

ABSTRACT

Fire Disturbance Effects on Regional Carbon Cycling in a Sub-humid Woodland

Jian Yao, Ph.D.

Mentor: Joseph D. White, Ph.D.

Fire disturbance affects many ecosystem processes, especially carbon (C) cycling. In addition, fire is routinely used as a management tool in wildland ecosystems. In this study, I measured the fire-affected C storage, vegetation composition, habitat suitability for an endangered bird species (golden-cheeked warble), and charcoal content in juniper-oak woodlands with documented past surface fires within Balcones Canyonlands National Wildlife Refuge. Using this information, I modified a process-based model of ecosystem biogeochemical cycling (Biome-BGC) to simulate the effects of different fire types, the production and loss of fire-derived charcoal, and the charcoal effects on soil water availability. From my field measurements, I found significantly different total aboveground biomass C with average values of 5.25, 6.86, and 9.18 kg m⁻² for 60 plots with known fire histories that categorized into the recent (<40 year), old (≥40 year), and no fire group, respectively. These data also showed that higher oak recruitment was associated with fires that occurred in years with low summer precipitation. I concluded that fire may have a dual effect on habitat suitability with catastrophic wildfire damaging potential habitat and significantly reducing regional C storage, and moderate intensity

fires in dense young juniper stands promoting tree species diversity. From the laboratory analysis of soils derived from these same plots, I estimated that the regional average soil charcoal concentration to be $1.40 \text{ g C kg}^{-1} \text{ soil}$ ($20.8 \text{ g C kg}^{-1} \text{ SOC}$) based on the methods of ^{13}C nuclear magnetic resonance and mid-infrared spectroscopy, with fire-affected sites having significantly higher soil charcoal concentrations than the non-fire sites. I calculated the regional annual soil charcoal loss rate to be 4.7%, potentially due to soil erosion on steep slopes. Finally, the modified Biome-BGC model was able to reasonably simulate fire-affected C and charcoal storage changes. The model also indicated that the effects of fire on the ecosystem properties (vegetation C, leaf area index, and net ecosystem exchange) were closely associated with the severity of fire. The fire-derived charcoal did not appear to have significant effects on the simulated ecosystem properties. My results provided detailed ecological information regarding fire-affected processes in these woodland ecosystems.

Fire Disturbance Effects on Regional Carbon Cycling in a Sub-Humid Woodland

by

Jian Yao, B.S., M.S.

A Dissertation

Approved by the Institute of Ecological, Earth, and Environmental Science

Joseph D. White, Ph.D, Chairperson

Submitted to the Graduate Faculty of
Baylor University in Partial Fulfillment of the
Requirements for the Degree
of
Doctor of Philosophy

Approved by the Dissertation Committee

Joseph D. White, Ph.D., Chairperson

Rebecca J. Sheesley, Ph.D.

Sascha Usenko, Ph.D.

Steve I. Dworkin, Ph.D.

William C. Hockaday, Ph.D.

Accepted by the Graduate School
December 2012

J. Larry Lyon, Ph.D., Dean

Page bearing signatures is kept on file in the Graduate School.

Copyright © 2012 by Jian Yao

All rights reserved

TABLE OF CONTENTS

TABLE OF CONTENTS.....	v
LIST OF FIGURES	vii
LIST OF TABLES	viii
LIST OF ABBREVIATIONS.....	ix
ACKNOWLEDGMENTS	xi
CHAPTER ONE	1
Introduction.....	1
Climate Change and Carbon Cycling.....	1
Fire Disturbance	2
Wildland Fire Management	3
Study Area Description.....	4
Study Objectives	6
CHAPTER TWO	7
Fire Effects on Carbon Sequestration and Vegetation Composition, and its Implications on Habitat Managements	7
Introduction.....	7
Methods.....	9
Plot Selection	9
Field Survey	10
Laboratory Analysis.....	12
Carbon Storage Assessment.....	12
Community Composition and Habitat Analysis	15
Statistical Comparison	16
Results.....	18
Aboveground Biomass Carbon	18
Soil C and N.....	19
Community Composition.....	21
Habitat Suitability	22
Discussion	23
Fire Effects on Carbon Sequestration	23
Fire Effects on Soil Geochemistry	27
Fire Effects on Community Composition	28
Fire Effects on Habitat Suitability	32

Implications for Fire Management: Balancing the Carbon Sequestration and Habitat Conservation.....	32
CHAPTER THREE	36
The Storage Change of Fire-derived Soil Charcoal in a Sub-humid Woodland	36
Introduction.....	36
Methods.....	38
Soil Sampling.....	38
Estimation of Total Soil Charcoal using the ¹³ C NMR Method	39
Estimation of Total Soil Charcoal using MIRS	43
Statistical Comparison	45
Results	45
Charcoal Estimated by ¹³ C NMR.....	45
Charcoal Estimated by MIRS	47
Discussion	51
Charcoal in the Ecosystem.....	51
Comparison between the BD and CP NMR	54
Factors Related to MIRS Predicted Charcoal	56
CHAPTER FOUR.....	58
Modeling Ecosystem Property Changes due to Fire Disturbance	58
Introduction.....	58
Methods.....	60
The Biome-BGC Model.....	60
Model Modification	63
Simulated Vegetation Types	68
Model Simulation and Statistic Comparison	69
Results	72
Fire Effects on Ecosystem Properties	72
Production and Loss of Fire-derived Charcoal	74
Effects of Vegetation Types and Fire Seasons	76
Soil Charcoal Effects on Ecosystem Properties.....	76
Discussion	78
Model Modification	78
Fire Effects on Ecosystem Properties	80
Simulated Charcoal Production and Loss	81
Effects of Vegetation Types and Fire Seasons	82
Charcoal Effects on Ecosystem Properties	83
Summary of Future Model Work.....	84
CHAPTER FIVE	86
Conclusions.....	86
REFERENCES	89

LIST OF FIGURES

Figure 1. The locations and tract boundary of the BCNWR.....	10
Figure 2. The average total biomass C for each fire group.....	19
Figure 3. Tree density of each species type for the three fire groups	20
Figure 4. nMDS ordination of the species tree density data	22
Figure 5. The mean habitat suitability indexes (HSI) for each fire group	23
Figure 6. The average stem densities for plots had fires in drought and wet years.	31
Figure 7. The CP and BD NMR spectra of charcoal-free soil	48
Figure 8. The plots of leave-one-out cross validation of PLSR model.....	50
Figure 9. The plots of soil charcoal concentrations against the time.....	54
Figure 10. MIR spectra and the PLSR cross-validation coefficient spectra	57
Figure 11. The simulation settings for each site.	70
Figure 12. The time series of simulations for the site of WEB002.....	73
Figure 13. The simulated charcoal storage (kg m^{-2}) changes	75
Figure 14. The differences between fire effects for enf and dbf.....	77
Figure 15. The simulated soil water differences.	77

LIST OF TABLES

Table 1. Allometric equations used for calculating AGBC of mature trees	17
Table 2. The average C storage and standard deviation (kg m^{-2}) for woodland living AGBC, dead AGBC, and soil C of each fire groups.	20
Table 3. Means and standard deviations of the soil chemical characteristics of sampled soil before and after the HF treatment.	46
Table 4. Means and standard deviations of concentrations estimated for the six biomolecule components.	49
Table 5. The combustion factors for different biomass pools for fires with different severities..	64
Table 6. The fire occurrence year, physical characteristic parameters, and vegetation composition for sites selected for simulation.....	70
Table 7. The mean of last year simulation results from sites for each group.	74

LIST OF ABBREVIATIONS

AGBC: aboveground biomass C

AGB: aboveground biomass

ANOVA: analysis of variance

BC: black carbon

BCNWR: Balcones Canyonlands National Wildlife Refuge

BD: bloch decay

Biome-BGC: Biogeochemical Cycles terrestrial ecosystem process model

C: carbon

CF: combustion factor

CP: cross-polarization

CWD: coarse woody debris

DEM: digital elevation model

DFA: discriminant function analysis

FIREMON: Fire Effects Monitoring and Inventory System Protocol

GCW: golden-cheeked warbler

HCl: hydrochloric acid

HF: hydrofluoric acid

HSI: habitat suitability index

MANOVA: multivariate analysis of variance

MIRS: mid-infrared spectroscopy

N: nitrogen

NEE: net ecosystem exchange

NMDS: nonmetric multidimensional scaling

NMR: nuclear magnetic resonance

PDSI: palmer drought severity index

PLAI: projected leaf area index

PLSR: partial least squares regression

SL: severity level

SLA: specific leaf area

SOM: soil organic matter

SSURGO: Soil Survey Geographic database

TOC: total organic carbon

TSI: topographic saturation index

RMSEP: root mean square error of prediction

ACKNOWLEDGMENTS

I would like to thank my mentor, Dr. Joseph D. White for his guidance in my journey of pursuing PhD. I would also like to thank my other committee members, Dr. William C. Hockaday, Dr. Steve I. Dworkin, Dr. Sascha Usenko, and Dr. Rebecca J. Sheesley for their support and scientific opinions on this project. I thank my colleague Darrel B. Mary for his help in the field work and the development of this dissertation. I also thank my other colleagues in the Baylor Spatial Ecology Lab: Arjun Adhikari and Ramu Neupane.

Biome-BGC version 4.2 was provided by Peter Thornton at the National Center for Atmospheric Research (NCAR), and by the Numerical Terradynamic Simulation Group (NTSG) at the University of Montana. NCAR is sponsored by the National Science Foundation.

This research was funded by the U.S. Fish and Wildlife Agreement #20181AJ601 with Baylor University. Additional funding was provided by the Glasscock Foundation at Baylor University. I thank D. Holle, C. Schwope, C. Sexton, and D. Maple from the BCNWR for their support during the field data collection.

I would also like to thank my family for supporting me to study abroad. I thank all my friends who helped me during this time. Finally, I thank my Fiancée, Shu Feng, for standing at my back throughout this entire process.

CHAPTER ONE

Introduction

Climate Change and Carbon Cycling

Radiative forcing by the carbon dioxide (CO₂) is one of the primary drivers of the Anthropocene climate change. The global atmospheric concentrations of CO₂ have increased from a pre-industrial value of about 280ppm to 392ppm in 2011 (Keeling and others 2005, Tans and Keeling 2012). The highest carbon (C) emission rates occurred in the past two decades concurrent with the highest global temperature on record (Raupach and others 2007). The main anthropogenic CO₂ fluxes identified are emissions from the combustion of fossil fuels and net emissions from land use changes (Canadell and others 2007).

Estimates indicate that photosynthesis by terrestrial plants removes approximately 120 petagrams (Pg) of C per year from the atmosphere and about 610 PgC is stored in plants at any given time (Steffen and others, 2005). The largest terrestrial C sinks occur in young, growing forests with older forests and soils accumulating C at significantly lower rates. Perturbations of terrestrial ecosystems may elevate ecosystem respiration and significantly change C storage (Baldocchi 2008). The changes of ecosystem C fluxes are related to natural perturbations and large-scale human activities, such as deforestation, agriculture activities, and land use changes (Amiro and others 2010) that may account for 25% of the anthropogenic C emissions (Running 2008). Therefore, estimates of terrestrial C balances should incorporate episodic disturbances (such as wildfire) in addition to land-use changes

Fire Disturbance

An ecological disturbance is an event that results in a sustained disruption of ecosystem structure and function (Pickett and White, 1985). Physical, chemical, and biological effects of disturbances all play roles in the post-disturbance C budget (Glaser and Amelung 2003; Goetz and others 2007; Wan, Hui, Luo 2001a). Disturbance events can cause CO₂ emission to the atmosphere from the loss of terrestrial biomass; however, these impacts are a major uncertainty in understanding the global C cycles (Canadell and others 2007).

Fire is a dominant disturbance in many wildland ecosystems worldwide and directly contributes CO₂ to the atmosphere (Amiro and others 2006; Kurz and Apps 1999; Law and others 2004). The impacts of fire on ecosystems include C storage change, vegetation community shift, disrupted nutrient cycling, and alteration of soil properties. However, not all fires have the same effect. The three basic types of fires (surface, ground, and canopy fires) may burn differently depending on the kind of available fuel (Whelan, 1995). A surface fire burns fuels that are on the ground, generally with low temperatures and fast fire movement. In woodlands, surface fires can help keep surface fuels from building up and stimulate herb and shrub regrowth. A ground fire burns the organic layer with slower fire movement as compared to a surface fire. A canopy fire burns the higher leaves and branches of trees and shrubs, moves from tree to tree through the foliage. For a surface or ground fire, ladder fuels are required in order to move the fire to canopy.

The magnitude of fire effects can be described in the terms of fire intensity and severity (Morgan and others 2001). Fire intensity describes the physical combustion

process and energy output from fire, while fire severity emphasizes on the percentage of fuel combusted and the post-fire effects (Keeley, 2009). Usually, high-intensity fires are associated with high fire severity. Therefore, in this study, I primarily used the term “intensity” to describe fire, except for using the “severity” when describing the percentage of fuel combusted. The nature of fires (different frequency, magnitude, seasonality, and spatial patterns) occurring over an extended period of time is referred to as fire regime (Brown 1995; Morgan and others 2001).

Changing climate may affect the natural fire regimes that sustain certain ecosystems (Dale and others 2000), with fires predicted to be more frequent, severe, and extensive (Flannigan, Stocks, Wotton 2000). For example, projections of future climate suggest a doubling of area burned in Canada boreal forest by the end of this century. Other boreal areas, such as Siberia, may also see similar increases in fire (Bergeron and others 2004). In addition to climate change, recent invasions by non-native grasses into grassland have increased the amount and continuity of fuels which has increased the frequency of fire in a variety of ecosystems worldwide (Brooks 2007). The changes of fire frequency are expected to affect vegetation community (Paine, Tegner, Johnson 1998).

Wildland Fire Management

Current fire management strategies in wildlands include (a) letting wildfires burn unhindered, (b) reducing the risk and spread of wildfire through landscape level fuel management, or (c) using prescribed burns as a fuel reduction method. Potentially, selecting the “optimal management strategy” based on the states of ecosystems and management objectives may be assessed if the frequency of fires is known and the

woodland successional pathway is established (Richards, Possingham, Tizard 1999). Managing fire is always challenging because it is difficult to predict when and where wildfires will occur. However, managers can reduce the risk of wildfires by banning fires during certain weather conditions to lessen the chance of wildfire ignition, reducing the intensity of fires by mechanically reducing fuel loads, and suppressing the spread of wildfires by creating fuel breaks and active firefighting. Prescribed fire is also an important ecosystem management tool that utilizes low-intensity surface burns to reduce C emissions by burning off fuel to potentially avoid large intense wildfires (Haines, Busby, Cleaves 2001; Wade and Lunsford, 1989; Wiedinmyer and Hurteau 2010). Prescribed burns may also shift vegetation community composition by increasing mortality of fire sensitive species (Brown, Agee, Franklin 2004; Burton and others 2011; Hann and Bunnell 2001). However, fire applied too broadly, as a function of ambitious habitat restoration in ecosystems primed for high-intensity fires, could reduce C storage, affect nutrient availability, homogenize the landscape, and damage wildlife habitat (Brown, Agee, Franklin 2004; Fulé and others 2004; Tiedemann, O. Klemmedson, Bull 2000).

Study Area Description

For my study, I assessed fire effects on the woodlands of Balcones Canyonlands National Wildlife Refuge (BCNWR). Woodlands are a phytogeographic subset of forests generally composed of low density, short-statured trees found in climates that are growth-limited by temperature, precipitation, or evaporative demand (Woodward 1987). Economically, harvesting firewood or small-boled trees or for lumber is limited due to low productivity in woodlands. Historically, woodlands were used for livestock grazing

due to extensive open herbaceous areas found within woody vegetation patches (Peterken 1981).

This BCNWR refuge consists of 7109 hectares (ha) located on the eastern edge of the Edwards Plateau, 15 kilometers northwest of Austin, Texas, USA. The refuge is composed of non-contiguous tracts of land ranging in size from 38 to 1655 ha and is a part of a larger habitat protection area for two endangered bird species including the golden-cheeked warbler (GCW) (*Dendroica chrysoparia*) and the black-capped vireo (*Vireo atricapilla*) (USFWS, 1992). The refuge area is climatically classified as sub-humid, with mean annual precipitation of 855.0 mm, and mean temperatures range of 5.7–16.8 °C in winter and 22.4–33.5 °C in summer (NCDC, 2011a). The topography of the area is characterized by steep canyons with broad plateaus mainly consisting of limestone bedrock from the marine-derived Glen Rose formation of Cretaceous origin (Sellards, 1933).

The dominant woody vegetation of BCNWR is the evergreen Ashe's juniper (*Juniperus ashei*), with subdominant species including broad-leafed hardwoods, such as Texas red oak (*Q. buckleyi*), plateau live oak (*Q. fusiformis*), scalybark oak (*Q. sinuata* var. *breviloba*), post oak (*Q. stellata*), and escarpment black cherry (*Prunus serotina* var. *eximia*) (Diamond, 1977; Gehlbach 1988). The remnant mixed juniper-oak woodlands are critical habitat for the GCW which uses stringy, sloughed bark from mature Ashe's juniper exclusively for nesting material (USFWS, 1992, Pulich, 1976). The warbler also requires, as an important food source, Lepidopteran (Geometridae) larvae that feed on broad-leafed deciduous foliage (e.g. *Quercus* spp.) during the spring breeding season. Kroll (1980) described that high suitability GCW habitat should have a high density of

mature trees including old (>40 year) junipers, with a ratio of juniper to broad-leaved species of approximately 1.35:1.

Study Objectives

With increasing interest in C sequestration and C credit trading related to mitigating atmospheric CO₂ concentrations responsible for the current climate warming, woodlands may serve as significant C sinks as the extensive fire suppression continued. Woodlands are bio-diverse and serve as potential habitats for specialized wildlife species due to the large extent of edge that provides broad-scale ecotones (Barrett, Ford, Recher 1994). In Central Texas, woodlands may have been historically maintained by fire (Bray 1904; Clark 1991). Maintaining these woodlands as both C sinks and habitat may require potential anthropogenic disturbance, such as prescribed fire that facilitates successional pathways. However, little has been known about fire effects on this ecosystem, which leads to uncertainty of outcomes of reintroducing fires into this landscape. In this study, I investigated historic fire effects on site C storage, soil charcoal content, vegetation composition, and habitat suitability of GCW in juniper-oak woodlands within BCNWR. I also modified a biogeochemical model to simulate effects of different fire types on various ecosystem properties. As part of this model, I developed a new sub-model to simulate charcoal production from burned vegetation, charcoal loss due to erosion, and the effect of charcoal on soil water availability for different soil types. The objective of this study was to provide detailed ecological information regarding fire-affected ecosystem processes in order to increase knowledge of fire effects on the regional woodland ecosystem for helping decision-making of future fire management policy in this area.

CHAPTER TWO

Fire Effects on Carbon Sequestration and Vegetation Composition, and its Implications on Habitat Managements

This chapter published as: Yao J, Murray DB, Adhikari A, White JD. 2012. Fire in a sub-humid woodland: The balance of carbon sequestration and habitat conservation. *Forest Ecology Management* 280(0):40-51.

Introduction

Fire is an important ecosystem process in woodlands (Bowman and others 2009; Fuhlendorf, Smeins, Grant 1996; Van Auken, 2008) affecting C sequestration, tree species composition, and biogeochemical cycling (Amiro and others 2006; DeLuca and Aplet 2008; Goetz and others 2007; Knicker 2007; Wan, Hui, Luo 2001b). However, not all fires are equivalent. In juniper woodlands, high-intensity, stand replacement fires dramatically reduce C storage to amounts similar to stand initiation (Reemts and Hansen 2008). Low-intensity surface fires reduce stored C slightly by consuming understory vegetation, downed woody debris, and leaf litter (Burton and others 2011). Fire also affects post-fire vegetation recruitment due to different responses of species to fire (Hoffmann and Solbrig 2003; Morrison and Renwick 2000). High-intensity fire can shift the entire community structure; while low-intensity fires primarily affect young individuals and seedling recruitment. Therefore, ecosystems with mixed-fire regimes must be fully characterized in order to meet multiple management objectives (Nelson and others 2009; Olschewski and Benítez 2005; Turner and others 2011).

Compositional changes of vegetation communities in woodlands have been observed due to fire suppression at both regional and global scales (Archer 1994;

Henderson and Long 1984; Lloret, Pausas, Vilà 2003). Management plans to restore many ecosystems to pre-settlement conditions call for restoration of pre-settlement fire regimes, which can improve habitat quality for some endangered species (Blake 2005). However, for many ecosystems, the natural fire regime is unknown. In addition, fire suppression has also led to woody fuel accumulations which have increased the probability of historically unprecedented large, high-intensity wildfires (Flannigan and others 2009; Graham and others, 2004). Because fire suppression has occurred for nearly a century in some wildlands, there has been mixed conclusions about basic understanding of long-term ecological impacts of fire on different ecosystems (Carter and Foster 2004; Elliott and Vose 2005; Lavoie and others 2010; Pyne, 1997; Varner III and others 2005). Therefore, the suggestion of returning fire to woodland ecosystems as an ecosystem restoration tool (Abrams 2005; Brose and others 2001) requires a complete understanding of ecological consequences, with careful comparison of alternative management practices such as mechanical/manual “fire surrogates” treatments (Weatherspoon and Skinner, 2002).

