). Plants in woodland ecosystems often respond to a rise in atmospheric carbon dioxide by increasing the carbon allocation to the roots (Lipson et al. 2014). However, the fine root system in the riparian woodland was not influenced by carbon dioxide or climate. The limited effect of atmospheric carbon dioxide and climate indicated other factors altered the fine root system in the riparian woodland. The difference in effects by carbon dioxide and climate were plausibly due to differences in habitat. The location of the riparian woodland relative to the North Bosque River possibly altered fine root growth (Kreuzwieser et al. 2004). Also, high occurrence of flooding in the riparian woodland compared to the upland woodland overrode any atmospheric carbon dioxide or climate affect. The clay soils became waterlogged during flooding and conceivably limited the growth of the fine root system in the riparian zone. The oxygen deprivation due to anoxia associated with flooding influences carbon metabolism of plant roots. Plants slow root growth and other energy consuming processes under flooded conditions and decrease the demand for carbon. Photosynthesis can also be influenced as stomatal closure increases due to the altered closure signals that occur in roots. The leaf water potential may potentially decrease as the stomata closure changes.

Photosynthesis was affected by the increased availability of atmospheric carbon dioxide (Ryan 1991). The carbon dioxide available in the atmosphere can enhance or limit the amount of carbon dioxide sequestered into plant biomass. The atmospheric carbon dioxide concentrations increased over time, which resulted in higher carbon uptake during photosynthesis (Zachos et al. 2008).

4.10 Conclusions

The woody tree carbon differed between the upland woodland (Figure 4.1) and the riparian woodland (Figure 4.2).

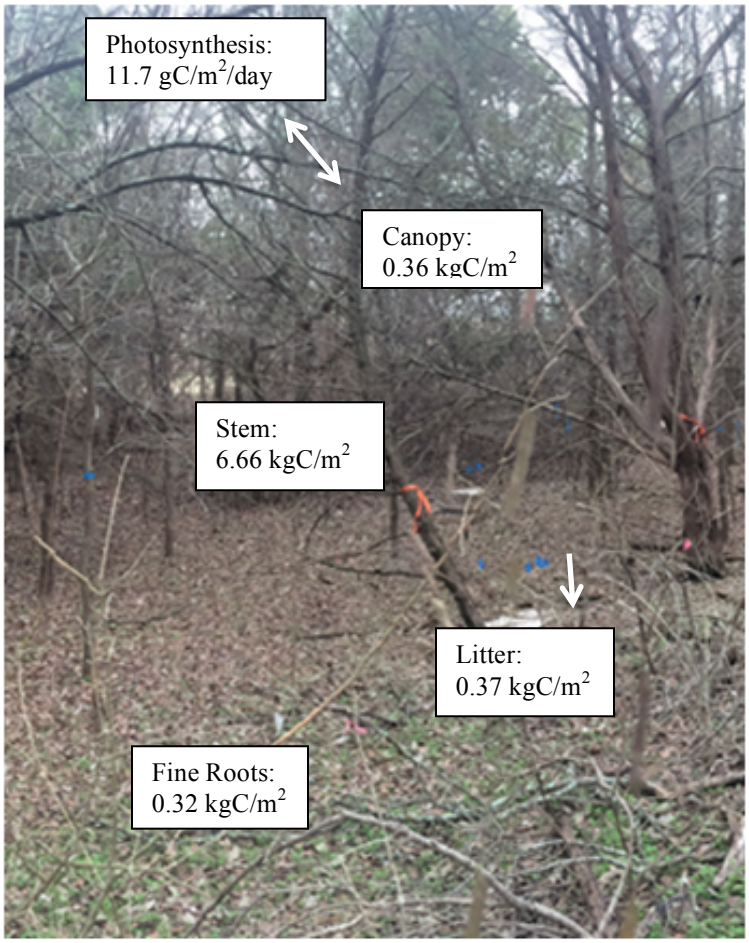

Figure 4.1 Upland Carbon Pools: Different carbon pools in woody tree species were estimated in the upland and riparian woodland.

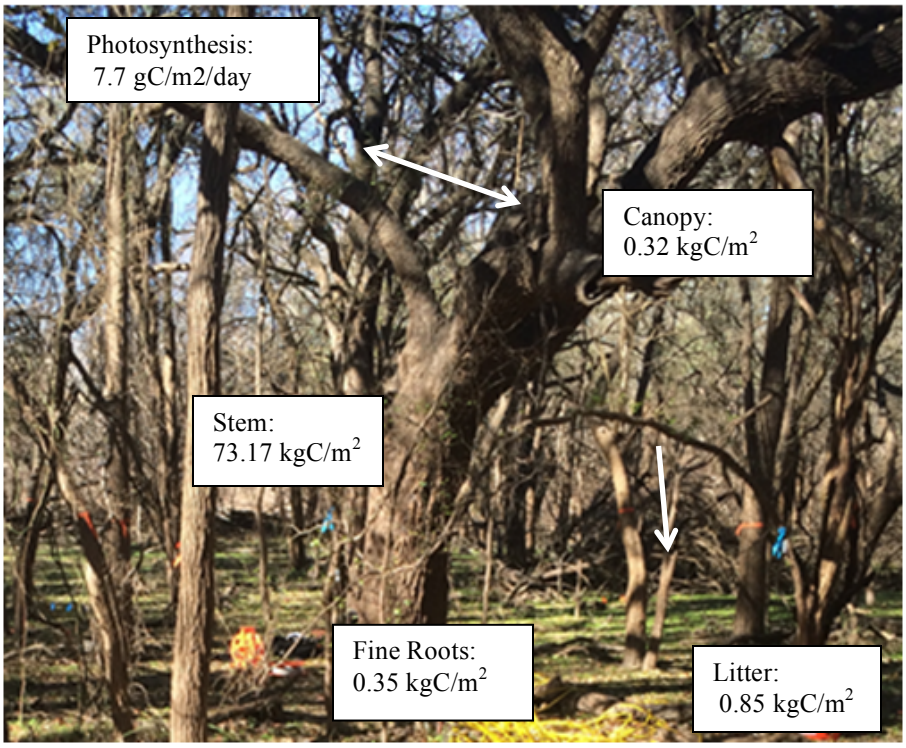

Figure 4.2 Riparian Carbon Pools: Different carbon pools in woody tree species were estimated in the upland and riparian woodland.

The woodland carbon budgets were associated with habitat differences between the upland and riparian woodlands. The total carbon in the tree stem and canopy was different between the upland and riparian woodlands. The fine root carbon pool was not different between the upland and riparian woodlands; however, the carbon flux into the fine root system was different between the woodlands. The canopy carbon, including foliage and branches, and fine root carbon did not influence each other. The upland woodland had more carbon in the canopy compared to the riparian woodland; however, the upland and riparian woodland had the same amount of carbon in the fine root system. The carbon in the canopy and root systems do not limit or enhance the capacity of carbon sequestration into the other. The upland woodland had more carbon in the canopy but no

more carbon in the form of litter material compared to the riparian woodland. The increase in canopy carbon did not coincide with an increase in the amount of litter carbon over time. The increase in the woody debris slows the decomposition rate of litter and decreased the woody-to-foliage ratio (Dearden et al 2006). The foliage in the canopy increased; however, the proportion of leaf litter in total litter material did not change over time as the woody litter proportion increased.

The canopy carbon and carbon taken up by photosynthesis did not correspond with each other. The upland woodland had higher canopy carbon compared to the riparian woodland; however, under high light conditions, the upland woodland did not have higher photosynthesis rates than the riparian woodland. The decline of photosynthesis efficiency occurred in leaves under low light (Kitao et al 2000). Species vary in shade tolerance. The upland woodland trees absorbed carbon under low light while the riparian woodland trees released carbon, which suggested that the upland woodland trees had a higher shade tolerance.

I found the woodland carbon budgets changed over time. The amount of stem biomass measured in 2005 differed from the stem biomass measured in 2015. There was a significant increase between 2005 and 2015. The abundance of total litter biomass did not change over time. The increase canopy biomass did not result in an increase in the amount of litter.

The soil moisture was different between the upland and riparian woodlands although both woodlands had the same soil type. The Biome-BGC model investigated the carbon sequestration in the context of climate and increased atmospheric carbon dioxide levels. The Biome-BGC model indicated that the growth of the woodland systems was affected

by climate, carbon, and water. The growth in the woodlands was distinguished from natural growth. Overall, climate, increased atmospheric carbon dioxide, or both affected the sequestration of carbon into tree species in the woodlands.

4.11 Future Carbon Budgets

The climate is expected to change further in the future in central Texas (climatewizard.org). Compared to the past fifty years, the mean temperatures are expected to increase from 15.6 to almost 26.7 °C by 2080. In addition, the precipitation is expected to change from an average of 912mm to 950 mm.

The carbon dioxide concentrations will likely increase in the upland and riparian woodlands of the Lake Waco Wetlands by the year 2100. The projected carbon dioxide by 2100 varies based on future climate change mitigation strategies (IPCC, http://www.ipcc-data.org/observ/ddc_co2.html). Depending on climate mitigation strategies, the future carbon dioxide concentration would range from nearly 600 ppm to almost 1,000 ppm.

From my study, projections for continues increase in atmospheric carbon dioxide concentrations will contribute most to the carbon budgets of the woodlands at the Lake Waco Wetlands. The leaf area index (LAI) increased over time and is sensitive to the increase in atmospheric carbon dioxide. The continuing increase in atmospheric carbon dioxide will lead to future higher in the LAI, which will result in an increase in canopy carbon and canopy surface area. The surface available for leaf gas exchange will increase in woody vegetation. The adjusted leaf gas exchange will increase photosynthesis absorption of carbon dioxide and the release of water during transpiration. This relationship is reflected in the sensitivity of photosynthesis to the increase in atmospheric

carbon dioxide. Transpiration rates may rise with increased leaf surface area; however, the observed soil moisture decreased over time. As soil moisture decreases in the future, the primary productivity of the woodland ecosystem will be limited due to the lower water availability.

The increase in carbon dioxide absorption allows for the increase in root biomass, as reflected by the sensitivity of roots to atmospheric carbon dioxide. Root growth increases the demand for carbon resources, the increased atmospheric carbon dioxide will allow for higher root growth in the future. In contrast, future climate change will slow root growth due to the increased risk of flooding. Observed data indicates that deep floods slow root growth due to the decreased oxygen levels of the soil.

The observed stem carbon increased but was not sensitive to atmospheric carbon dioxide. The stem carbon changed over time and will change in the future due to climate change or other stress factors. However, the response of the stem carbon to increased atmospheric carbon dioxide will require time and drastic changes to the climate. Litter carbon did not change over time and was not sensitive to atmospheric carbon dioxide. As atmospheric carbon increases in the future, the litter carbon will be slow to adjust. While the amount of litter carbon may not drastically change in the future, the decomposition of litter will potentially change based on climate change and changes in soil moisture. Higher observed decomposition rates were associated with higher soil moisture; however, decreased soil moisture over time may lead to slowed decomposition rates. Slowed decomposition will slow the amount of carbon dioxide released from soil microbes into the atmosphere.

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