In this study, I investigated the effects of past surface fires on woodland C storage, woody vegetation community composition, and habitat suitability for an endangered bird species in a U.S. national wildlife refuge. Utilizing a “chronosequence” approach, I grouped and compared stands at different successional stages following fire disturbance (Amiro and others 2010). Fire impacts on the aboveground biomass C (AGBC), soil C and N, and vegetation community composition were assessed based on differences between plots grouped according to different apparent stand ages. Finally, fire effects on

current and potential GCW habitat were assessed based on differences in community composition and a habitat suitability index (HSI) developed for this bird species.

Methods

Plot Selection

To assess fire impacts on C storage, vegetation community characteristics, and GCW habitat suitability, I established a series of study plots in the BCNWR. The total of 60 plots was established in 2010 located next to trees that were sampled for a previous dendrochronology study (Murray and White, in review). In that study, 5 cm tree slab sections of trees were cut with a chainsaw < 1 m above the root flare from randomly selected downed and dead hardwood trees in the refuge area. These slabs were then analyzed to determine the number of tree rings, width of rings, and presence and number of fire scars. Based on the age and fire scar years derived from these tree slabs, I categorized and sampled 20 plots in each of the following three groups: recent-fire (<40 year), old-fire (>40 year), and no-fire group (Figure 1). I chose 40 years as half of the developmental age of these woodlands based on previous studies that showed formation of dense-canopy woodland after approximately 80 years without fire (Fuhlendorf, Smeins, Grant 1996; McLemore, Kroh, Pinder III 2004). To avoid confounding effects of multiple fires for the fire-affected groups, I selected sites with single fire events from the tree ring study. To reduce potential bias of spatial autocorrelation, I ensured independence of each plot by selecting plots associated with trees that were fire-scarred during different years, and filtering these plots with a minimum distance of 300 m as fires burn relatively small areas within these woodlands (Murray and White, in review). Most

of the burned plots were characterized as having low-intensity, surface burns due to minor fire scar injuries observed in the trees rings. These low-intensity burns were suspected to consume predominantly seedlings and saplings, and only occasionally kill mature trees.

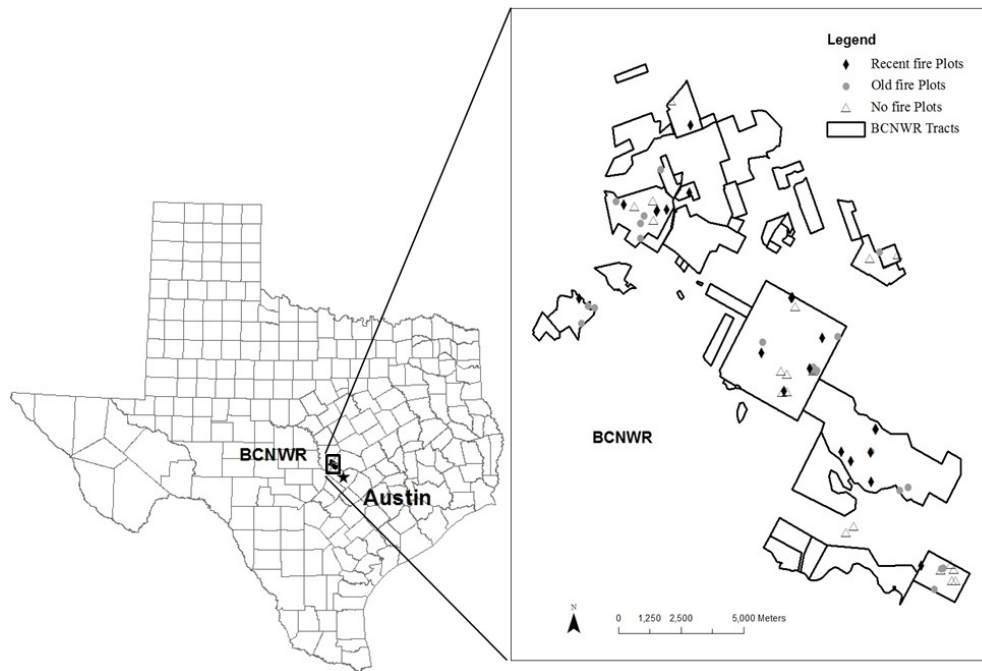


Figure 1. The locations and tract boundary of the BCNWR are shown above with the locations of 60 selected sampled points for the recent, old and no fire groups.

Field Survey

Data measured for each plot followed the Fire Effects Monitoring and Inventory System Protocol (FIREMON) (Lutes et al., 2006). I centered plots on the location of the trees sampled for the tree ring study. Each plot encompassed an 11.28 m radius circle for a total sampled area of 0.04 ha. Because my data was area-related, sampling on different slopes using a fixed-area plot could under-predict the results and affect the extrapolation of my results at the landscape level. To correct for slope, I determined the effective

sampled area by projecting the circular plot on a horizontal surface as an eclipse plot (Equation 1), which was used to calculate all area-related results from the plot measurements.

$$\text{Effective sampled area} = \pi \cdot r^2 \cdot \cos\theta \quad \text{Equation 1}$$

Variables measured in the 0.04 ha plot included species name, tree diameter at breast height (dbh), and height for individual mature trees (dbh > 10 cm), and saplings (ht > 1 m and dbh < 10 cm). For the biomass calculation, the diameters of multi-stemmed juniper and oak tree stems that diverged above the root crown were measured separately. For the analysis of community composition, multi-stemmed individuals were counted as single trees to avoid pseudo-replication. Saplings were measured by identifying the species and counting the number of individuals within the plot within dbh classes: 0–2.5, 2.5–5, 5–7.5, and 7.5–10 cm. For seedlings (ht < 1m), a subplot encompassed by a circle with 1.78 m radius was centered within the 11.28 m plot. Seedling species were identified, and the number of plants was counted for four height classes: 0–0.2, 0.2–0.5, 0.5–0.8, and 0.8–1 m. I estimated dbh values of 0.1, 0.3, 0.6, and 0.9 cm for each seedling's height class based on field measurements.

I also collected data on downed woody debris and litter depths from three 25 m transects in each plot based on the FIREMON line intercept sampling method. Ten samples of litter with various depths were collected from a 0.25 m² quadrat into paper bags from 10 different plots to estimate plot litter mass. To assess soil C and N, I collected two soil samples below the litter layer 5 m from the circle center in the south and west directions from each plot and at least 1 m away from any standing trees to avoid roots which may have biased my samples. Soil was sampled to a depth of 10 cm by a soil auger of 1.75 cm in diameter. At each site, I also recorded environmental data such as

elevation, slope, aspect, and the percentage of surface rock. Potential direct solar radiation was calculated from the recorded slope and aspect data using the method of Buffo et al. (Buffo, Fritschen, Murphy 1972).

Laboratory Analysis

Litter and soil samples were dried at 60 °C for 48 hours and weighed. Dried soil samples were ground into fine powder using a 3 inch ceramic mortar and pestle. Pulverized soil samples were added to silver capsules (3.2 × 4 mm, Costech Comp.) and acidified using concentrated sulfuric acid every two hours, which I repeated 20 to 25 times in a 60 °C gravity oven to volatilize inorganic C (e.g. calcite). The capsules were then capped with tin foil, and C and nitrogen (N) concentrations determined by thermal combustion within an elemental analyzer (Costech Comp. Model 4010).

Carbon Storage Assessment

I divided site C into three pools: living biomass C, dead biomass C, and soil C. Living AGBC was calculated by summing the C from the pools of mature trees, saplings, and seedlings. Mature tree aboveground biomass (AGB) was calculated from published allometric equations (Clark et al., 1985; Clark et al., 1986 a & b; Hahn, 1984; Schnell, 1976; Wiant, 1977) using field measured values for each species (Table 1). For species with no existing published allometric equation, I used equations for similar species. For unique species without specific equations, a generalized allometric equation was used (Jenkins et al., 2003). Sapling and seedling AGB were estimated using allometric equations designed specifically for trees with small dbh (Williams and McClenahan 1984). These allometric equations account for differences in wood specific gravities of

small juniper (0.40) (Equation 2) and oaks and other broad-leafed species (median=0.53) (Equation 3) where biomass was calculated based on the midpoint dbh of each class.

$$\text{Log}_{10} \text{Biomass} = 1.2727 + 1.4039 \text{Log}_{10} (\text{dbh}^2) \quad \text{Equation 2}$$

$$\text{Log}_{10} \text{Biomass} = 1.1843 + 1.5327 \text{Log}_{10} (\text{dbh}^2) \quad \text{Equation 3}$$

Dead AGBC was calculated from summing the C from the pools of standing dead trees, downed woody debris, and litter biomass. For standing, non-damaged dead trees with a complete stem structure and species identifiable, I used the same allometric equations for live trees to estimate biomass. If the trees were damaged, I calculated the biomass using the volume of remaining cylinder of tree stumps multiplied by the species specific wood specific gravity values (Jenkins and others 2003). For downed woody debris, I used the method developed by Brown (1974) based on data from the line intercept sampling. For litter, I first established a least squares linear regression model between the depth of litter and dry litter biomass and then measured average litter depths of each plot. I combined living and dead AGB to calculate the total site AGBC assuming C comprised 50% of biomass (Clark and others 2001; Malhi and others 2004; Pregitzer and Euskirchen 2004).

The soil C in this study was calculated as a function of soil depth, soil bulk density, rock fragment contents, and soil C concentration. The soil types of sampled plots and their associated soil bulk density, rock fragment content, and maximum soil layer depth were derived from the Soil Survey Geographic (SSURGO) database (USDA 2011). Point-specific soil depths were calculated using topographic integration (Zheng, Hunt Jr., Running 1996). I used the topographic saturation index (TSI) (Beven and Kirkby 1979) (Equation 4) as a surrogate for topographic correction to scale the maximum soil depth value derived from SSURGO data to calculate point soil depth.

$$TSI = \ln(\alpha / \tan \beta) \quad \text{Equation 4}$$

where α is the upslope drainage area (m²), and β is the topographic slope (degree). The α and β were calculated using the *Flow accumulation* and *Slope* function in ArcGis 9.3 (ESRI), based on a 30 m resolution U.S. Geological Survey digital elevation model (DEM) data (downloaded from Texas Natural Resources Information System, <http://www.tnris.org>). The maximum TSI values for each soil type were also derived for the calculation of point soil depth (m) (Equation 5).

$$SoilDepth = MaxSoilDepth (TSI / MaxTSI)^{0.5} \quad \text{Equation 5}$$

where the coefficient 0.5 is an empirical value used in other woody ecosystems (Jensen et al., 1997).

The soil depth to bedrock was less than 50 cm thick for most of sites, except those located in valley bottoms. Because of the dominance of thin soils within my plots, I assumed that the soil C concentration decreased within the soil profile with 50% of organic C in the top 20 cm of the soil surface (Jobbágy and Jackson 2000). I used a modified log-log model (Zinke, Sabhasri, Kunstadter 1978) developed from the global average soil organic C percent by depth data (Jobbágy and Jackson 2000) to describe the C concentration variation in the soil profile (Equation 6).

$$\log_{10} Y = -0.625 \log_{10} d + \log_{10} A - 0.619 \quad \text{Equation 6}$$

where Y is the soil C concentration at specific depth (%), d is the soil depth (m), and A is the average soil C concentration for the top 10 cm (%). I then calculated total *soil C* (kg m⁻²) based on this model (Equation 7).

$$Soil\ C = \rho \times (1 - \beta) \times \int_0^D Y = \rho \times (1 - \beta) \times 0.643 \times A \times D^{0.375} \quad \text{Equation 7}$$

where ρ is the soil bulk density (kg m^{-3}), β is the rock fragment content (%), and D is the total soil depth (m).

Community Composition and Habitat Analysis

I classified recorded species data into three species types: juniper, oaks, and others. I then calculated tree density for each species type in size classes of mature trees, saplings, and seedlings. By treating each size class as a separate group in the analysis, I attempted to capture the size-structured population information in my community composition analysis (McCune and Grace 2002). I used R software (version 2.13.1) to conduct a nonmetric multidimensional scaling (nMDS) of species tree density data of the three fire groups to examine the relationships of fire with community composition. This ordination method is generally the most appropriate for ecological community data that are non-normal and discontinuous (McCune and Grace 2002). In addition, I used the Bray-Curtis coefficient as the measure of distance (Faith, Minchin, Belbin 1987), and selected a two-dimensional ordination based on a Monte Carlo permutation test. After the ordination procedure was completed, environmental variables including elevation, slope, aspect, surface rock percent, and potential direct solar radiation were added graphically to the ordination space with the horizontal axis rotated to correspond with the maximum correlated variables. I also displayed the calculated aboveground biomass C of individual plots in the ordination space as different-sized symbols. For visualization, I calculated and illustrated the ordination spaces occupied by each fire group (eclipse convex hulls) based on a 0.8 confidence level within the ordination space.

I calculated the HSI for each plot from a linear model based on a stepwise discriminant function analysis (DFA) performed on various habitat variables, including

(1) presence or absence of oaks and Ashe's juniper; (2) distance (m) between trees; (3) density (stems per hectare) of mature oaks and Ashe's juniper; (4) height (m) of stand; and (5) age of Ashe's juniper (Kroll 1980). The distances between trees were calculated from all vegetation densities. The ages of Ashe's juniper were calculated using the linear regression model between tree diameter and age of juniper, where $diameter\ (cm) = 0.875 + 0.374 \times age\ (year)$ (Kroll 1980). Mean values of each variable were multiplied by the appropriate unstandardized discriminant coefficients from the DFA and then were summed for the HSI (Kroll 1980). Lower HSI values indicated increased habitat suitability.

Statistical Comparison

All data were \log_e transformed to meet the normality assumption of parametric tests used in my analysis. The difference between the fire groups was assessed using ANOVA (SPSS 18.0.0) for each single derived variable followed by Tukey's *post-hoc* test to determine which group was significantly different from others. I used the MANOVA test (McCune and Grace 2002; Stroup and Stubbendieck 1983) followed by Tukey's *post-hoc* test for comparing multiple variables between the fire groups at the same time to test for the composite fire effects, such as fire effects on C storage and community composition. An independent *t-test* was used where two variables were compared. Significance level was set *a priori* at 0.05.

Table 1. Allometric equations used for calculating AGBC of mature trees

Species	Wood specific gravity (Jenkins et al., 2003)	Replacing species	Allometric equations		Reference
<i>Juniperus ashei</i>	0.44	<i>Juniperus virginiana</i>	$Y = 0.1632 \times X^{2.2454}$	(14cm ≤ X ≤ 43cm)	(Schnell, 1976)
<i>Quercus buckleyi</i>	0.56	<i>Quercus falcata</i>	$Y = 1.95177 \times \left(\frac{X}{2.54}\right)^{2 \times 1.28848} \times 0.45$	(X ≤ 28 cm)	(Clark et al., 1986a)
			$Y = 2.60305 \times \left(\frac{X}{2.54}\right)^{2 \times 1.28848} \times 0.45$	(X ≥ 28 cm)	
<i>Ulmus crassifolia</i>	0.57	NA	$Y = 2.17565 \times \left(\frac{X}{2.54}\right)^{2 \times 1.2481} \times 0.45$	(X ≤ 28 cm)	(Clark et al., 1986b)
			$Y = 2.04282 \times \left(\frac{X}{2.54}\right)^{2 \times 1.25464} \times 0.45$	(X ≥ 28 cm)	
<i>Quercus stellata</i>	0.6	NA	$Y = 2.2365 \times \left(\frac{X}{2.54}\right)^{2 \times 1.24077} \times 0.45$	(X ≤ 28 cm)	(Clark et al., 1986a)
			$Y = 6.79066 \times \left(\frac{X}{2.54}\right)^{2 \times 1.00918} \times 0.45$	(X ≥ 28 cm)	
<i>Quercus sinuate</i> <i>var. breviloba</i>	0.6	NA	$Y = \exp(-0.20127 + 2.4342 \ln x)$	(2.5cm ≤ X ≤ 73cm)	(Jenkins et al., 2003)
<i>Quercus fusiformis</i>	0.6	NA	$Y = \exp(-0.20127 + 2.4342 \ln x)$	(2.5cm ≤ X ≤ 73cm)	(Jenkins et al., 2003)
<i>Celtis laevigata</i>	0.49	NA	# $Y = -0.00004 X^3 H + 0.049 X^2 H - 0.00005 X^3 + 0.05 X^2$ (X ≥ 12.7cm)		(Hahn, 1984)
<i>Juglas nigra</i>	0.51	NA	# $Y = -0.00003 X^3 H + 0.067 X^2 H - 0.00005 X^3 + 0.06 X^2$ (X ≥ 12.7cm)		(Hahn, 1984)
<i>Fraxinus texensis</i>	0.53	<i>Fraxinus pennsylvanica</i>	$Y = 2.76583 \times \left(\frac{X}{2.54}\right)^{2 \times 1.15849} \times 0.45$	(X ≤ 28 cm)	(Clark et al., 1985)

Y: Biomass in kg; X: dbh in cm; H: height in m

#: Equations were reconstructed from multiple steps calculation of biomass method of Hahn, 1984

Results

Aboveground Biomass Carbon

The average slope of sampled plots was 14.25 ± 11.97 degrees for the recent-fire groups, 17.75 ± 9.41 degrees for the old-fire group, and 13.75 ± 9.20 degrees for the no-fire group. The apparent stand ages (years after fire) ranged from 3 to 39 years (s.d.=12.1 years) for the recent-fire group, and 42 to 88 years (s.d.=7.4 years) for the old-fire group. For the no-fire group, the stand ages (years after stand initiation) ranged from 48 to 136 years (s.d.=21.8 years).

For living AGBC, only C stored in mature tree biomass was significantly different between groups ($F_{(2,57)}=20.52$, $p < 0.001$) based on ANOVA, with the no-fire group having the highest value of mature tree AGBC and the recent-fire group having the lowest value (Table 2). For dead AGBC, only the litter was significantly different between groups ($F_{(2,57)}=3.27$, $p=0.048$), with the no-fire group having the highest value. The no-fire group also had slightly more, but not significantly so, downed woody debris than those of other two groups. The site AGBC, including both living and dead AGBC, was significantly different between groups ($F_{(2,57)}=20.58$, $p<0.001$), which was attributed to the difference in the mature tree AGBC that represented approximately 80% of the site AGBC stored in the system. Tukey's *post-hoc* test of site AGBC showed that all groups were significantly different from each other with the highest value for the no-fire group and the lowest for the recent-fire group (Figure 2).

Soil C and N

For soil C, I identified 8 soil types from the SSURGO database for my sampled plots. I found that the soil C pool was 4 to 6 time larger than the AGBC pool with large standard deviations among different plots mainly due to the large variations in the soil depths (Table 2). I also found no significant difference of soil C storage between groups. For the soil C concentration, the average value was estimated to be $7.84 \pm 1.87\%$ for the recent-fire group, $7.38 \pm 2.64\%$ for the old-fire group, and $8.12 \pm 2.43\%$ for the no-fire group, with no significant difference between groups. The average soil N concentration was estimated to be $0.54 \pm 0.14\%$ for the recent-fire group, $0.50 \pm 0.16\%$ for the old-fire group, and $0.54 \pm 0.14\%$ for the no-fire group with no significant difference between groups.

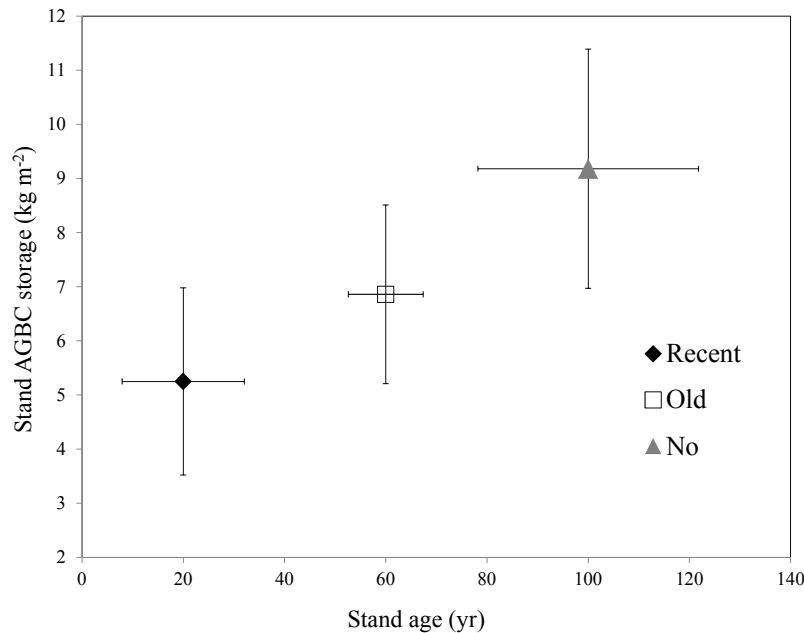


Figure 2. The average total biomass C for each fire group are shown. The vertical error bars represent the biomass C standard deviations, and the horizontal error bars represent the standard deviations of stand ages (year).

Table 2. The average C storage and standard deviation (kg m^{-2}) for woodland living AGBC, dead AGBC, and soil C of each fire groups.

Fire group	Living AGBC			Dead AGBC			AGBC*	Soil C
	Trees*	Saplings	Seedlings	Standing	Downed	Litter*		
Recent	3.58±1.59	0.26±0.17	0.0014±0.0014	0.24±0.24	0.77±0.48	0.56±0.18	5.42±1.81	34.01±18.65
Old	5.44±1.95	0.23±0.11	0.0010±0.0011	0.21±0.17	0.81±0.40	0.51±0.19	7.20±1.86	33.25±18.34
No	7.29±1.86	0.25±0.14	0.0013±0.0010	0.23±0.44	1.04±0.59	0.64±0.12	9.45±2.31	36.04±19.47

* indicates the variable was significant different among three groups at 0.05 significance level.

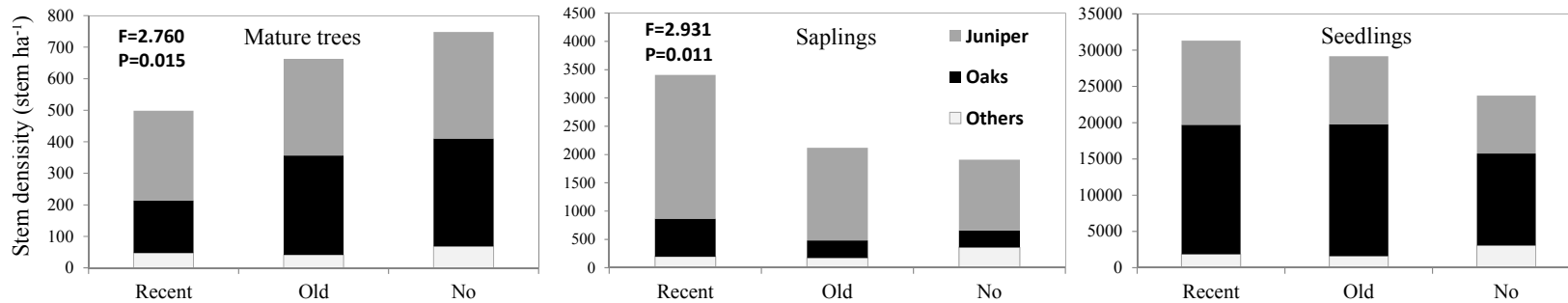


Figure 3. Tree density of each species type (juniper, oak, and others) in the size class of mature trees, saplings, and seedlings for the three fire groups are shown. The MANOVA test results of community composition difference between the fire groups, if significant, are indicated on the upper left corner of individual graphs. Note the differences in the scales of y-axes for each individual graphs.

Community Composition

Overall, Ashe's juniper was the dominant species comprising 50% of mature trees, 70% of saplings, and 35% of seedlings for all plots. Oaks comprised approximately 40% of mature trees, 25% of saplings, and 55% of seedlings for all plots. Total mature tree stem densities were lowest for the recent-fire group and highest for the no-fire group, while the sapling and seedling densities were highest for the recent-fire group and lowest for the no-fire group (Figure 3).

For community composition, I found that mature tree densities of each species type differed significantly between groups (Wilks' $\lambda = 0.758$, $F(2,57) = 2.760$, $p=0.015$), with higher, but not significantly, mature juniper density in the recent-fire group and higher mature oaks and other species densities in the no-fire group. I also found that sapling densities of each species type were also significantly different between groups (Wilks' $\lambda = 0.747$, $F(2,57) = 2.931$, $p=0.011$). The juniper sapling densities (average 72%) were significantly higher than the other two species types (average 17% for oaks and 11% for other species) for all three groups. For seedlings, no significant difference of seedling densities was found between groups, although average oaks seedling densities were higher (58%) than juniper (34%) and other species (8%).

The nMDS ordination of species tree density data showed that the groups were defined within the ordination space with some overlap (Figure 4). High density of juniper saplings was characteristic of the recent-fire group, while the no-fire group had higher density of mature trees. In addition, mature oaks density (mostly *Q. buckleyi*) was highly correlated with the topographic slope, while juniper density was correlated with

potential solar radiation. The soil C and N concentrations were highly correlated with the density of oaks.

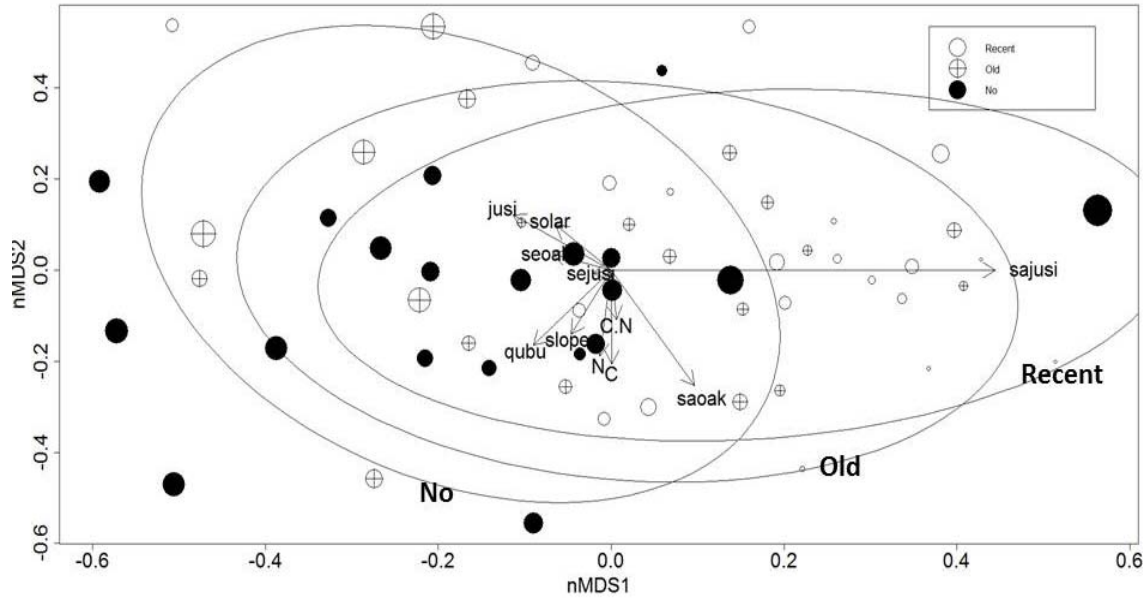


Figure 4. nMDS ordination of the species tree density data (mature tree, saplings, and seedlings) of the three fire groups is shown. The eclipse circles represent calculated ordination space occupied by each fire group at the 80% confidence level. The size of the symbol is proportional to the total aboveground biomass C storage calculated for each plot. The arrows represent the vegetation and environment variables*, with direction showing correspondence to the nMDS axes, and the length indicative of the relative strength of derived correlations.

*jusi: Ashe's juniper; qubu: oaks, mainly *Q. buckleyi*; sajusi and saoak: sapling junipers and oaks; sejusi and seoa: seedling junipers and oaks; C and N: soil C and N concentration; C.N: soil C to N ratio; solar: potential solar radiation.

Habitat Suitability

All of my plots contained both juniper and oak species, with more than half of the plots (53.3%) containing at least one mature tree species other than oak or juniper. The mean age of juniper was estimated to be 25.59 ± 12.45 years for the recent-fire group, 26.88 ± 8.98 years for the old-fire group, and 31.05 ± 16.49 years for the no-fire group. The mean height of the stands was estimated to be 7.25 ± 1.00 m for the recent-fire group,

7.60±1.03 m for the old-fire group, and 8.52±1.22 m for the no-fire group. Based on the above information, I calculated the HSI for each plot and found no significant difference between fire groups (Figure 5).

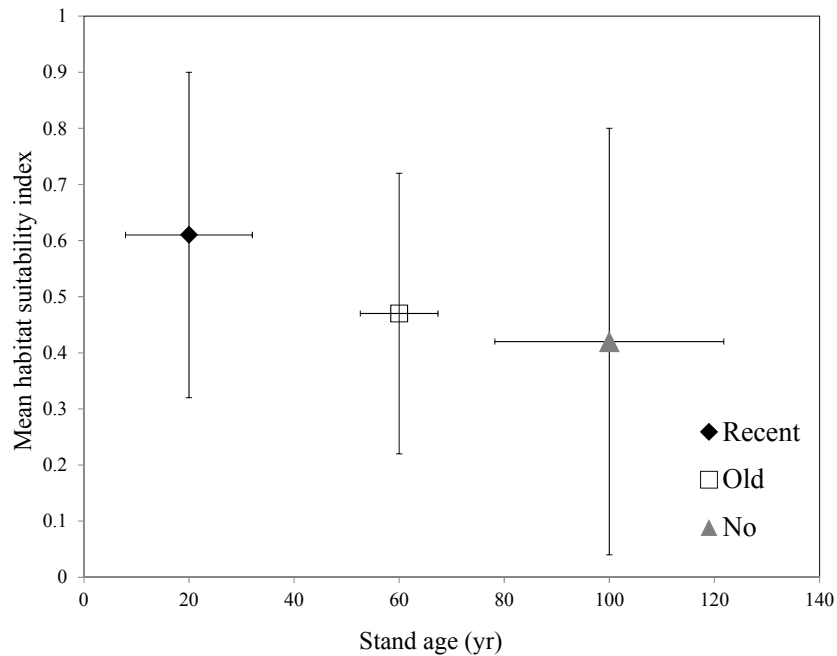


Figure 5. The mean habitat suitability indexes (HSI) for each fire group are shown. Lower HSI indicates better habitat suitability. The vertical error bars represent the index standard deviations, and the horizontal error bars represent the standard deviations of stand ages (yr).

Discussion

Fire Effects on Carbon Sequestration

Continued C accumulation in sub-humid woodlands may play an important role in mitigating rising atmospheric CO₂ concentration and associated global climate warming because adapted woody species with opportunistic life history traits may occupy broad bioclimatic zones with high tolerance for variable site water availabilities (Asner and others 2003; Birdsey et al., 2007; Pregitzer, 2007; IPCC, 2007). The average AGBC for

this Central Texas woodland ecosystem was estimated to be 7.36 kg m^{-2} , with a range of $2.66\text{--}16.15 \text{ kg m}^{-2}$, which was similar to other forest and woodland ecosystems C storage estimates in the U.S. with an average 6.75 kg m^{-2} for the southeast region, 6.48 kg m^{-2} for the south central region, and 7.14 kg m^{-2} for the entire U.S. (Birdsey and Heath 1995; Houghton, Hackler, Lawrence 1999). My estimates of average living AGBC for this woodland ecosystem were 5.68 kg m^{-2} , which was slightly higher than the national average of 3.84 kg m^{-2} for all woodlands across the U.S. (Goodale and others 2002; Houghton 2005).

The belowground biomass C was not included in this study because no study had been conducted to determine the belowground biomass for individual species in this ecosystem. The root to shoot (R/S) ratio, an index routinely used to calculate belowground biomass from aboveground biomass, range from 0.19 to 0.31 for woody species from various studies (Cairns and others 1997; Cannell 1982). However, shallow, calcareous soil overlaying fractured Cretaceous limestone in this ecosystem may restrict vertical root growth. The maximum rooting depths of most species in these woodlands varies from 3 to 7 m, but the roots of the evergreen oak, *Q. fusiformis*, may be found below 10 m embedded in fractured bedrock (Jackson and others 1999). Large lateral root development in thin soils of dry environments may help plants maximize uptake of shallow soil (Schenk and Jackson 2002). However, root space competition can limit lateral root growth due to high densities of saplings similar to the woodlands in my study area (Schenk 2006). Therefore, using a constant R/S ratio to calculate belowground biomass may not result in high stand-level accuracy. By excluding belowground biomass C in my analysis I am unable to assess the full effects of fire on stored total biomass C.

Because the no-fire group had higher densities of mature trees, I expect the absolute differences in total C between fire and no fire stands to be larger due to higher belowground C storage for the no-fire group. In addition, belowground C storage may potentially be important as an indicator of vegetative reproduction potential for oaks (Floyd, Romme, Hanna 2000; Reemts and Hansen 2008) and should be a focus of future study.

Previous studies indicated that low to moderate-intensity fires have less effects on live biomass C storage than high-intensity fires and C loss would be likely to stabilize in a relatively short period of time (less than a decade) (Hurteau and North 2010; van Mantgem and others 2011). Fire-related tree mortality is thought to be age-specific and density-related, where large sparse trees with thicker bark are more resistant to fire damage (Fuhlendorf, Smeins, Grant 1996; Hood and others 2007). The impact of low-intensity fire on C storage increases for sites with higher proportions of biomass in small trees with dbh < 20 cm (Cook and others 2005). My study showed that even low-intensity fire reduced C storage significantly in this woodland ecosystem, as a consequence of higher densities of small trees which were affected most by surface fires. Although my study focused on stands with single fire events, my results may also be used to project outcomes for multiple fire events which I predict would limit mature tree densities and keep C storage at a relatively low level.

Fire had no clear effects on soil C storage that ranged from 5.17 – 63.59 kg m⁻². Variation of estimated soil depths within the sampled area most likely confounded the results. Feedbacks between climate, vegetation cover, disturbance, and topography affect soil C accumulation (Wood, Murphy, Bowman 2011). Species distributions on hillslopes

are influenced mostly by soil depth and water holding capacity. For example, steep slopes result in small soil depths, low soil moisture, and slow soil C accumulation (Tromp-van Meerveld and McDonnell 2006). In my study area, tree harvesting intensity and fire for the past century were at their highest during the 1950s (Murray and White, in review), which also coincided with a drought of record. Large rain storms that followed this drought potentially resulted in higher than average soil erosion rates that were accelerated by the removal of vegetation cover and have contributed to regionally thin soils (Allen and others 2011). Because soil accumulation may require 50 to 500 years to recover depending on the severity of disturbance and ecosystem type (Burke, Lauenroth, Coffin 1995; Knops and Tilman 2000; Schlesinger 1986), I conclude that the current soil C in my study area is a reflection of soil formation and recovery.

Woodland sites with deeper soil depths were located in valley bottoms potentially with higher topographic moisture. Most of my no-fire sites were located in valleys which had higher AGBC storage and soil C storage. Also, for these valley sites, the calculated soil C storage was significantly larger than the AGBC pool ($P < 0.001$), making it the largest C pool for site C storage. These large soil C pools affected my estimated average soil C values of 34 kg m^{-2} , which were larger than Central Texas regional soil C values of 13 kg m^{-2} estimated from the SSURGO database (USDA, 2011). This difference was consistent with the assessment by the National Cooperative Soil Survey (NCSS) in which SSURGO derived soil organic C values were about 50 to 60% less than NCSS pedon database lab measured soil C values (NCSS, 2010; West et al., 2010).

Fire Effects on Soil Geochemistry

The average soil C concentration of 8% for my study was higher than the average 5% measured in a nearby afforested prairie pasture (White and Moore 2010)(White and others 2010). Also, my soil C concentration values were higher than the average global value for Entisols, the most common soil unit found in my study area (USDA Soil survey of Texas, 1974), of approximately 1% (Batjes, 1996). The average soil N concentration for my study area (0.53%) was also higher than the values from the nearby afforested prairie pasture with an average value of 0.19% and the average global N concentration value for Entisols of 0.10%.

I did not find a significant effect of fire on soil C and N concentration, however site variances were apparent. Soil C and N concentration values for my study were correlated to topographic slope (Figure 4), which I attribute to the effects of slope on soil erosion and nutrient leaching rates (Weiler and McDonnell 2006). Vegetation composition may also explain the site soil C and N differences (Hobbie 1992), which is supported by my data where oak-dominated sites had higher soil C and N concentration than juniper-dominated sites (Figure 4). Higher N in the mature oak-dominated woodlands is likely due to annual contribution of low-lignin litter from these deciduous oak species. In contrast, high lignin content in juniper leaves may have increased litter residence time (Bates, Svejcar, Miller 2007; Tiedemann and Klemmedson 1995), which decreases N availability similar to other juniper-dominated sites (Roberts and Jones 2000).

Soil C and N are also dependent upon fire intensity. Low-intensity fire causes little initial loss in mineral soil C and N (Johnson and Curtis 2001). In this ecosystem,

low-intensity fires may release N bound in litter organic matter, which may benefit nutrient-limited species such as Ashe's juniper and affect regeneration and competition (Hobbie 1992; Knicker 2007; Zou and Bashkin 1998). Repeated low-intensity fires may also deplete nutrient stocks in the soil (Jackson 2000). High-intensity fire can increase soil C due to vertical transport of hydrophobic organic matter from surface (Johnson and Curtis 2001).

Fire Effects on Community Composition

Periodic surface fire has maintained many forests by favoring fire-tolerant species, such as oaks (*Quercus* spp.) (Abrams 1992; Hutchinson and others 2008; McEwan and others 2007; Tharp, 1939). Central Texas woodlands may have been historically maintained by fire (Bray 1904; Clark 1991). Fire frequency has decreased over the last century in my study area due to active fire suppression and ranching on the eastern Edwards Plateau which poses a threat to the health and persistence of certain species within this woodland ecosystem (Foster, 1917; Russell and Fowler 2002). Unfortunately, no other information about earlier fire history beyond this range is available due to the short-lived nature of these woody species. Murray and White (in review) estimated a 5.5 year fire return interval in the BCNWR which was comparable to fire return intervals in other mixed-oak woodlands in the U.S. of 5.3 to 8.4 years (Stambaugh and others 2009). However, this estimate may not reflect the true site fire return which might be 40–70 years based scarring from multiple fires analyzed for BCNWR.

Although I suspected that low-intensity fire may benefit juniper through soil nutrient mineralization, lack of fire may inhibit oak adult recruitment by increasing the density of fire-sensitive juniper species and reducing the survival and growth of oak

seedlings (Abrams 1992; Russell and Fowler 2002). For my study, I found that sites with a single fire disturbance had higher oak seedling density than juniper seedling density, though not significant (Figure 3). For saplings, higher juniper densities were observed in the recent-fire group compared to the other two groups. Because survivorship of junipers was high overall, I expect that in the absence of future fires these sites will be dominated by junipers.

The significant difference of mature tree densities I observed between the fire groups is attributed to fire-affected tree recruitment, the influence of topography, herbivory, and historical climate. Topography plays an important role in mediating the fire–vegetation–soil feedbacks (Wood, Murphy, Bowman 2011; Wood and Bowman 2012). In my study, the high correlation of *Q. buckleyi* to topographic slope was consistent with the previous observation related to slope-associated soil processes and fire susceptibility (Figure 4) (Diamond, 1997). Stands located in valley bottoms with thick soil layers may have access to seasonally sustained topographic moisture which reduces fire occurrence (Wood, Murphy, Bowman 2011). These topographic position sites provide “fire refugia” for vegetation in this landscape, which was demonstrated by the higher number of my no-fire stands located in valley bottoms. Ashe’s juniper was highly correlated with the potential solar radiation (Figure 4), which was associated with topographically exposed dry sites with higher fire frequency. This is consistent with the high water use efficiency of junipers (Merrill and Young, 1959). These sites have shown higher recruitment rates for Texas red oak in the past (Murray and White, in review), however recent lack of recruitment on these sites may be linked to soil loss since the 1950’s.

The dominance of oaks, rather than Ashe's juniper for the old-fire group, may be due to a higher oak recruitment rate observed from 1900 to 1935 potentially related to lower whitetail deer (*Odocoileus virginianus*) population sizes (Russell and Fowler 2004). Deer preferentially browse on oak seedlings and saplings. After 1935, deer densities increased associated with eradication of the infectious screwworm (Calliphoridae), which corresponded with observed lower oak recruitment and Ashe's juniper dominance in the recent-fire group. Deer populations potentially peaked in the 1980s and have remained very large, around 30 deer km⁻², despite increased hunting pressure (Russell and Fowler 2002; Young and Richards, 1996).

The old-fire group, which represented stand initiation during 1930 to 1970, showed higher oak densities, which may also be explained by a prolonged drought that occurred from 1947–1956. Based on the historical Palmer Drought Severity Index (PDSI) (NCDC, 2011b; Palmer, 1965), 12 out of 20 of the plots within the old-fire group had fire scars during these drought years. Of these 12 plots, oak percentages were significantly higher than the other old-fire group plots ($t=1.877$, $p=0.074$) (Figure 6). The mechanism for higher oak densities may be attributed to increased probability of fire with greater intensity under drought conditions due to the presence of dead individual trees and dry canopy fuels. With more intense fire, mortality rates would be expected to be different between fire-sensitive juniper and fire-resistant oak. High-intensity fires in this environment decrease juniper densities and favor oak species recruitment through asexual reproduction from basal sprouting (Floyd, Romme, Hanna 2000; Reemts and Hansen 2008). For plots with low-intensity fires, juniper sapling densities would be expected to be higher. Previous studies have indicated that Ashe's juniper seedling establishment and

survival are highest in shaded conditions but with higher growth at canopy edges and in grasslands (Reemts and Hansen 2008; Van Auken, Jackson, Jurena 2005). Current prescribed burning on the refuge is limited to grasslands using wooded areas as fire breaks under moderate burning conditions. These low-intensity burns in woodlands may favor continued juniper recruitment, while high-intensity fires, from wildfires, may favor recruitment of shade-intolerant oak. Fire effects on community composition are also related to fire frequency. Although not a focus in this study, I predict that, for stands with multiple fire disturbances instead of only single fire events for a long period, fire effects on community composition would be more substantial. Frequent fire may help to shift an entire woodland community towards a grassland ecosystem (Briggs, Hoch, Johnson 2002; Cloudsley-Thompson, 1975; Habselka et al., 2007; Ruthven III and Synatzske 2002).

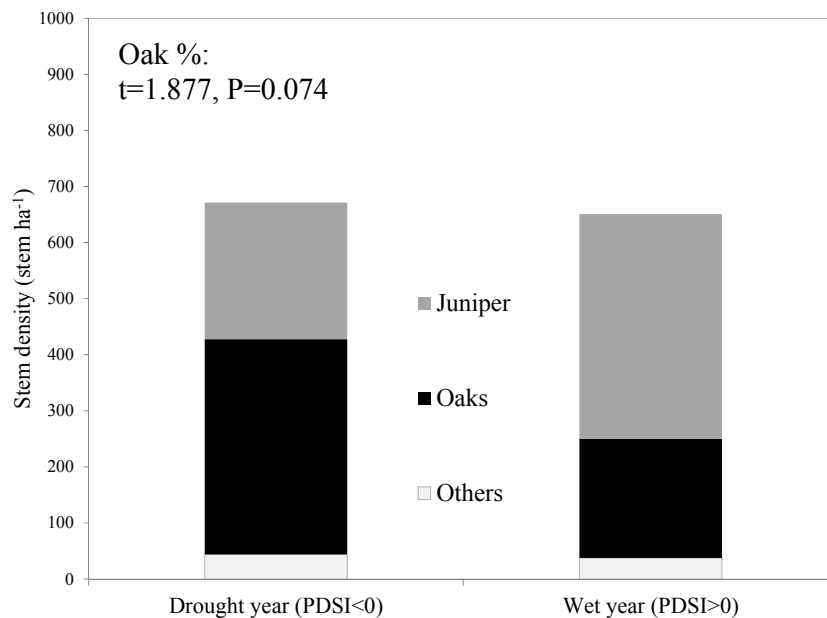


Figure 6. The average stem densities of each species type for the plots that had fire in drought years (PDSI<0, total 12 plots) and in wet years (PDSI>0, total 8 plots) of the old fire group are shown. The plots had fire in the drought years had significantly higher oak percent than the plots had fire in wet years at $\alpha=0.1$ confidence level ($t=1.874$, $p=0.077$).

Fire Effects on Habitat Suitability

The calculated HSI for most of my plots ranged from 0.3 to 0.8, which was significantly higher than the value of 0.12 Kroll (1980) proposed as a threshold value for quality habitat. The value of 0.12 Kroll used was derived from the midpoint of the HSI value range of his study area. The difference in the derived HSI values between my study and Kroll's may be attributed to tree density differences between the two study areas. This may be a result of different local ecosystem characteristics and tree sampling methods. Kroll's study was confined to a small area at the eastern edge of the Edwards Plateau approximately 100 km north of the BCNWR. Also, whether Kroll accounted for multi-stemmed juniper trees in the density calculation is unclear. To estimate an appropriate threshold HSI value for quality habitat in BCNWR, future study needs to associate long term warbler observation data with calculated HSI values for stands in the refuge.

The calculated HSI were not significantly different between groups, and I found that fire effects on habitat suitability for birds, such as GCW, can be dichotomous (Blake 2005). In my study, fire reduced mature tree density, which had a negative impact on habitat suitability indicated by higher average HSI values for the no-fire group than the recent-fire group. However, I also observed that high-intensity fire was related to higher oak recruitment which has the potential to sustain GCW habitat for the future.

Implications for Fire Management: Balancing the Carbon Sequestration and Habitat Conservation

Managing lands in BCNWR to sustain GCW habitat may require both mechanical treatment and use of fire in the woodlands. Critical core breeding habitat for GCW

includes stands considered as old-growth in this ecosystem, which are composed of large, mature junipers (> 40 years old) and > 36% oak species mixture (Kroll, 1980), should be protected from wildfire. To reduce the risk of intense fire, mechanical thinning of understory and removal of downed dead woody fuel can be employed in these core habitats (Albrecht and McCarthy 2006). For at least two decades, expansion of low-density residential development at the wildland–urban interface has greatly increased fire risks in many wildlands, with my study area classified as having a high wildland fire hazard (Theobald and Romme 2007). Human population densities and land management activities are likely to affect both the ignition and suppression of future fires, which is complicated by the potential for future warmer and drier climates (Archibald and others 2009). As the BCNWR lands are discontinuous and surrounded by grass pastures with scattered single home ranches, there is a risk of fire initiating in these adjacent areas of fine fuel and spreading onto BCNWR. Current management policy includes informing public about the level of fire danger, placing fire bans accordingly across the area in both refuge lands and exterior lands, and creating “shaded fuel breaks” around the refuge tract boundaries using mechanical thinning to remove understory ladder fuels in order to prevent canopy fires in the woodland. While mechanical treatment such as this can reduce site C storage, it is compensated by subsequent ecosystem production with little impact on site C storage or community composition over the long term (Boerner, Huang, Hart 2008; Graham et al., 2004; Hurteau and North 2010).

I note that management must also take into account oak recruitment failure in young stands. Naturally occurring wildfires in monoculture stands of dense young Ashe’s juniper with poor HSI values may be allowed to burn. This may potentially increase oak

recruitment where root and seed stock are viable with negligible impacts on juniper, landscape level survivorship (Glenn-Lewin 1977). However, because of the large wildland-urban interface of the refuge, wildfires are dangerous to humans. The management of the refuge may require innovative prescribed burnings that mimic some of the mixed intensity fire behaviors of wildfires within acceptable risk limits (Abrams 2005; Brose and others 2001; Hubbard and others 2004). Prescribed fire has already been used in grasslands and may be expanded into woodlands in this area with appropriate future study on woodland succession and habitat impacts.

Climate also plays a role in shaping current and future woodland community composition. Drought and associated fire appear to favor oak persistence, not dominance, over time. The future climate is expected to have more drought events for this region (IPCC, 2007), similar to the weather patterns of the 1950's and the recent drought of 2011. Therefore, future management needs to consider climate-related effects when timing potential prescribed fires. Because fire in this woodland ecosystem reduces C storage significantly, use of prescribed burning should consider the post-fire climate as well, as it affects vegetation productivity. The higher C storage in these woodlands may be attributed to higher surface temperature with an increased growing season length (Sterl and others 2008), which would limit the impact of burning on C storage especially for low-intensity surface burns (Boerner, Huang, Hart 2008). The relationships between fire, C storage, and climate indicate the need for managers to be adaptable to different management techniques especially when dedicating land area for long-term C sequestration (Ellenwood, Dilling, Milford 2012).

Management of public lands requires careful consideration of short and long-term outcomes of restoration and conservation activities (Loomis, 1993). However, dichotomous policies, such as broad fire exclusion or use, may arise from externally derived mandates such as the Endangered Species Act or the U.S. Department of Interior's recent decision to achieve C neutrality on its landholdings (Ellenwood, Dilling, Milford 2012). This study primary focused on the southern semi-humid woodland community with management emphasis on conserving endangered species specific to this ecosystem. However, I demonstrated that multiple conservation and ecosystem service objectives may be accomplished for a wildlife refuge. This requires detailed, community-level, ecological information that encompasses longer time scales. Based on this need, an "integrative complexity" quantitative measurement approach may be used to choose a balanced dichotomous policy within public lands (Carroll and Bright 2010). This supports evidence that land management policies should come from integrated approaches that support action based on robust scientific evidence (McDermott, Noah, Cashore 2008).

CHAPTER THREE

The Storage Change of Fire-derived Soil Charcoal in a Sub-humid Woodland

Introduction

Fire affects the terrestrial C cycle on 40% of the Earth's land surface by consuming biomass and producing charcoal from incomplete combustion (Alexis and others 2007; Chapin, Matson, Mooney 2002; Fuhlendorf, Smeins, Grant 1996). Terrestrial ecosystem fires are estimated to consume 4 to 8 Pg of biomass C annually and produce 0.5 to 1.7 Pg of charcoal (Reeves and others 2008). Because, charcoal is a compound that contains polyaromatic, heterocyclic black carbon (BC), it is highly recalcitrant to biological decomposition in soil (MacKenzie and others 2008). With extremely slow decomposition rates potentially requiring hundreds to thousands years, BC may represent a substantial sink for biospheric C (Kuhlbusch and Crutzen 1995). Currently, the global BC reservoir has been estimated to be 300-500 Gt C, composed of 5-30% of total organic carbon (TOC) from soil, river water, and sediment (Hockaday and others 2007; Lehmann, Gaunt, Rondon 2006; Masiello 2004; Preston and Schmidt 2006; Rodionov and others 2010).

The pool size of BC highlights the importance of fire-derived charcoal in terrestrial ecosystems; however more information is also needed to characterize terrestrial soil charcoal fluxes and potential feedbacks on biogeochemical cycling and ecosystem functions. Charcoal is a C-enriched substance that may affect terrestrial nutrient cycling and soil water holding capacity (DeLuca and Aplet 2008). In boreal and temperate forests, charcoal has been shown to facilitate nitrification of soil organic materials

through increasing microbial activity and water holding capacity (Berglund, DeLuca, Zackrisson 2004; Lehmann and others 2011; Zackrisson, Nilsson, Wardle 1996a). The potential benefits of charcoal for agriculture may have been understood by tribal peoples in the Amazon rainforests who added charcoal to soils of cleared forests which potentially increased soil fertility by increasing cation exchange capacity from oxidation (Glaser and Amelung 2003).

Due to its chemically-heterogeneous nature, charcoal in ecosystems has been difficult to quantify as analytical methods capture only parts of the continuum of BC materials that range from soot to slightly charred biomass (Hammes and others 2007). Solid state ^{13}C nuclear magnetic resonance (NMR) spectroscopy can identify condensed aromatic C in order to estimate charcoal concentrations in soil (Hockaday and others 2007; Simpson and Hatcher 2004; Skjernstad, Taylor, Smernik 1999). The advantage of ^{13}C NMR spectroscopy is that it can quantitatively determine the amount of organic C in different functional groups, such as alkyl, O-alkyl, aromatic and phenolic, in a complex media, like soil (Smernik and Oades 2000). Because NMR is expensive and time consuming, this may limit the number of samples that can be analyzed. Alternatively, mid-infrared spectroscopy (MIRS) may be used to predict various organic and inorganic soil properties based on statistical analysis of spectral absorption features (Bornemann and others 2008; Janik and Skjemstad 1995; Janik, Skjemstad, Raven 1995; Viscarra Rossel and others 2006). Aromatic C may be detected with MIRS and can be used to estimate soil charcoal in an efficient way as compared to NMR (Colthup, Daly, Wilberley 1990; Reeves and others 2008). However, MIRS can only be used as a quantitative measurement when there were reference samples with known concentrations of targeted

compounds. Also, the similarity of the functional groups found in charcoal and the other materials such as humic acids, etc., may affect the quantitative accuracy of MIRS when these compounds are present in soil (Reeves and others 2008).

While charcoal-C may be an important long-term storage pool of terrestrial C, there is little information about its persistence in different ecosystems. In this study, I assessed the amount of charcoal, derived from residual burned biomass in soil from sites in a sub-humid woodland where I previously reconstructed the fire history using an extensive tree ring survey (Hammes and others 2007; Yao and others 2012). I carefully selected sites that had only experienced single fire disturbance since the stand initiation and had no evidences of nearby fire occurrence based on the information provided by the tree ring study to extract soil samples. From these samples, I estimated charcoal concentration using NMR and MIRS techniques, and compared derived concentrations for sites with recent, old, and no documented fire occurrences. I hypothesized sites with recent fire occurrences should have higher charcoal concentration than sites with older fire occurrences. Using information about time since last fire occurrence and site charcoal concentration, I calculated a potential regional loss rate of soil charcoal. By analyzing my results using topographic data and redox state of the charcoal, I proposed mechanisms for charcoal loss from the soils.

Methods

Soil Sampling

To assess charcoal associated past fire events, I analyzed two soil samples collected from each the established 60 plots in the BCNWR (Yao and others 2012). Rock

fragments and biomass residuals were manually removed from soil samples followed by drying at 60 °C for 48 hours in a gravity convection oven. From these samples, 5 g soil was ground to fine powder using a 3 inch ceramic mortar and pestle.

Estimation of Total Soil Charcoal using the ^{13}C NMR Method

Because of the expense and time required for the NMR analysis, I only analyzed a subset (18 samples) of all soil samples (120 samples) by randomly selecting six soil samples from different plots of each fire group using this method. To prepare for NMR analysis, I added approximately 3 g of the pulverized soil, referred to as w_1 , into 50 ml centrifuge tubes (VWR International LLC., Ultra-high performance) for each sample. I acidified these samples using 10-20 ml gaseous 10% HCl to volatilize inorganic C (e.g. calcite), which was visually identified by bubbling within the solution (Harris, Horwáth, van Kessel 2001). The HCL treated soil solution was then centrifuged at 8000 rpm for 10 minutes followed by removal of any supernatant. Samples were treated with fresh HCL every two hours until no bubbling was visible in the tubes. Because the chemical composition of soil organic matter (SOM) using solid-state ^{13}C NMR spectroscopy is limited by high iron oxide concentration and low organic C concentration in soil (Gonçalves and others 2003), I also treated the soil samples with diluted 10% (w/w) hydrofluoric acid (HF) to remove paramagnetic material and to concentrate the amount of SOM (Preston, Schnitzer, Ripmeester 1989; Schmidt and others 1997). This was accomplished by adding 25 ml of 10% HF in each tube, followed by sealing the tube and putting on a shaking machine for 12 hours. Subsequently, samples were centrifuged at 8000 rpm for 10 minutes followed by supernatant removal and addition of new HF, which I repeated 3 times. The soil samples were then washed with deionized water for 3

times using the same procedure and dried in a gravity convection oven 50 °C for 48 hrs and weighed for mass referred to as w_2 . The C and nitrogen (N) concentrations of the HF-treated soil samples were then determined by thermal combustion with an elemental analyzer (Costech Comp. Model 4010). The recovery rates of C after the HF treatment were calculated as:

$$\text{C recovery (\%)} = \frac{\%C_{HF} \times \theta}{\%C_{original}} \quad \text{Equation 8}$$

where $\%C_{HF}$ is the percentage of C concentration in HF-treated soil, $\%C_{original}$ is the percentage of C concentration in the original soil (Chapter 1), and θ is the percent of soil mass remaining after HF treatment (%).

The solid-state ^{13}C NMR spectra of HF treated soil samples were obtained using magic angle spinning (MAS) techniques on a Bruker Avance III 300MHz spectrometer operating at a ^{13}C resonance frequency of 75 MHz and using a commercial Bruker double-bearing probe. Approximately 250 to 300 mg pulverized soil was packed into a 7 mm diameter cylindrical zirconia rotor, sealed with a Kel-F end-cap and spun at 5k Hz. I collected NMR spectra using two techniques, the Cross-polarization (CP) and the Bloch decay (BD), and then compared the results and selected the better one for the further analysis based on the mixing model prediction errors discussed later. The CP NMR spectra were acquired following a 90° ^1H excitation pulse, a 1 ms ^1H – ^{13}C contact pulse, and with a 5 s delay between acquisitions for 3000 scans. The chemical shift frequency was referenced to glycine as an external standard. To reduce noise to signal ratio of spectra, line broadenings of 30 Hz were applied prior to Fourier transformation. The BD NMR spectra were acquired from a single, direct excitation of ^{13}C atoms at 90° with a 90 s delay between acquisitions for 800 scans. For the BD spectrum, the signal from the

Kel-F rotor end-cap can significantly affect spectra (Smernik and Oades 2000), therefore, the end-cap spectrum was obtained as background and later subtracted from measured soil BD spectra.

Each spectrum (CP and BD) was phase and baseline corrected prior to integration. The spectra were first integrated between 0 and 220 ppm so that signals from all resonances were included for calculating the NMR observability of the ^{13}C nuclei in the sample (C_{obs}). The integrations of signal intensity were conducted by an adapted integration routine supplied with the instrument software (Topspin 3.0, Bruker Biospin). The C_{obs} was assessed by using glycine as standard, and assuming the C_{obs} of glycine was 100% (Smernik and Oades 2000). The C_{obs} was then determined for each sample as:

$$C_{\text{obs}} = \frac{I_{\text{sample}} \times m_{\text{glycine}} \times \%C_{\text{glycine}}}{I_{\text{glycine}} \times m_{\text{sample}} \times \%C_{\text{sample}}} \quad \text{Equation 9}$$

where I was intensity determined from integration, m was the mass of the sample in the NMR rotor, and $\%C$ was the percentage C concentration. (Smernik and Oades 2003) showed that CP NMR intensity of HF treated soils is often underestimated by the above equation because the magnetization intensity (I_{sample}) relaxes more rapidly than I_{glycine} during the 1ms contact time, via a process known as $T_{1\rho}^{\text{H}}$ relaxation. No attempt was made here to correct CP NMR spectral intensities for the difference in $T_{1\rho}^{\text{H}}$ relaxation. Therefore, my C_{obs} values for CP NMR were likely a conservative measure of C_{obs} .

The spectra were then integrated for seven major functional groups associated with chemical shift regions: alkyl C (0 to 45 ppm), N-Alkyl/Methoxyl C (45-60 ppm), O-Alkyl C (60 to 95 ppm), Di-O-Alkyl C (95 to 110 ppm), aromatic C (110 to 145 ppm), phenolic C (145 to 165 ppm), and amide/carboxyl C (160 to 215 ppm) (Knicker and Lüdemann 1995). These integration results, along with C and N concentrations, were

used as inputs into a molecular mixing model to estimate the concentrations of six biomolecules including carbohydrate, protein, lignin, lipid, carbonyl, and charcoal (Baldock and others 2004; Nelson and others 1999; Nelson and Baldock 2005a). Assignments of ^{13}C NMR signal intensity in the chemical shift regions associated with each component of the molecular mixing model and their molar elemental concentrations normalized to C concentration were derived from parameters of a previous study using standard references materials of each component to parameterize the mixing model for soil ecosystems (Baldock and others 2004). The predicted proportions of each molecular component calculated by the model are expressed on a TOC basis (%). These values were then adjusted according to the mass loss during the acid treatment to calculate biomolecular concentrations in untreated soil ($\text{g charcoal C kg}^{-1}$ soil). For example, the charcoal C concentration in untreated soil can be calculated as:

$$\text{Charcoal C (g C kg}^{-1} \text{ soil)} = 10 \times \rho \times \%C_{\text{TOC-HF}} \times \left(\frac{w_2}{w_1} \right) \quad \text{Equation 10}$$

where ρ is the proportion of charcoal component to TOC calculated by the mixing model (%), $\%C_{\text{TOC-HF}}$ is the percentage of C concentration in HF-treated soil determined by elemental analyzer, and w_1 is the weight of soil before treatment and w_2 is the weight of soil after HF acid treatment. I referred to the results of the molecular mixing model using CP and BD NMR data as CP NMR + model and BD NMR + model, respectively. To confirm detectability of charcoal in soil using the NMR method, I obtained a laboratory-produced charcoal standard derived from chestnut wood with $682.0 \text{ g C kg}^{-1}$ and 1.6 g N kg^{-1} (Hammes and others 2006) that I added to a sample soil from a site without known evidence of fire to produce a 14% wt/wt charcoal/soil mixture. The CP and BD NMR spectra were then obtained and compared for the charcoal-free soil, pure

charcoal, and soil-charcoal mixture. I also calculated the oxidation state values (Cox) of all organic materials in soil based on the mixing model in order to evaluate the potential charcoal decomposition (Baldock and others 2004).

Estimation of Total Soil Charcoal using MIRS

All pulverized soil samples (120 samples) were scanned in a Thermo Scientific Nicolet 380 FT-IR spectrometer (Thermo Electron Scientific Instruments LLC, Madison, WI, USA) equipped with a “Smart Performer” attenuated total reflectance accessory (model 0039-555) with proprietary Germanium on KBr beam splitter and a deuterated glycine trisulfate detector. Each sample was scanned in the wave numbers range of 4000 to 400 cm^{-1} (i.e. wavelengths range from 2500 to 25,000 nm) at 4 cm^{-1} resolution for 32 scans to produced one spectrum and using Helium Neon as reference laser. Two repeated scans were conducted for each soil sample under the constant flow of N_2 gas through the spectrometer, and measurements were automatically corrected for water vapor and atmospheric CO_2 .

To account for measurement variations of diffuse reflectance spectroscopy of powdery samples (Janik, Merry, Skjemstad 1998), spectra were applied with appropriate treatments before comparison, including baseline correction and mean standardization. Baseline corrections were completed using the instrument software (EZ OMNIC 7.3, Thermo Electron Corporation) to correct for uneven baselines. Spectra were then mean centered using the spectral regions that correspond to the most invariable zone (1861 to 2561 cm^{-1} in this study) where the standard deviation values were close to or equal to zero as the reference zone for standardization (Cadet and Offmann 1996).

To estimate soil chemical properties, I used partial least squares regression (PLSR) based MIR absorption data. Biomolecule component concentration data estimated by the NMR analysis were firstly transformed by calculating the square root of the data before entry into the PLSR model in order to minimize non-linearity in the calibration (Janik and others 2007). The calibration of the PLSR was completed by combining the square roots of biomolecule component concentrations estimated by the NMR + model method from the 18 soil samples (6 for each fire group) with the MIR absorption spectra, followed by transformation into a smaller set of orthogonal PLS loadings with derived scaling terms (Haaland and Thomas 1988; Janik and others 2007). Best fit calibration models were developed using the one-out cross validation procedure (Efron 2004). Although PLSR is a full spectrum method, from my preliminary analysis, I found that removal of certain spectral ranges enhanced the accuracy of the PLSR models. The optimal spectral range to use in the final PLSR calibration was selected to be 4000-1030 cm^{-1} based on the root mean square error of prediction (RMSEP) and the coefficient of determination (R^2) between measured and predicted values (Geladi and Kowalski 1986). After calibration, the PLSR model was used to predict the square roots of biomolecule component concentrations for the remaining 42 samples (14 for each fire group). Calibrations and predictions of PLSR model were performed for the six biomolecule component concentrations separately using R (version 2.13.1, The R foundation for statistical computing). The results predicted from the PLSR model were squared to obtain the predicted biomolecule component concentrations values, and results of two soil samples from each plot were then averaged to calculate plot means.

Statistical Comparison

The difference of six biomolecule component concentrations between three fire groups was assessed using ANOVA (SPSS 20) for results from both the NMR + model methods and the MIRS method (McCune and Grace 2002; Stroup and Stubbendieck 1983). I used the independent Student's t-test to assess differences of biomolecule component concentrations between any two fire groups. Significance level was set a priori at 0.05.

Results

Charcoal Estimated by ^{13}C NMR

For the 18 HF-treated soil samples prepared for the NMR analysis, the average soil mass loss due to the removal of calcite, iron oxides, and silicates by acid treatment was $83.8 \pm 5.3\%$ (one standard deviation). After the HF treatment, the soil C and N concentrations increased as compared to the values before the HF treatment, with no significant differences found between different fire groups (Table 3). The recovery of C after the HF treatment was estimated to be $84.7 \pm 12.8\%$.

The average C_{obs} was estimated to be $62.9 \pm 3.9\%$ for the CP NMR and $109.4 \pm 6.1\%$ for the BD NMR with no significant differences between fire groups. The CP and BD NMR spectra both showed that SOM was potentially dominated by organic matter with chemical shift regions associated with alkyl C (0 to 45 ppm), O-Alkyl C (60 to 95 ppm), and amide/carboxyl C (160 to 215 ppm) groups (Figure 7). I also found clear differences in the chemical shift region associated with aromatic C (110 to 145 ppm) for the charcoal-free soil, pure charcoal, and soil-charcoal mixture which demonstrated the ability of NMR technique to detect potential charcoal. Based on the NMR spectra data

inputs into the mixing model, dominant biomolecules of SOM were lignin, protein, and carbohydrate for both CP and BD NMR measurements (Table 4).

Table 3. Means and standard deviations of the soil chemical characteristics of sampled soil before and after the HF treatment, and associated mass loss rates. The Cox values from the mixing model based on the results of two NMR methods have been shown to indicate the oxidation states of bulk soil C pools for different fire groups.

Fire	C _{pre-HF}	N _{pre-HF}	Mass loss	C _{post-HF}	N _{post-HF}	Cox (CP)	Cox (BD)
group	(g kg ⁻¹)	(g kg ⁻¹)	(%)	(g kg ⁻¹)	(g kg ⁻¹)		
Recent	78.43	5.41	83.48	430.52	29.44	-0.23	-0.13
	(18.71)	(1.42)	(3.63)	(62.64)	(5.94)	(0.04)	(0.10)
Old	73.82	5.05	83.19	406.57	29.37	-0.22	-0.06
	(26.45)	(1.67)	(6.84)	(38.93)	(3.21)	(0.07)	(0.03)
No	81.28	5.47	84.59	442.95	28.08	-0.29	-0.13
	(24.35)	(1.43)	(5.10)	(52.91)	(1.84)	(0.12)	(0.09)

No significant difference in biomolecule concentrations among the three fire groups were found for the CP or BD NMR measurements based on ANOVA. However, the charcoal concentration predicted by the CP NMR + model method for the recent fire group was higher than the value of the old fire group, and significantly higher than the value of the no fire group based on the independent Student's t-test ($p=0.005$). The charcoal concentration predicted by the BD NMR + model method for the recent fire group was also higher than the value of the old fire group, and the value of old fire group was significantly higher than the value of the no fire group based on the independent Student's t-test ($p=0.038$). The charcoal concentration predicted by the BD NMR +

model method (average 1.40 ± 2.64 g C kg⁻¹ soil for all 18 samples) were higher, but not significantly, than the values predicted by the CP NMR + model method (average 0.87 ± 1.41 g C kg⁻¹ soil). The mixing model predictions based on the BD NMR spectra had higher accuracy (4.32 ± 4.3), indicated by the sum of square error, than the model predictions based on the CP NMR spectra (10.07 ± 5.78). Due to the higher sensitivity for aromatic C and better fit of the mixing model (lower sum of square error) of the BD NMR data, I used the BD NMR + model predicted soil biomolecule component concentrations to calibrate the PLSR of MIRS.

Charcoal Estimated by MIRS

The derived 8 components PLSR calibration model showed very high correlation of MIRS and the BD NMR + model predicted values for charcoal, protein, lignin, and lipid indicated by low RMSEP and high R² values. The PLSR calibration correlation slightly decreased for carbohydrate and carbonyl (Figure 8). The average values of biomolecule component concentrations predicted by the MIRS methods were similar to the results of the NMR + model methods (Table 4). There were no significant differences of any biomolecule component concentration among three fire groups. Only the charcoal concentration in the recent fire group was significantly higher than the value of the old fire group ($p=0.005$). By considering six biomolecule components together, I found that the results predicted by the MIRS method were not significantly different from the results predicted by the two NMR methods. However, the charcoal concentrations predicted by the MIRS method were higher than the results predicted by the NMR + model methods, especially significant for the no fire group ($p<0.001$).

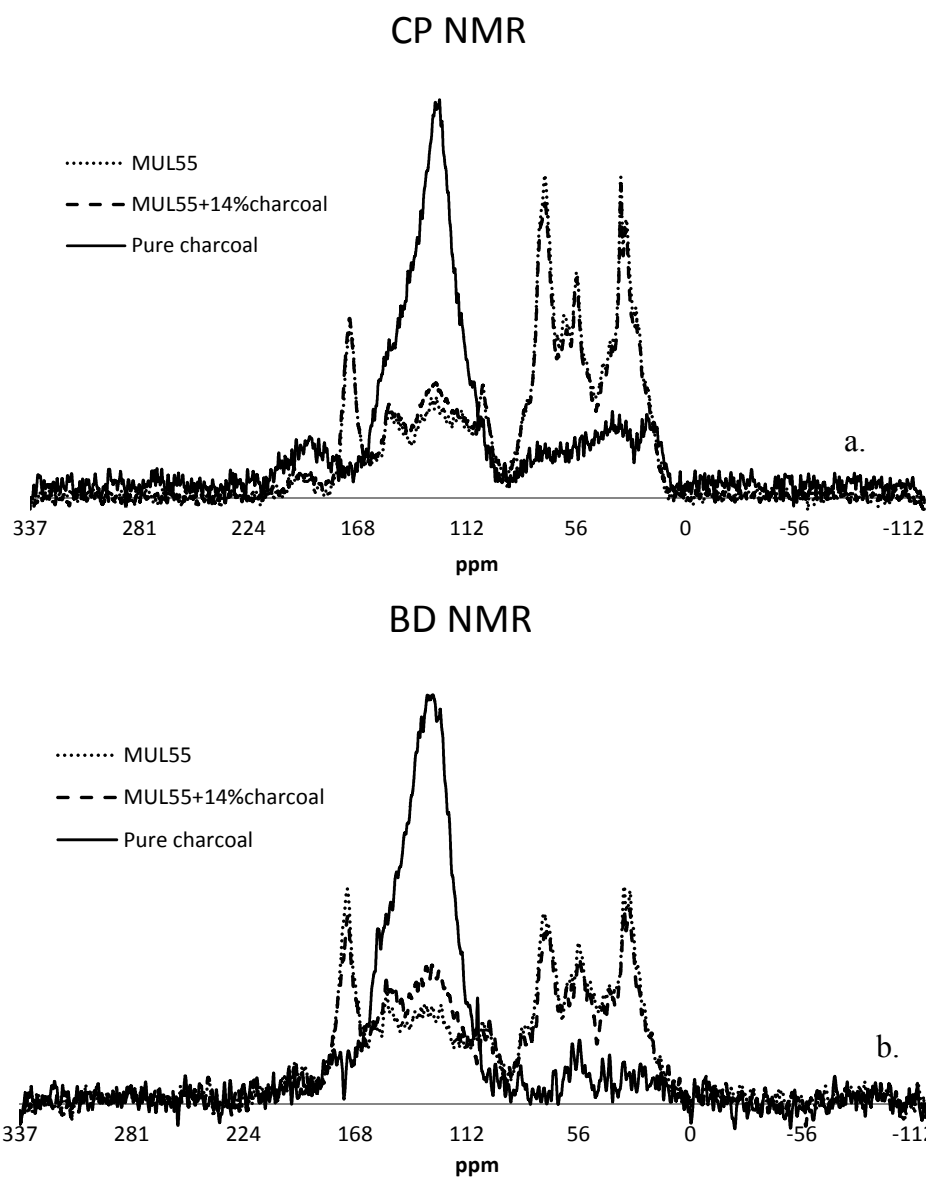


Figure 7. The CP and BD NMR spectra of charcoal-free soil for the site of MUL55, charcoal-free soil and standard charcoal reference mixture (MUL55 + 14% charcoal), and pure charcoal. The major chemical shift region for aromatic C is from 110 to 145 ppm. All spectra were scaled to represent same intensity integration from 0-220 ppm. (a) CP NMR spectra; (b) BD NMR spectra.

Table 4. Means and standard deviations of concentrations (g C kg⁻¹ soil) estimated for the six biomolecule components from the soil of the three fire groups predicted by the NMR + model and MIRS methods.

Fire group	Techniques		Charcoal	Carbo-hydrate	Protein	Carbonyl	Lignin	Lipid
Recent	NMR (6)	CP	1.79 ^a (1.80)	13.14 (3.21)	15.53 (5.02)	2.43 (1.34)	29.20 (8.25)	9.70 (3.20)
		BD	2.73 (3.06)	9.90 (3.45)	15.53 (5.02)	4.83 (2.11)	32.15 (9.92)	6.65 (3.01)
	MIR ^b (14)		2.65 (2.27)	10.01 (2.06)	14.23 (2.59)	3.29 (1.90)	26.47 (4.54)	6.75 (2.27)
Old	NMR (6)	CP	0.59 (0.88)	13.28 (7.03)	15.28 (6.64)	2.45 (0.99)	29.07 (14.20)	9.66 (5.50)
		BD	1.21 (1.70)	10.00 (4.35)	15.28 (6.64)	5.39 (2.89)	32.72 (18.48)	5.73 (2.05)
	MIR (14)		1.40 (1.04)	10.03 (3.79)	12.66 (5.08)	3.89 (2.94)	29.93 (11.36)	9.16 (4.97)
No	NMR (6)	CP	0.08 (0.18)	13.46 (5.83)	13.49 (5.31)	1.85 (0.99)	29.01 (10.71)	11.91 (6.29)
		BD	0.05 (0.11)	9.03 (3.13)	12.59 (4.31)	5.20 (2.21)	33.84 (13.52)	8.19 (4.19)
	MIR (14)		1.47 (1.69)	10.94 (2.62)	14.30 (4.22)	2.94 (1.94)	28.64 (9.53)	7.51 (2.91)

a: All NMR-predicted values were transformed from g C kg⁻¹ TOC to g C kg⁻¹ soil by adjusting to mass losses due to both HCL and HF acid treatments.

b: all MIRS-predicted values were based upon calibrations developed against the BD NMR derived results.

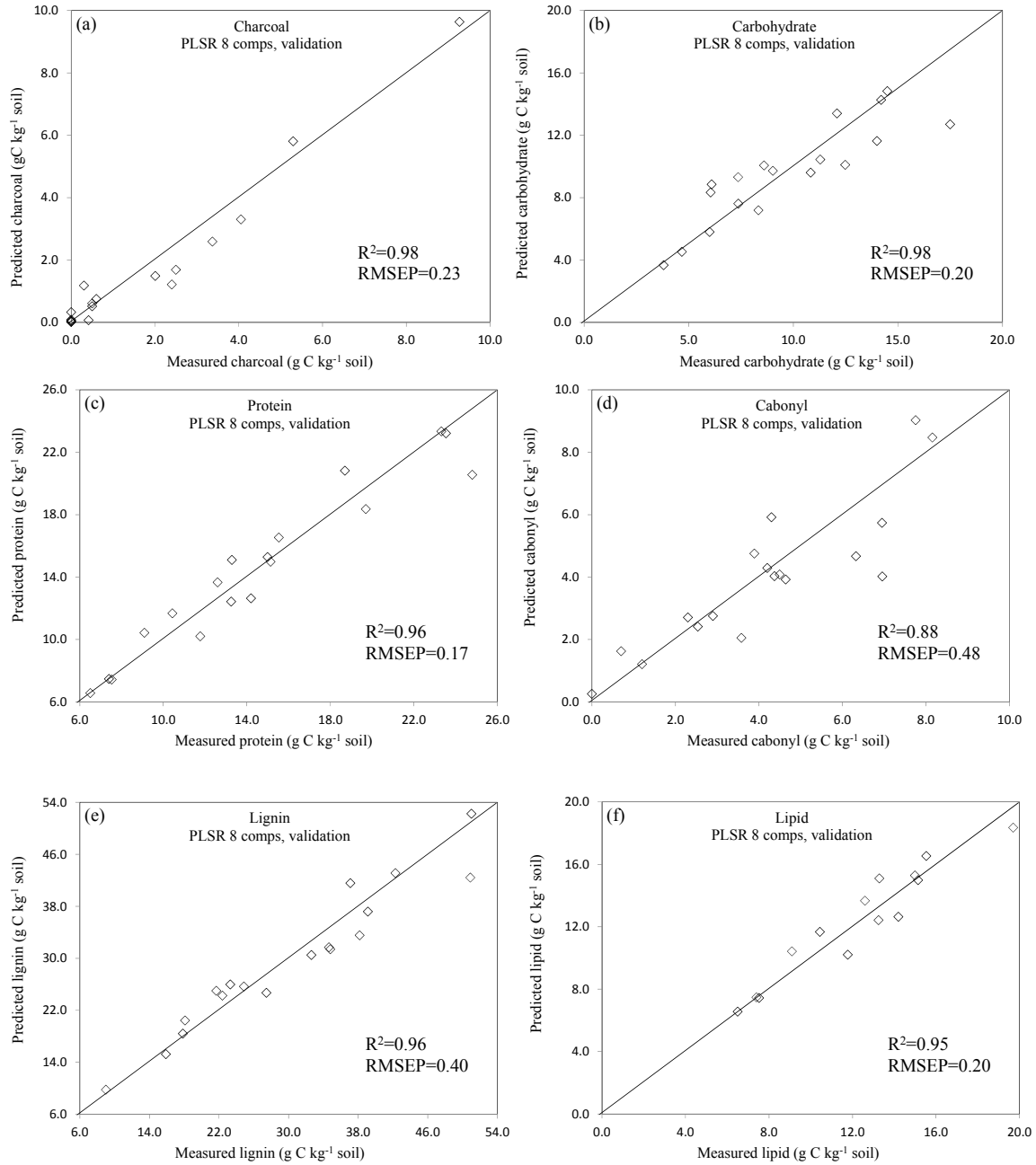


Figure 8. The plots of predicted versus measured values of leave-one-out cross validation of PLSR model for (a) charcoal, (b) carbohydrate, (c) protein, (d) carbonyl, (e) lignin, and (f) lipid with R^2 and RMSEP values shown on graphs. The PLSR was developed for the square roots of the measured biomolecule components concentrations. Therefore, the predicted results were transformed back to concentration values (g C kg^{-1} soil) by squaring. The RMSEP values were also adjusted by squaring.

Discussion

Charcoal in the Ecosystem

The regional soil charcoal concentrations estimated ranged from 0 to 9.27 g C kg⁻¹ soil (0 to 104.5 g C kg⁻¹ SOC) with an average value of 1.40 g C kg⁻¹ soil (20.8 g C kg⁻¹ SOC) predicted by the BD NMR + model; while the values predicted by the MIRS method ranged from 0.01 to 6.77 g C kg⁻¹ soil with an average value of 1.84 g C kg⁻¹ soil. The wide range of the predicted charcoal concentrations may be associated with variability of topography, change in vegetation cover over time, and fire histories in my study area. My estimates of charcoal concentration for the BCNWR woodlands are within the range of values for upper soils from other studies. For example, in a temperate mixed-grass savanna of the southern Great Plains of the U.S., a previous study found that charcoal comprised 50-90 g C kg⁻¹ SOC at 0-10 cm, and 70-130 g C kg⁻¹ SOC at 10-20 cm with the 2-3 years fire return interval having only a minor effect on the soil charcoal pool size (Dai and others 2005). In soils of an Alaskan black spruce forest, mean BC stocks in surface mineral soil were estimated to range from 25 g C kg⁻¹ SOC to 404 g C kg⁻¹ SOC (Kane and others 2010). In my study area, charcoal was estimated to comprise > 2% of the soil C pool (20.8 g C kg⁻¹ SOC). Therefore, charcoal represents an important part of the total C budget as soil C accounts for the major part of total C in the BCNWR woodlands (Chapter 1).

As each fire-affected site only had one fire disturbance, the differences in charcoal found in the old fire sites versus the recent fire sites may be used as a space for time substitution to estimate potential loss of charcoal from ecosystem for which I estimate at 4.7% (Figure 9a). Due to this high charcoal loss rate, the potential “legacy

charcoal” in soil from historical fires before the stand initiation (at least 80 years ago) should not be a confounding factor in estimating the regional charcoal loss rates. The mixing model derived Cox values indicate the decomposition states of the terrestrial organic residue, with lower values indicating a more reduced condition resulting from the accumulation of lipid and lignin molecular components (Baldock and others 2004). I did not find significant differences in the Cox values between different fire groups from neither the CP nor the BD NMR + model results (Table 3). Although the Cox values from my study were calculated for bulk soil C pool, I suspected the none-difference Cox values between fire groups can still be viewed as an indicator of no detectable charcoal decomposition in my soil samples due to the relatively short time since last fire (average 48 years).

The loss of charcoal may be attributed to off-site transport by erosion (Czimczik and Masiello 2007). Charcoal with a mean diameter < 53 μm is very mobile (Skjernstad, Taylor, Smernik 1999). Charcoal that remains on the soil surface is susceptible to loss caused by overland flow during high precipitation events. Surface charcoal may be translocated into lower soil horizons potentially due to mass movement with clay and silt, and biological activity (Dai and others 2005; Fedoroff, Courty, Thompson 1990). However, most of my study area is covered with a thin soil layer (<30 cm), which reduces charcoal translocation into deeper soil.

For the BCNWR, fire may be more prevalent on hillsides due to insolation and differential heating effects of fuels (Murray et al. in review). Because the average topographic slope of my plots was $15.3 \pm 13.9^\circ$, the charcoal transportation should be fairly substantial in this region. I suspected charcoal erosion loss should be closely

related to site slope with high slope tends to have higher loss rate during precipitation events than on flat surfaces (Rumpel and others 2006; Rumpel and others 2009). When I plotted the measured soil charcoal concentrations from the BD NMR + model method against the year since last recorded fire for high slope and low slope sites separately, I found a significant exponentially decreased soil charcoal concentrations with time trend for NMR analyzed sites ($F=7.16$, $p=0.02$), with the estimated annual charcoal lost rate for high slope sites of 5.3% and low slope sites of 4.2%, (Figure 9a). The coefficient of determination value (0.40) found for all values indicates that time since fire is a dominant variable describing charcoal soil concentrations. The analysis of charcoal and time since fire by slope categories showed that slope is influential. Higher topographic slopes had more predicted loss of site charcoal, with higher variation. This variation is likely due to site differences where upslope drainage, vegetation interception of precipitation, and slope shape are likely to affect site charcoal retention.

I did not find significant decreasing trends of soil charcoal with time since last fire based on the CP NMR + model nor the MIRS method (Figure 9b, 9c). The CP NMR + model method had lower detectability and sensitivity of charcoal indicated by lower predicted charcoal values and higher mixing model errors. The lack of significance from the MIRS method was likely due to the sensitivity of the MIRS to detect the lower range of charcoal concentration values. Because the MIRS estimates are based on multiple linear regression of absorption associated with different biomolecule concentrations, the bulk-sample approach I used in this study might introduce confounding factors for the underlying linear mechanistic light absorption assumption and limit detection of

compounds like charcoal at low concentrations under the interaction of other biomolecules.

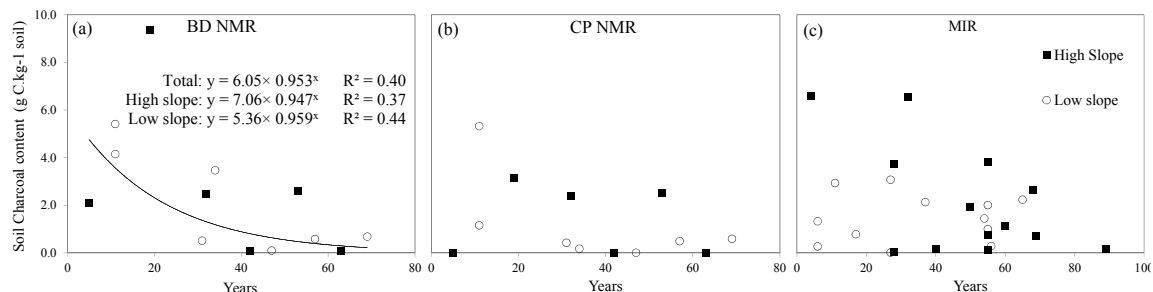


Figure 9. The plots of soil charcoal concentrations (g C kg⁻¹ soil) against the time since last recorded fire. The solid rectangulars represent plots with high slopes (≤ 20 degree), while the open circles represent plots with low slopes (0-20 degree). (a) The sites from both the recent and old fire group (12 sites) analyzed using the BD NMR + model method. Exponential models were applied for all sites together, and for high and low slope sites separately, with equations, R^2 values, and the exponential line for all sites together shown. (b) The sites from both the recent and old fire group (12 sites) analyzed using the CP NMR + model method. (c) The rest sites from both the recent and old fire group (28 sites) analyzed using the MIRS method. No exponential model line were showed for (b) and (c) due to no significant relationship was detected.

Comparison between the BD and CP NMR

The combined use of ¹³C NMR, C and N elemental analysis and the biomolecular mixing model has been shown to be an accurate method for characterizing the molecular composition of natural SOM across a range of diverse environments (Baldock and others 2004; Nelson and others 1999; Nelson and Baldock 2005a). In this study, I found the BD NMR + model method may accurately measure soil charcoal concentrations with sufficient detection sensitivity to differentiate charcoal concentration differences for sites with fire happened within the past 80 years. The calculated C_{obs} values for the BD NMR from my study were slightly higher than the values from a previous study that reported C_{obs} can range from 79 to 107 % for different organic materials (Smernik and Oades 2000). The high C_{obs} indicated the BD NMR is a quantitative method and can

theoretically detect all C atoms in this soil. The C_{obs} value of CP NMR from my study ranged from 57 to 69 %, indicating that CP method can only detect part of C in this soil.

The BD NMR + model may also be a more efficient method to assess soil charcoal because of its ability to detect highly aromatic structures that are likely to be under-represented in CP NMR spectra due to their low protonation (Smernik and Oades 2000). For the BD technique, ^{13}C nuclei are directly irradiated with a radiofrequency pulse. The CP technique first magnetizes ^1H nuclei by a radio frequency pulse that is subsequently transferred from the ^1H atoms to local ^{13}C nuclei. In highly condensed aromatic C structures like charcoal, ^{13}C nuclei can be many bond-lengths away from the nearest ^1H nucleus. Because of this, CP NMR does not efficiently magnetize highly condensed or graphitic ^{13}C atoms from nearby protons (Smernik and others 2002). Therefore, the soil charcoal concentrations predicted by the BD NMR + model method were higher, but not significantly, than the values predicted by the CP NMR + model method (Table 4).

Statistically, the BD NMR + model method was favorable because the lower sum of square errors of the mixing model. The range of sum of square error from both CP and BD NMR + model methods were similar to a previous study examining soil samples from a range of diverse environments (Baldock and others 2004). However, the lower sum of square error from the BD NMR mixing model indicated higher prediction accuracy for charcoal. From my soil samples, I found high lignin concentrations possibly due to inputs from the evergreen juniper leaves litter (Tiedemann and Klemmedson 1995). Because lignin also contains aromatic C structures similar to those found in charcoal, high lignin concentrations in my soil samples potentially contributed to the lower

prediction error by the BD NMR + model method as compared to the CP NMR + model method. Another possible factor that can result in high errors from the mixing model was the concentration of “humic” structures. The “humic” substances, formed by abiotic mechanisms rather than biotic processes, were not included in the mixing model (Nelson and Baldock 2005b).

Factors Related to MIRS Predicted Charcoal

MIRS is theoretically based on light absorption by vibrations of covalent bonds associated with a particular chemical functional groups (Janik and others 2007). Data from the MIRS contained fewer mechanistic absorption spectra associated with specific chemical bonds as compared to other studies (Figure 10) (Janik and others 2007). This might be due to the fact that soil in my study area contains high levels of goethite and calcite, which can obscure the MIR signal of SOM and may reduce the predictability of organic groups using MIRS (Janik, Skjemstad, Raven 1995). The benefits of PLSR are the significant compression of information, the ability to handle collinear data sets and some types of non-linearity, as well as the discrimination between relevant spectral information and systematic error in measurement or spectral noise (Haaland and Thomas 1988). By using PLSR on MIRS data and using the BD NMR + model results as the reference data for calibration, MIRS showed high accuracy in predicting all biomolecule component concentrations (Figure 8). For the model predictions to be considered sufficiently robust, the calibration spectra must be characterized by spectral features associated with various forms of organic matter, rather than co-variance due to other features such as clay content or mineralogy (Janik and others 2007). For instance, I compared the MIR spectra and the PLSR cross-validation coefficient spectra of the

average of first 6 loading weights for charcoal, and found that weight loadings for charcoal pronounced peak characteristic of aromatic C near 1581 and 1393 cm^{-1} , which were similarly indicated in previous studies to be possible signature chemical shift ranges for aromatic C (Figure 10) (Janik and Skjemstad 1995; Janik and others 2007).

The predictions by MIRS of charcoal as well as other biomolecule component concentrations were similar to the predictions by the BD NMR + model method, except for the high average charcoal concentration for the no fire group. I found this high average value for the no fire group was caused by high charcoal concentrations estimated (about 4 and 6 g C kg^{-1} soil) in 2 plots out of total 16 plots. I suspected that these two plots actually had fires, but were not recorded by the tree ring study. Another possible source of error in the PLS prediction of charcoal was due to the uncertainty of not having accounted for all of the soil charcoal in the reference data. I used the charcoal concentration predictions from the BD NMR + model as the reference, but this method also only predicts a proportion of charcoal in total soil BC continuum.

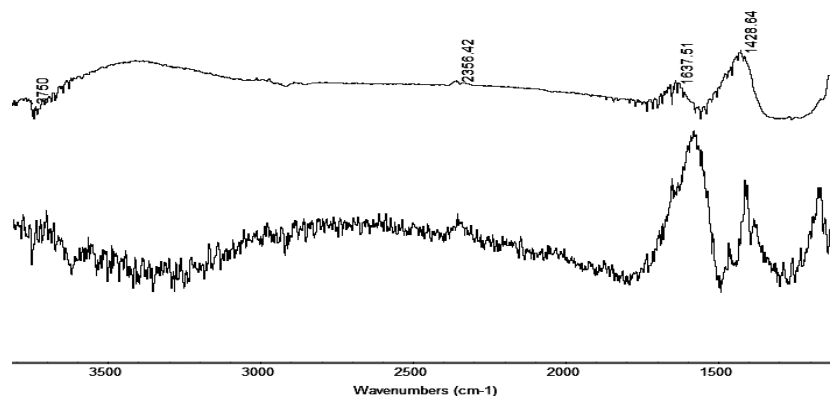


Figure 10. MIR spectra of a soil sample with 3.37 g C kg^{-1} soil of charcoal predicted by the BD NMR + model method (top); the PLSR cross-validation coefficient spectra of the average of first 6 loading weights for charcoal (bottom).

CHAPTER FOUR

Modeling Ecosystem Property Changes due to Fire Disturbance

Introduction

The effects of different fire types on wildland ecosystems may include decreasing C storage, changing vegetation communities, altering soil properties, and affecting water yield (Amiro and others 2006; DeLuca and Aplet 2008; Goetz and others 2007; Knicker 2007). Fire can significantly reduce biomass C storage with up to 98% directly combusted depending on fire severity (Stocks and Kauffman 1997; Chapter 2). The effects of fire are also thought to be related to the seasonality of fire, as fire can disrupt plant growth, affect the available seed banks, or top-kill root sprouting species (Knapp, Estes, and Skinner 2009). The composite fire effect on C cycling may be reflected in the net ecosystem exchange (NEE) which is defined as the net primary productivity minus episodic C loss due to non-respiratory processes such as natural or anthropogenic disturbances. One of the less-understood parts, however, is the production of charcoal. The simple definition of NEE, however, does not account for the charcoal production.

Fire-derived charcoal represents a potentially important part of terrestrial C cycling due to its long persistence in soil (Kuhlbusch and Crutzen 1995; MacKenzie and others 2008). Charcoal is recalcitrant to biochemical alteration and may require hundreds to thousands of years to decompose depending on the percentage of polyaromatic BC in charcoal and conditions of the surrounding environment (Nguyen, Brown, Ball 2004). The production of fire-derived charcoal may vary for different ecosystems (Alexis and others 2007). Charcoal production is higher for large intact woody material and lower for

foliage and understory herbaceous vegetation (Nocentini and others 2010). In areas with a high frequency of fire, the amount of charcoal in the soil may be high (MacKenzie and others 2008). Therefore, total soil organic C content may not be a good indicator of C substrate available for microbes or a good predictor of site-level decomposition as soil may contain charcoal in addition to labile C (Clein and others 2000). Because decomposition of charcoal is relatively slow, loss of charcoal may be primarily due to soil erosion controlled by the slope and surface runoff (Rumpel and others 2006; Rumpel and others 2009).

Fire may increase surface runoff due to the removal of vegetation (Inbar, Tamir, Wittenberg 1998; Oguntunde and others 2008). However, charcoal inclusions into the soil profile increase soil water availability due to the presence of porous charcoal that retains water. This is especially effective in coarse-textured soils and soils with large amounts of macropores (Glaser, Lehmann, Zech 2002; Piccolo, Pietramellara, Mbagwu 1997). Tryon (1948) found that volumetric soil water increased by 18% with an addition of 45% (by volume) charcoal to a sandy soil. For a clay soil, he found volumetric soil water decreased approximately 20% with the same charcoal treatment. The impact of changed soil water availability associated with the fire-derived charcoal additions on the primary productivity has yet to be evaluated.

Models may be used to develop basic theoretical understandings of ecosystem functions that are generally difficult to assess by field-based experiments. However, many current ecosystem process models do not mechanistically simulate the various effects of fire disturbances (White and others 2000). In this study, I modified an ecosystem process model (Biome-BGC, Thornton and others 2002) to simulate the

effects of fire disturbance with different severities and seasonality on C cycling related ecosystem properties, the production and loss of charcoal, and charcoal-affected soil water availability. Using site data on fire history and vegetation composition from my previous study (Yao et al. 2012), I applied the modified model on the Central Texas woodland ecosystem to assess the effects of fire on ecosystem properties, specifically, vegetation C, projected leaf area index (PLAI), and NEE. The overall fire effects were first tested between sites with different fire histories by accounting for simulations across different settings. The fire effects were also compared between different fire severities, seasons, and vegetation types. The charcoal production and loss were also simulated and compared for a range of fire severities, seasons, vegetation types, and topographic slopes. The feedback effects of fire-derived charcoal on soil water availability were assessed for different types of soil by examining the site water balance related PLAI and NEE (Grier and Running 1977).

Methods

The Biome-BGC Model

The Biogeochemical Cycles terrestrial ecosystem process model (Biome-BGC 4.2, Thornton and others 2002, available on <http://www.ntsg.umn.edu/project/biome-bgc>) simulates the biological and physical processes controlling C, N, and water dynamics, and can estimate fluxes and storage of energy, water, C, and N for the vegetation and soil components of terrestrial ecosystem at areas ranging from 1 m² to the entire globe (White and others 2000). The primary purpose of the model is to study global and regional interactions between climate, disturbance and biogeochemical cycles (Thornton and

others 2002). The Biome-BGC 4.2 runs on prescribed site conditions, meteorology, and parameter values. Theory and applications of the Biome-BGC model are widely available. For example, the Biome-BGC 4.2 was used to produce a C budget for the forested region of Oregon, and to determine the relative influence of differences in climate and disturbance among the ecoregions on C stocks and fluxes (Law and others 2004).

The Biome-BGC 4.2 is a one dimensional model as it represents a point in space with all fluxes and stocks scaled to a per square meter basis (Thornton 1998). The Biome-BGC 4.2 simulates dynamics at a point of a plant functional type and ignores successional dynamics. Model structure is discussed by Thornton (1998). Briefly, the model simulates primary production with the Farquhar photosynthesis model (Farquhar, Caemmerer, Berry 1980) from leaf C pools based on leaf temperature, CO₂ concentration, leaf C to N ratio, and incoming solar radiation. This process is controlled by the simulation of the stomatal conductance on both the sunlit and shaded canopy leaves. Evaporation and transpiration are important processes that control the water availability for leaf photosynthesis, and are estimated using the Penman-Monteith equation (Monteith and Unsworth 2008; Thornton and others 2002). Two types of autotrophic respiration are simulated in the Biome-BGC 4.2 model, including maintenance respiration, which is an exponential function of tissue mass, N concentration, and temperature, and growth respiration, which consumes a proportion of newly assimilated C. The assimilated C is allocated to other plant structures under the consideration of N availability based on a set of fixed fractions defined by model user. The biomass C is transferred through different biomass pools by allocation processes and finally removed from the system by the decomposition and disturbance processes. The major biomass pools of the Biome-BGC

4.2 model include leaves, stems, coarse woody debris (CWD), litter, and SOM. The litter C is divided into three different pools that undergo chemical degradation at different rates, which creates a connected series of SOM pools. The assimilation and decomposition processes compete for one pool of soil mineral N. PLAI (m^2 leaf area per m^2 ground area), calculated by multiplying leaf C with the average specific leaf area (SLA), controls canopy radiation absorption, water interception, photosynthesis, and litter inputs to detrital pools and is central to the Biome-BGC 4.2 representation of N cycling. The C to N ratios of different biomass and SOM pools define nutrient requirements for new growth, plant respiration rates, photosynthetic capacity, litter quality, and decomposition rates, therefore, are important constraints of ecosystem processes.

Meteorological data required by the Biome-BGC 4.2 model include daily minimum temperature (T_{\min}), daily maximum temperature (T_{\max}), precipitation, humidity, solar radiation, and day length. In this study, I obtained the regional meteorological data, including T_{\min} , T_{\max} , and precipitation primarily from the National Oceanic and Atmospheric Administration (NOAA) National Climate Data Center (<http://www.ncdc.noaa.gov/cdo-web/>) for the station of Burnet, TX, US (30.76° , -98.23° ; elevation 391.7 m; NOAA station ID:USC00411250). The available meteorological data from this station is from 1893 to 2012; however continuous quality data is from 1953 to 2005 with data coverage above 99%. I also downloaded meteorological data for the period of 2006-2011 from the Remote Automated Weather Stations (RAWS) Climate Archive (<http://www.raws.dri.edu/wraws/>) located at Balcones, Texas, USA, which has data coverage above 99%. Missing data were filled with the average values from the dates before and after the missing periods. I combined these two

datasets to create the meteorological data of a 59-year span ranged from 01/01/1953 to 12/31/2011. These meteorological data (Tmax, Tmin, and precipitation) were used as input data for the MT-CLIM 4.3 (Thornton and Running 1999; available from <http://www.ntsg.umd.edu/project/mtclim>) to calculate other model required meteorological data, such as vapor pressure deficit and solar radiation, for each specific location by accounting for the differences in elevation, slope, and aspect.

Model Modification

In order to simulate fire effects on ecosystem properties, I modified the Biome-BGC 4.2 model to be able to simulate different severities of fire disturbance happening at any given time, referred to here as the Biome-BGC 4.3 model. In the new model, fire consumption of individual biomass pool was set to be associated with the user-defined severity of each fire. I also added sub-models of the fire-derived charcoal production, loss, and effect on soil water availability. Model processes not mentioned in the following text remain unchanged from the 4.2 version model.

Fire disturbance. The Biome-BGC 4.2 model simulates fire as a part of a daily mortality process, which is modeled as daily losses of living and dead biomass based on a fixed fire turnover rate. These losses are assumed to be transferred directly to the atmosphere and lost from the system. In order to simulate different fire events that can happen at any given time, I modified the model to include a custom time series file specifying the dates and severities of individual fire events. For each fire event, a fire severity level (SL) was assigned ranging from 1 to 3 (1: low severity surface fire; 2: moderate severity fire; 3: high severity crown fire). Biomass pools affected by different

SL fires were different with the amount of biomass consumed depending on the combustion factor (CF) scalars (Table 5). For this function, I assumed low severity surface fires (SL=1) would only affect the surface litter and CWD biomass pools, while moderate and high severity fires (SL=2 and 3) would affect the litter, CWD, leaf, and stem pools. The root biomass pool was not affected by fire in this function. The CF scalar represents the percentage of available fuel consumed during a single fire, which varies greatly between different ecosystems (ranged from 19% to 98%) and is closely related to fire severity (Conard and A. Ivanova 1997; Kauffman, Cummings, Ward 1994; Stocks and Kauffman 1997). Based on the CF scalars from the previous studies, I assumed the fire with the lowest severity (SL=1) had CF scalar of 27% for my study area. The CF scalars for higher severity level fires were assumed to be positively related to the SL values. Therefore, the Biome-BGC 4.3 model simulated moderate severity fires (SL=2) with the assigned CF scalar of 54% ($27\% \times 2$), and high severity fires (SL=3) with the CF scalar of 81% ($27\% \times 3$).

Table 5. The combustion factor (CF) scalars for different biomass pools for fires with different severities.

Severity Level	Fire Type	Combustion Factor (CF) scalar			
		Litter	CWD	Leaf	Stem
1	Low severity surface fire	27%	27%	NA	NA
2	Moderate severity fire	54%	54%	54%	54%
3	High severity crown fire	81%	81%	81%	81%

Because the Biome-BGC 4.2 does not include the post-disturbance regeneration process, the preliminary simulations showed vegetation C recovery following an intense

crown fire was very slow due to the low photosynthesis rate as a result of foliar loss due to fire. Therefore, I added a sub-model of vegetation regrowth by assuming a small fraction of the live stem C (0.05%) was transferred to the live leaf C pool when the leaf C was $< 0.1 \text{ kg m}^{-2}$ due to fire loss.

Charcoal production. The charcoal production rate varied in different ecosystems with the estimated range of 0.6 % to 8 % and most estimates below 2.5% from various studies (Alexis and others 2007; DeLuca and Aplet 2008; Kuhlbusch and Crutzen 1995). The amount of charcoal production during a fire event is small in comparison with the atmospheric losses, as indicated by a study in a scrub oak ecosystem in Florida that fire-related atmosphere C loss was approximately 21 times the amount of charcoal-C being produced with the estimated charcoal production rate at 4-6% (Alexis and others 2007). Therefore, in the sub-model of charcoal production, I calculated the fire-derived charcoal by assuming the fire-combusted biomass C that lost to the atmosphere was 21 times larger than the charcoal being produced, which resulted in charcoal production rates ranging from 1.3% to 4.3% in my study. I then calculated the percent of charcoal (charcoal%) in soil by dividing the simulated total charcoal mass into the total soil mass that was calculated from the input soil bulk density and soil depth.

Charcoal loss. Fire-derived charcoal is generally deposited on forest floors until it is mixed into the soil or lost from the site (DeLuca and Aplet 2008; Lynch, Clark, Stocks 2004). A variety of processes, including freeze–thaw events, tree overthrow, and soil disturbance by animals, may mix surface charcoal into the mineral soil (Gavin 2003). Direct measurements of the proportion of surface charcoal mixed into the mineral soil are

lacking, but the large range of charcoal contribution to mineral soil C suggests that the proportion is highly variable (DeLuca and Aplet 2008). Due to the lack of field measured data on soil charcoal movement, I calibrated the parameters of the charcoal loss sub-model (the charcoal mix into soil rate, the charcoal loss scalar for a single maximum outflow event, and the soil-charcoal loss scalar as introduced in the following text) based on the data from my previous charcoal storage change study (Chapter 3). The model calibration was performed on one of the study sites (WEB002) with fire occurring in 1956. The calibration included adjusting the charcoal loss parameters to achieve an annual charcoal loss rate similar to the previous study estimated value of 4.7%. From the calibration, I assumed an average of 20% of the fire-derived charcoal on the woodland floor would be mixed into deeper soil layer every year. Charcoal remains on woodland floor is vulnerable to loss through erosion, while the charcoal mixed with the mineral soil is considered more stable and resistant to loss (Zackrisson, Nilsson, Wardle 1996b; Chapter 3). I assumed the loss rate of soil-mixed charcoal to be only 10% of surface charcoal loss rate in this study. The erosion loss of charcoal was simulated for both surface and soil mixed charcoal as a function of two factors: the slope and the total outflow (Rumpel and others 2006; Rumpel and others 2009).

$$Charcoal\ loss = \partial \times \delta \times \frac{outflow}{outflow_{max}} \times charcoal \times f(slope) \quad \text{Equation 11}$$

where ∂ is the correction factor for mixture condition of charcoal within the soil (1 for surface charcoal, and 0.1 for soil mixed charcoal in this study). The δ is the charcoal loss rate scalar for a single maximum outflow event with the value set to be 20%. This value was within the charcoal loss rate range of 7 to 29% from Rumpel and others (2009).

The $\frac{outflow}{outflow_{max}}$ is a scalar for erosion intensity of individual surface overland flow event

based on the maximum surface overland flow ($outflow_{max}$). I set the $outflow_{max}$ to a value of 70 kg m^{-2} based on preliminary simulations which provided a range of overland flow values for different slopes and vegetation types. The *charcoal* variable represents the storage of charcoal in either surface or soil charcoal pool. The $f(slope)$ variable is a slope correction factor for charcoal loss, which was relativized to the regional average slope value (15°) in this study.

$$f(slope) = \sqrt{\frac{\sin \theta}{\sin 15^\circ}} \quad (1 \leq \theta \leq 90) \quad \text{Equation 12}$$

where θ represents the site slope in degree from 1 to 90, which resulted in the $f(slope)$ values ranged from 0.25 ($\theta = 1$) to 2 ($\theta = 90$). The $f(slope)$ value is set to 0.20 on a flat surface ($\theta = 0$), which is slightly lower than the $f(slope)$ value on a 1 degree slope.

Charcoal effects on soil. In this study, I focused on assessing the effects of charcoal addition on the available soil water content. The soil type information for my study area was derived from the Soil Survey Geographic (SSURGO) database (USDA 2012), which showed that regional soils are dominated by gravelly clay loam from bracket-rock outcrop complex (80%), along with some stony clay from Tarrant soils (14%) and some silty clay loam (6%). The gravelly clay loam soil has high sand and low clay content (approximately 45% sand, 30% silt, and 25% clay), which is different from the stony and silty clay soils that have higher clay content (approximately 25% sand, 25% silt, and 50% clay). In this study, I compared the charcoal addition effects between the high sand content (45% sand, 30% silt, and 25% clay) and high clay content (25% sand, 25% silt, and 50% clay) soils. Tryon (1948) studied the effects of charcoal on the soil water content by adding charcoal in different soils and found that charcoal can linearly

decrease available soil water for high clay content soils (Equation 3) while increasing available soil water for high sand and silt content soils (Equation 4,5). For the sub-model of charcoal addition effects in the Biome-BGC 4.3 model, the adjustments factors for soil water associated with each soil type were calculated based on the %charcoal:

$$\text{Clay soil: } \Delta_{\text{sw_clay}} = -0.111 \times \text{Charcoal\%} \quad \text{Equation 13}$$

$$\text{Sand soil: } \Delta_{\text{sw_sand}} = 0.065 \times \text{Charcoal\%} \quad \text{Equation 14}$$

$$\text{Silt soil: } \Delta_{\text{sw_silt}} = 0.015 \times \text{Charcoal\%} \quad \text{Equation 15}$$

where Δ_{sw} is the change of available soil water in % for each soil type in the presence of charcoal.

The effect of charcoal addition on the soil volumetric water content at saturation (vwc_sat) was calculated by assuming the charcoal effects on soil clay, sand, and loam parts were independent (Equation 6).

$$\text{vwc_sat_c} = (1 + a \times \Delta_{\text{sw_clay}} + b \times \Delta_{\text{sw_sand}} + c \times \Delta_{\text{sw_silt}}) \times \text{vwc_sat} \quad \text{Equation 16}$$

where vwc_sat_c is the charcoal affected volumetric water content at saturation (dimensionless), a is the percent of clay in the soil (%), b is the percent of sand in the soil (%), c is the percent of silt in the soil (%).

Simulated Vegetation Types

The woodland vegetation in my study area is dominated by two vegetation types including: evergreen needle-leaf (enf , e.g. Ashe's juniper) and deciduous broad-leaf (dbf , such as Texas red oak and black cherry). Evergreen broad leaf species like live oak are found in my study area, however showed limited stand dominance therefore were not included in the study. Because the Biome-BGC 4.3 model simulates one vegetation type at a time and does not include forest succession dynamics, I ran simulations for both enf

and dbf vegetation type separately and then calculated composite site results according to site specific vegetation composition derived from the previous field measurements (Chapter 2). I used the default eco-physiological constant values from the Biome-BGC 4.2 model for the both enf and dbf vegetation types to reduce the number of variables that may be influencing the results of my study.

Model Simulation and Statistic Comparison

In this study, I selected six sampled sites from my previous studies (Chapter 2) with a range of fire occurrences (1956 to 2000), slope values (0 to 40 degrees), and vegetation compositions, to utilize as representative simulation locations (Table 6). For each vegetation type, the Biome-BGC 4.3 model was first run in the “spin-up” mode without fire disturbance to bring the model state variables into a steady-state. The “spin-up” run began with no SOM and a very small initial vegetation component (Thornton and others 2002). After average 2000 simulation years, the model reached a steady state defined as changes in annual average daily soil C stocks $< 0.0005 \text{ kg m}^{-2} \text{ yr}^{-1}$ (Thornton 2010). These resultant model parameters (such as SOM) were output as an “endpoint” file. The “endpoint” file was then used to define initial conditions for my simulations of fire disturbance for each study sites. Using steady states as the simulation start points allowed comparison across sites in order to assess the potential effects of fire on the changes of vegetation C, PLAI, NEE and charcoal production.

To establish a model baseline, I first ran the Biome-BGC 4.3 model without fire for the 1953 to 2012 period based on the mean site attributes identified from the sites without fire (Chapter 2). Each site was simulated 24 times accounting for different fire and environment settings (Figure 11). In the simulations, winter fire occurred on the first

day of the year, while summer fire occurred on year day 200, approximately the coldest and hottest time of the year in Central Texas, respectively, indicated by both the NOAA and RAWS data.

Table 6. The fire occurrence year, environmental characteristic parameters, and vegetation composition for sites that selected to represent the recent and old group.

Fire group	Site	Fire year	Slope (degree)	Soil depth (m)	Aspect	Elevation (m)	Enf (%)	Dbf (%)
Old	WEB002	1956	15	0.88	120	349	50	50
	GAI059	1964	5	0.33	110	375	25	75
	WEB004	1969	30	0.27	30	322	5	95
Recent	WEB011	1972	40	0.07	30	380	50	50
	FLX024	1984	20	0.78	30	294	60	40
	ROG201	2000	0	0.43	NA	397	45	55

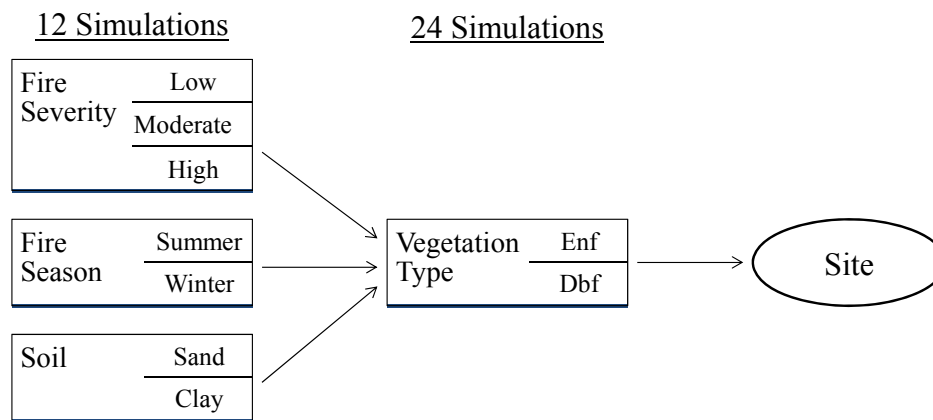


Figure 11. The simulation settings for each site. Each site was simulated 24 times, which accounted for three different fire severity levels (low, moderate, and high), two fire seasons (winter and summer), two soil types (sand-dominated and clay-dominated), and two vegetation types (enf and dbf).

From these simulations, I selected vegetation C, charcoal C, PLAI and NEE as outputs from the model to compare. Vegetation C represents the primary site C storage that can be directly affected by fire. PLAI can also be directly affected by fire and controls the post-fire biomass accumulation. PLAI is thought to be primarily related to site water balance (Grier and Running 1977). Therefore, I expected it to detect the changes associated with charcoal-affected soil water availability. NEE not only indicates the immediate fire-affected C flux but also relates to the post-fire productivity and the decomposition of fire-affected biomass. I also suspected that site water balance affected by fire-derived charcoal might potentially lead to changes on the photosynthesis rates and would be reflected on NEE. In order to better detect any slightly changes of fire-affected NEE, the NEE anomaly values were also calculated by subtracting the NEE baseline from the simulated fire-affected NEE. I used the last simulation year (end-year) annual mean values of each parameter as the primary model output values. I assumed that the simulated end-year values may represent the current stand states that can be compared with field measured values (Chapter 2). However, this study was not intended to use the modified Biome-BGC 4.3 model to simulate a specific location, rather to calibrate the model values and assess ecosystem processes associated with different types of fire disturbance and the inclusion of fire derived charcoal.

For each site, the outputs from 12 simulations of each vegetation type were averaged and then were weighted according to the site specific vegetation composition to obtain site composite values. The results were also compared between different fire severities, fire seasons, slopes, and soil textures. For example, to test the effects of different fire severities, outputs from simulations for all sites with the same fire severity

(but different fire seasons, slopes, and soil types) were grouped and compared with simulations with the other fire severities. To exclude the effects of fire and isolate the effects of fire-derived charcoal on site water balance and other ecosystem properties, I also developed an option in the Biome-BGC 4.3 model to not add the fire-derived charcoal in the soil that referred to as the “no charcoal in soil” option. All the simulations were performed again with the “no charcoal in soil” option, and then compared with the normal model runs to assess the soil charcoal effects.

Independent student t-test was applied to compare results between two variables. I used one-way ANOVA followed by the *post-hoc* t-test to compare the results differences between three variables. Significance level was set a priori at 0.05.

Results

Fire Effects on Ecosystem Properties

From my simulations, high severity fires reduced nearly 50% of total vegetation C, while low severity fires only slightly reduced vegetation C due to model specification of only surface litter C was consumed for this fire type (Figure 12a). Following simulations of high severity fires, the total vegetation C took average 50 years to recover to the pre-disturbed state with a recover rate of $0.09 \text{ kg m}^{-2} \text{ yr}^{-1}$. The moderate and high severity fires reduced the simulated PLAI significantly. However, the simulated PLAI increased quickly after both fire types requiring approximately five years to achieve pre-fire values (Figure 12b). Analysis of the NEE anomaly values indicated that fire-affected stands emitted slightly more C for 3-4 years after fires and then began to sequester more C than the non-fire baseline scenario for the most of simulation years (Figure 12c). For

sites with higher severity fires, the NEE anomaly values generally had slightly higher values, indicating higher C sequestration rates.

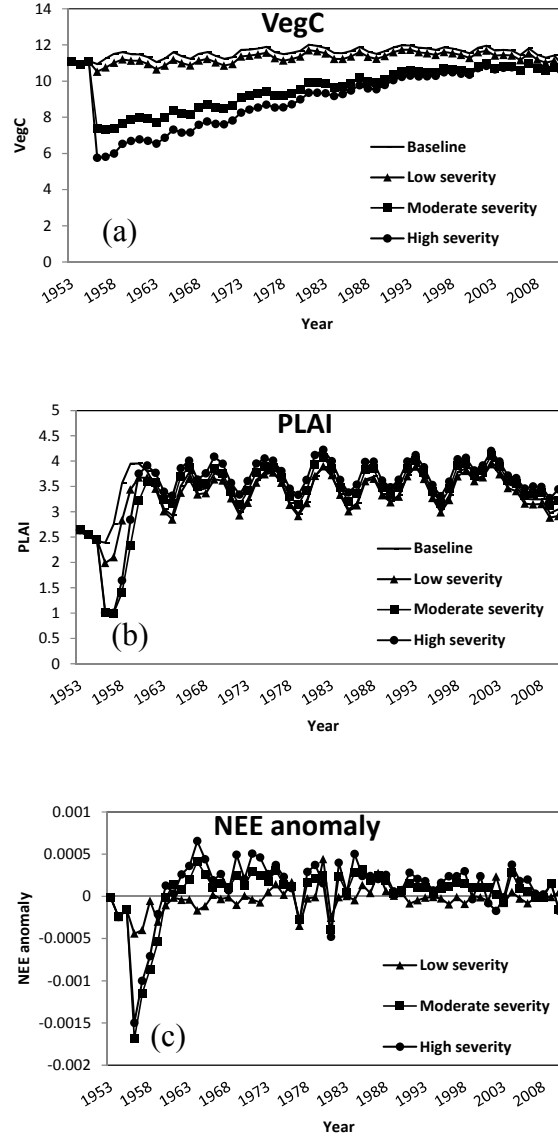


Figure 12. The time series of simulations for the site of WEB002 with fire happened in 1956. For each variable, all three severity fires were simulated and shown. For vegetation C and PLAI value, the baseline simulations with no fire disturbance were also shown. (a) Vegetation C (kg m^{-2}). (b) PLAI value. (c) NEE anomaly ($\text{kg m}^{-2} \text{ day}^{-1}$), calculated by subtracting the NEE baseline from the simulated fire-affected NEE.

By comparing simulated site composite results between different fire groups, I found that the simulated end-year vegetation C from the recent fire group was significantly lower than that of the old fire group ($F=22.73$, $t=3.49$, $p<0.01$), and both were lower than the non-fire baseline value (Table 7). However, there were no significant differences for simulated PLAI and NEE anomaly between groups. The simulated non-fire baseline had slightly higher PLAI values than the old fire group, and the old fire group also had slightly higher PLAI values than the recent fire group.

Table 7. The mean of last year simulation results from sites for each group. The group mean values were calculated from site mean values of three simulated sites for the both recent and old fire group. The site mean values were calculated from last year simulation results from 24 simulations associated with three fire severities, two fire seasons, two vegetation types, and two soil types. For the no fire group, results were averaged from two simulations of different vegetation types.

Fire group	Total vegetation C* (kg m ⁻²)	PLAI	NEE (kg m ⁻² day ⁻¹)	Charcoal C (kg m ⁻²)
Recent	7.81±1.52	2.52±0.64	0.0012±0.0006	0.028±0.030
Old	9.27±0.81	2.67±0.40	0.0012±0.0004	0.015±0.015
No	10.85	2.89	0.0015	0

Production and Loss of Fire-derived Charcoal

Charcoal production was primarily controlled by fire severity, with significantly different charcoal production of 0.016 ± 0.002 kg m⁻², 0.15 ± 0.01 kg m⁻², and 0.23 ± 0.02 kg m⁻² for the low, moderate, and high severity fires, respectively ($F=781.5$, $p<0.001$). The charcoal production from the high severity fires was slightly higher than the values from the moderate severity fires; however the moderate severity fires produced more than 10 times of charcoal than the low severity fires.

The losses of fire-derived charcoal were substantial for the first few years following the fire disturbances. For example, for the simulations of the site WEB002 with fire occurring in 1956, more than half of the initial fire-derived charcoal was lost within the first 4 to 5 years (Figure 13a). The charcoal loss rates following the high severity fires were found to be higher than the lower severity fires. After an initial loss period, the charcoal pool became relatively stable and only reduced slightly throughout the rest simulated years. I found that the average simulated end-year site charcoal was significantly different between the recent and old fire group ($F=12.53$, $t=1.62$, $p=0.001$), with the recent fire group sites having more charcoal (Table 7). The charcoal loss was closely related to the slope value with higher slope sites tending to have higher erosion rates of charcoal (Figure 13b). The average end-year charcoal storage in the high slope sites was nearly 70% less than the value from the low slope sites.

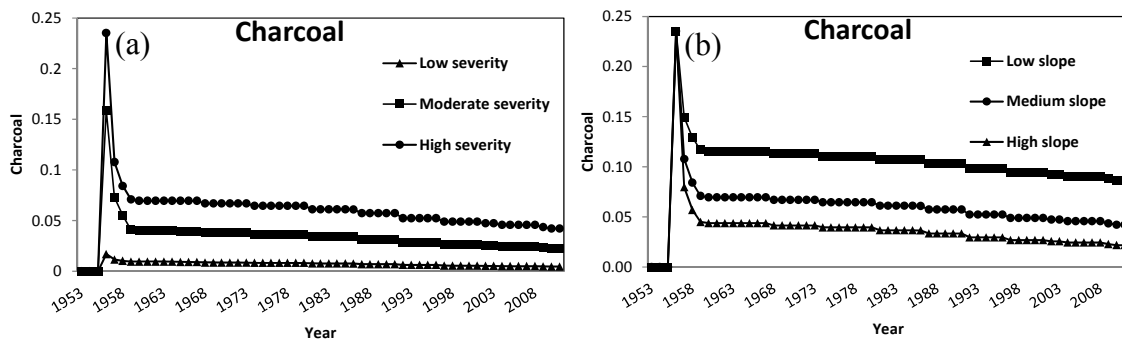


Figure 13. The simulated charcoal storage (kg m^{-2}) changes under different simulations for the site WEB002 with fire happened in 1956. (a) Charcoal storages changes for three different fire severities simulations. (b) As an example, the WEB002 site was simulated for a high severity fire with low (5°), medium (15°), and high slope (30°) to demonstrate the effects of slope on the charcoal loss.

Effects of Vegetation Types and Fire Seasons

The fire-affected vegetation C, PLAI, and NEE were not significantly different between the two vegetation types modeled. The simulated vegetation C of the enf vegetation type recovered slightly faster than the dbf (Figure 14a). However, the dbf vegetation type had simulated PLAI that returned to the pre-fire states faster and slightly higher NEE anomaly values immediately after fires (Figure 14b,c). The simulated PLAI of the dbf vegetation type did not show clear intra-annual variations as compared to the PLAI of the enf (Figure 14b). My comparison of average simulated site end-year results of the two vegetation types showed that only the average end-year charcoal storages were significantly different ($p < 0.001$), with the dbf vegetation type tending to have more charcoal remaining in the system (Figure 14d). I did not find significant differences between fires simulated for summer and winter seasons.

Soil Charcoal Effects on Ecosystem Properties

I did not find that the addition of charcoal to the soil C pool had any significant effects on the simulated PLAI or NEE. I compared the charcoal-affected soil water content differences for simulations conducted on two different types of soil, and found that charcoal addition in sand-dominated soil slightly increased the soil water content, while charcoal addition in clay-dominated soil slightly decreased the soil water content (Figure 15). However, the soil water changes due to charcoal addition were very small and in the order of $0.01\text{--}0.07 \text{ kg m}^{-2}$.

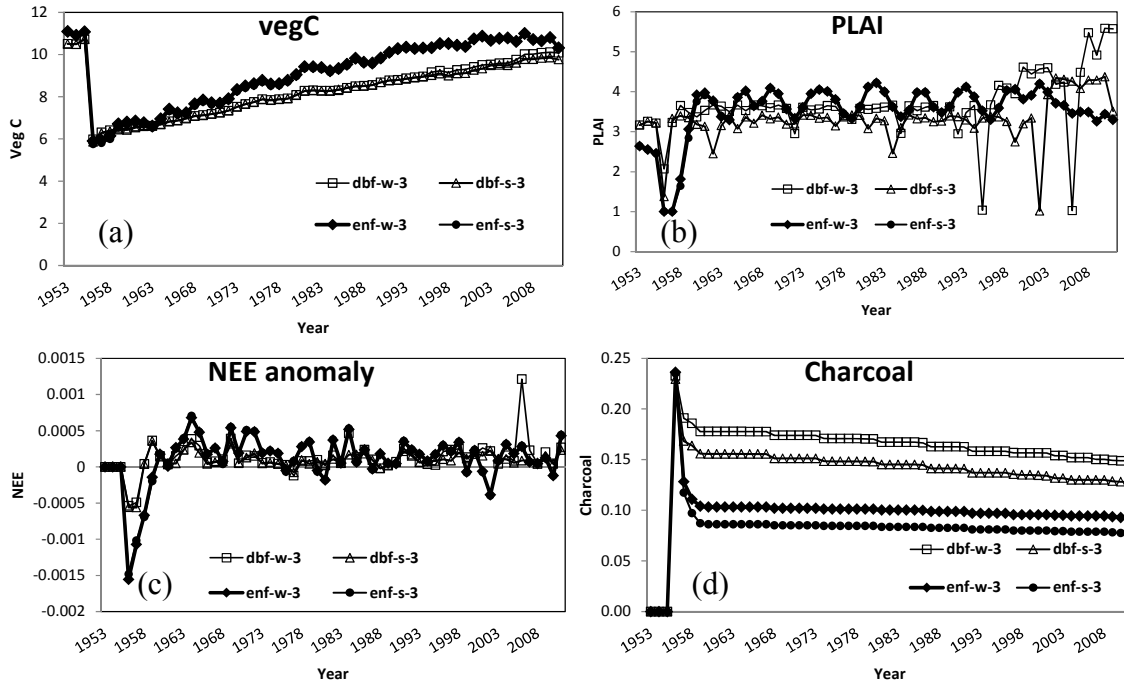


Figure 14. The differences between fire effects for enf and dbf, using the site of WEB002 with intense crown fire happened in 1956 as an example. For each variable, four simulations related to two vegetation types and two fire seasons (dbf-w-3: deciduous with intense crown fire happened in winter; dbf-s-3: deciduous with intense crown fire happened in summer; enf-w-3: evergreen with intense crown fire happened in winter; enf-s-3: evergreen with intense crown fire happened in summer) were shown. (a) Vegetation C (kg m^{-2}). (b) PLAI value. (c) NEE anomaly ($\text{kg m}^{-2} \text{day}^{-1}$), calculated by subtracting the baseline NEE. (d) Charcoal storage (kg m^{-2}).

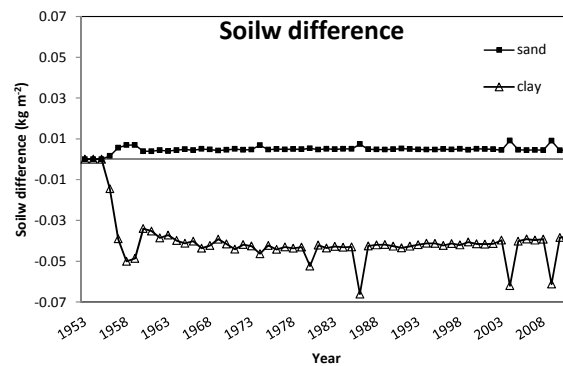


Figure 15. The simulated soil water differences, as compared to the “no charcoal in soil” simulations, for simulations on sand-dominated soil and clay-dominated soil. The charcoal addition slightly increased soil water content for sand-dominated soil, while decreased soil water content for clay-dominated soil.

Discussion

Model Modification

The modified Biome-BGC 4.3 model simulated fire effects on different biomass pools according to the user defined fire severities. This new version model provides a more mechanistic simulation of fire effects on vegetation C as compared to the previous model that simulated fire as a daily C loss process. The Biome-BGC 4.3 model showed that biomass consumptions were exponentially increased with increased fire severity, as both the number of affected biomass pools and the CF scalar increased with increased fire severity. In wildland fire, the severity for a single fire event varies due to the spatial heterogeneity of fire caused by the variations of fuel condition and topography.

Therefore, in order to consider the overall fire effects in this study, all three severity levels fire simulations were assessed collectively. Although I used a constant CF scalar for each SL in this study, the CF scalar may be different for each biomass pool in a single fire and strongly related to the surface-to-volume ratio of fuel. The CF scalar may also vary between different fire events due to differences in the prevailing climate conditions and conditions of available fuels. Therefore, the CF scalar should be calibrated for site-specific and fire-specific simulations in order to accurately model fire-affected biomass. In this study, I did not assess the fire effects on belowground root. Root, especially fine root, is a key component in site nutrient cycling and can be affected by intense fires (Ruess and others 2003). Therefore, a future model need to consider the fire impacts on root and its feedback effects on ecosystem properties. The new sub-model of vegetation regrowth after intense disturbance resulted in reasonable vegetation C recovery rates following fires. However, a more mechanistic regeneration process that includes the

sprouting from seeds and re-sprouting from both the aboveground and belowground vegetative parts might be needed in a future model version.

In this study, charcoal production depended on the available biomass, fire severity, and the CF scalar. However, other factors can affect the actual production of charcoal in a wildland fire, including the intensity, duration, and available oxygen during fire. Even in the same fire, the charcoal production rates from different vegetation parts may be different (Nocentini and others 2010). Stems tend to produce more charcoal, and leaves tend to combust completely. Therefore, similar to the CF scalar, the charcoal production rate in a future model needs to be improved by considering all the influencing factors.

Due to the relatively short simulation time range constrained by my field data, I did not include the simulation of charcoal decomposition in the Biome-BGC 4.3 model. The charcoal erosion loss process was primarily controlled by the amount of surface outflow in the Biome-BGC 4.3 model, which was closely related to the short-term precipitation patterns. The charcoal loss sub-model was calibrated on one study site according to the regional long-term average charcoal loss rate derived from the previous study. The long-term data based calibration might not produce accurate short-term charcoal loss rates associated with individual precipitation event. Therefore, more field-measured data about the charcoal movement will be required to refine the parameter setting. For the charcoal effects, I only examined the charcoal addition effect on soil available water in the Biome-BGC 4.3 model. However, charcoal addition may also affect surface albedo, cation exchange capacity, and soil nutrients, which can be addressed in future Biome-BGC model study (Berglund, DeLuca, Zackrisson 2004; Lehmann and others 2011; Zackrisson, Nilsson, Wardle 1996a).

Fire Effects on Ecosystem Properties

Significantly higher vegetation C losses predicted for moderate severity fires in comparison to low severity fires were due to modeled consumption of the stem biomass by moderate severity fires. The low post-fire total vegetation C accumulation rates from both moderate and high severity fires were due to the slow allocation of assimilated C to stem pool. Therefore, the simulated end-year vegetation C values for the recent fire group were significantly lower than the values of the old fire group. By considering all 24 simulations for each site together in the site comparison, the confounding effects of different fire severity, seasonality, and environmental characteristics were reduced. The simulated site average vegetation C values for the three fire groups (Table 7) had similar group differences but slightly higher values than the field measured values of 5.42, 7.20, and 9.45 kg m⁻² for the recent, old, and no fire group, respectively (Chapter 2). The lower field measured vegetation C values can be attributed to the fact that field measured values did not include the underground biomass. Therefore, the Biome-BGC 4.3 model simulated fire-affected site vegetation C changes were reasonable and compared favorably with the field measured values.

The simulated PLAI recovered quickly with no significant difference of end-year values between the recent and old fire group. This response can be attributed to the new leaf regeneration process I added in the Biome-BGC 4.3 model. Leaf controls the photosynthesis rate. The increase of PLAI after fire disturbance indicated the recovery of ecosystem to sequester C. A large decrease in C sequestration, indicated by the negative NEE anomaly values, was observed for several years after a high severity fire disturbance, until stand level photosynthesis returned to the pre-fire level (Conard and A. Ivanova

1997). The slightly higher C accumulation rates shortly after higher severity fires, indicated by the higher NEE anomaly values, may be related to less stress of competition for resources in the post-fire plant regeneration process.

Simulated Charcoal Production and Loss

The amounts of pre-fire available biomass were similar across the simulated sites, as all sites were started from steady mature states derived from the Biome-BGC 4.3 “spin-up” runs. Therefore, charcoal production was dominated by the fire severities, with the high severity fires producing significantly more charcoal. The higher charcoal loss rates after higher severity fires were caused by the increased amounts of outflow, which was related to the decreased canopy intercepted water losses due to the removal of canopy leaves by fire. Higher simulated outflow removed more surface charcoal not mixed into the soil pool. Simulated charcoal loss was greater for higher slopes which was consistent with findings in this woodland and the other ecosystems (Rumpel and others 2006; Rumpel and others 2009; Chapter 3). I also found that initial charcoal loss rates (the charcoal loss rates for the first few years after the fire) varied for different sites with different fire occurrence years. In the first few years following fire, most simulated fire-derived charcoal remained on the soil surface and was vulnerable for erosion. Therefore, the initial charcoal loss rates were closely related to site-specific precipitation patterns immediately following each fire.

The differences of end-year soil charcoal for the recent and old fire sites were primarily due to the charcoal loss process. The field-measured soil charcoal concentrations were 2.73 g C kg^{-1} soil for the recent fire group and 1.21 g C kg^{-1} soil for the old fire group (Chapter 3). From the field-measured charcoal concentration values,

the charcoal storage values were calculated based on the average soil depths (0.49 m for the recent fire group and 0.43 m for the old fire group) and the soil bulk density (20 kg m^{-3}) used for the Biome-BGC 4.3 model simulations, with the estimated value of 0.027 kg m^{-2} for the recent fire group and 0.011 kg m^{-2} for the old fire group. The estimated charcoal storage values were very similar to the average simulated charcoal storage values of 0.028 kg m^{-2} for the recent fire group and 0.015 kg m^{-2} for the old fire group, indicating the accuracy of the Biome-BGC 4.3 model on predicting fire-derived charcoal storage changes.

Effects of Vegetation Types and Fire Seasons

The faster accumulations of the simulated vegetation C for the enf vegetation type was potentially due to the fact that the evergreens did not need to shed leaves thus can accumulate C all year long. The faster increases of the simulated PLAI of the dbf vegetation type than the enf immediately after fires was potentially due to the higher SLA values of the dbf ($30 \text{ m}^2 \text{ kg}^{-1}$) than the enf ($12 \text{ m}^2 \text{ kg}^{-1}$) used in the Biome-BGC 4.3 model. The default allocation processes of the newly assimilated C from leaf to the other plant parts are the same for the dbf and enf vegetation types in the Biome-BGC 4.3 model. Therefore, with the same amount of vegetation C (also leaf C) accumulated, the increase of simulated PLAI for the dbf vegetation type was higher than the enf. The intra-annual variation patterns with a 5 years interval of the simulated PLAI for the enf vegetation type may be associated the regional precipitation pattern that related to large scale climate variation like the El Niño–Southern Oscillation (Ropelewski and Halpert 1986). The intra-annual variation was less clear for the simulated PLAI of the dbf, which might be attributed to the fact that the annual average PLAI values of dbf were strongly

influenced by the winter leaves shed. Although the initial simulated charcoal production for the enf and dbf vegetation type were similar, there were significant differences of the simulated end-year charcoal storages between these two vegetation types, which can be attributed to the different charcoal loss rates caused by the outflow differences. The simulated outflow of the dbf was less than the enf, primarily due to larger precipitation interception losses of the dbf as a result of larger leaf area (Matyssek 1986; Schulze 1982).

No significant differences were found between fires simulated for summer and winter season. In the Biome-BGC 4.3 model, the effects of fire seasonality were assessed by simulating fire disturbance on leaf C before or during the leaf growing season. However, the primary effects of fire seasonality were the differences in fuel consumption between seasons and the adaptations of plants to the timing of fire (Knapp, Estes, and Skinner 2009), both of which were not included in the current Biome-BGC 4.3 model. Future modifications of the model may include processes that estimate fire severities according to the prevailing climate and processes that can simulate the different adaption strategies of plants to different fire seasons.

Charcoal Effects on Ecosystem Properties

The lack of modeled effects of charcoal addition on ecosystem properties may be attributed to the small changes (0.02%) that charcoal induced on site soil water holding capacity. The effects of charcoal addition on soil water were different for different soil types, with increasing soil water content for sand-dominated soil and decreasing soil water content for clay-dominated soil. Fire frequency has decreased over the last century in this woodland due to active fire suppression and ranching, but still with an estimated

regional-level fire return interval of 5.5 years (Murray and White, in review) and approximately 40-70 years of fire return interval at stand-level (Chapter 2). The amount of charcoal in the soil may be higher for area with higher frequency of fire (MacKenzie and others 2008). Therefore, I suspect that the simulated charcoal effects may be larger in other sites with multiple historic fires, as compared to sites in this study that only had one recorded fire.

Summary of Future Model Work

This study increased the ability of the Biome-BGC model to mechanistically simulate the effects of different fire settings. However, this is just the first step to mechanistically model fire effects on the wildland ecosystems. Further modifications to the model are required. First, CF scalar values need to be better calibrated for specific fires by considering the prevailing climate during fires, the amount of available fuel, and the type of fuel, which will require more field-measured data on fire combustion. Also, the CF scalars should be dynamic for different biomass pools and need to be refined according to the conditions of fuel by using information such as the surface-to-volume ratio of fuel. The post-fire regeneration process also needs to be improved to include re-sprouting from both seeds and available vegetative parts. Second, the production and loss processes of charcoal need to be refined. Similar to the CF values, the production of charcoal should be related to fire severities, conditions of fuel, and available oxygen during fires. More field data on charcoal movement will be needed to improve the sub-model of charcoal loss. Future modeling work also needs to consider the potential charcoal decomposition process if modeling is performed on a longer time range. Last, this study has only explored the charcoal effects on soil water content. The charcoal

effects on soil nutrient availability, soil cation exchange ability, and surface albedo can be addressed in a future model.

CHAPTER FIVE

Conclusions

From the field measurement from sites in BCNWR, I found that fire significantly reduced site C primarily due to the reduced tree density, with average AGBC values of 5.25, 6.86, and 9.18 kg m⁻² for the recent, old, and no fire group, respectively. Fire has limited effects on soil C and N contents. I also found that fire affected community composition significantly, and therefore, it had been an important factor for maintaining Central Texas woodlands. The decreased fire frequency due to active fire suppression and ranching on the eastern Edwards Plateau over the last century threatens the health and persistence of certain endangered avian species within this woodland ecosystem. This poses an opportunity for future management to adopt prescribed fire as a potential management tool. Although the calculated habitat suitability index values for the GCW did not significantly differ between fire groups, I found increased oak recruitment associated with fires that occurred in low summer precipitation years. I suspect that fire may have a dual effect on habitat suitability. Catastrophic wildfires significantly reduce regional C storage and can decrease habitat suitability, while moderate intensity fires in dense young juniper stands promote tree species diversity and increase habitat suitability. Therefore, I propose a flexible management policy involving both mechanical treatment and use of fire in the woodlands to achieve multiple management objectives of C sequestration and habitat restoration.

Three different methods were used to derive the first estimates of soil charcoal concentration for this region, with an regional average value of 1.40 g C kg⁻¹ soil

representing 2% of soil organic C. As the soil C represents a major portion of total site C, BC in soil is important for C cycling in these woodlands. BC can be used as a long term C sink to mitigate elevated atmospheric CO₂ concentration. There were significant differences of the soil charcoal concentrations between the fire-affected sites and non-fire sites, with charcoal concentrations decreasing trend over time that I attributed due to soil erosion. I estimated the regional average annual soil charcoal loss rate to be about 4.7%, with highly variable rates potentially related to site topographic slope. The BD NMR + model method predicted higher concentrations of charcoal with lower mixing model errors as compared to the CP NMR + model method. The validation of PLSR calibration showed the ability of MIRS to predict the concentration of biomolecule components in soil with accurate calibration data from other prediction methods such as the BD NMR + model method. For the prediction of charcoal using MIRS, I found the signature vibrational frequencies for charcoal were near 1581 and 1393 wavenumber (cm⁻¹). From all three methods, only the charcoal concentrations predicted by the BD NMR + model method showed the expected decreasing trend of soil charcoal concentrations with time since last fire. Although charcoal concentrations estimated from the MIRS were not correlated with time since fire, it provided a cost-effective method to estimate average site charcoal.

From modeling results of the modified Biome-BGC 4.3 model, I found that moderate and high severity fires can significantly reduce vegetation C. The fire-affected PLAI and NEE anomaly values recovered quickly after fire disturbances. Simulated charcoal production was strongly related to pre-assigned fire severity levels, with moderate and high severity fires producing significantly more charcoal than low severity

fires. The loss rates of charcoal were found not only to be closely associated with slope values, but also may be related precipitation immediately following fires. The Biome-BGC 4.3 model can accurately simulate the storage changes of charcoal in this woodland ecosystem. The two simulated types of vegetation resulted in only minor differences in response to fire. The dbf vegetation type had smaller charcoal loss rates than the enf due to the lower outflow values caused by the larger precipitation interception losses.

Charcoal additions into soil had very limited influences on the simulated ecosystem properties, as the simulated charcoal-affected soil water content changes were very small and insignificant. This study increased the ability of the Biome-BGC model to mechanistically simulate the important ecosystem process of fire. However, more modifications will be required to include detailed fire-fuel-ecosystem interaction processes.

REFERENCES

- Abrams MD. 2005. Prescribing fire in eastern oak forests: Is time running out? *Northern Journal of Applied Forestry* 22(3):190-6.
- Abrams MD. 1992. Fire and the development of oak forests. *Bioscience* 42(5):pp. 346-353.
- Albrecht MA and McCarthy BC. 2006. Effects of prescribed fire and thinning on tree recruitment patterns in central hardwood forests. *For Ecol Manage* 226(1-3):88-103.
- Alexis M, Rasse D, Rumpel C, Bardoux G, Péchot N, Schmalzer P, Drake B, Mariotti A. 2007. Fire impact on C and N losses and charcoal production in a scrub oak ecosystem. *Biogeochemistry* 82(2):201-16.
- Allen PM, Harmel RD, Dunbar JA, Arnold JG. 2011. Upland contribution of sediment and runoff during extreme drought: A study of the 1947–1956 drought in the blackland prairie, texas. *Journal of Hydrology* 407(1-4):1-11.
- Amiro BD, Barr AG, Black TA, Iwashita H, Kljun N, McCaughey JH, Morgenstern K, Murayama S, Nesic Z, Orchansky AL, et al. 2006. Carbon, energy and water fluxes at mature and disturbed forest sites, saskatchewan, canada. *Agric for Meteorol* 136(3-4):237-51.
- Amiro BD, Barr AG, Barr JG, Black TA, Bracho R, Brown M, Chen J, Clark KL, Davis KJ, Desai AR, et al. 2010. Ecosystem carbon dioxide fluxes after disturbance in forests of north america. *J Geophys Res* 115:G00K02.
- Archer Steve. 1994. Woody plant encroachment into southwestern grasslands and savannas: Rates, patterns and proximate causes. *Ecological implications of livestock herbivory in the west.* ; 1994; Dever, CO. . 13-16 p.
- Archibald S, Roy DP, Van WILGEN BW, SCHOLLES RJ. 2009. What limits fire? an examination of drivers of burnt area in southern africa. *Global Change Biol* 15(3):613-30.
- Asner GP, Archer S, Hughes RF, Ansley RJ, Wessman CA. 2003. Net changes in regional woody vegetation cover and carbon storage in texas drylands, 1937?1999. *Global Change Biol* 9(3):316-35.
- Baldocchi D. 2008. TURNER REVIEW no. 15. "breathing" of the terrestrial biosphere: Lessons learned from a global network of carbon dioxide flux measurement systems. *Aust J Bot* 56(1):1-26.

- Baldock JA, Masiello CA, G  linas Y, Hedges JI. 2004. Cycling and composition of organic matter in terrestrial and marine ecosystems. *Mar Chem* 92(1–4):39-64.
- Barrett G, Ford H, Recher H. 1994. Conservation of woodland birds in a fragmented rural landscape. *Pacific Conservation Biology* 1(3):245-256 Yes.
- Bates JD, Svejcar TS, Miller RF. 2007. Litter decomposition in cut and uncut western juniper woodlands. *J Arid Environ* 70(2):222-36.
- Bergeron Y, Flannigan M, Gauthier S, Leduc A, Lefort P. 2004. Past, current and future fire frequency in the canadian boreal forest: Implications for sustainable forest management. *AMBIO: A Journal of the Human Environment* 33(6):356-60.
- Berglund LM, DeLuca TH, Zackrisson O. 2004. Activated carbon amendments to soil alters nitrification rates in scots pine forests. *Soil Biol Biochem* 36(12):2067-73.
- Beven KJ and Kirkby MJ. 1979. A physically based, variable contributing area model of basin hydrology / un mod  le    base physique de zone d'appel variable de l'hydrologie du bassin versant. *Hydrological Sciences Bulletin* 24(1):43-69.
- Birdsey RA and Heath LS. 1995. 4. carbon changes in U.S. forests. In: Productivity of america's forests and climate change. Joyce LA, editor. Gen. Tech. Rep. RM-GTR-271. ed. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest Experiment Station. 56-70 p.
- Birdsey RA, Jenkins JC, Johnston M, Huber-Sannwald E, Amero B, Jong Bd, Barra JDE, French N, Garcia-Oliva F, Harmon M, Heath LS, Jaramillo VJ, Johnsen K, Law BE, Marn-Spiotta E, Masera O, Neilson R, Pan Y, Pregitzer KS, 2007. North American forests. In: King AW, Dilling L, Zimmerman GP, Fairman DM, Houghton RA, Marland G, Rose AZ, Wilbanks TJ (Eds.), *The First State of the Carbon Cycle Report (SOCCR): The North American Carbon Budget and Implications for the Global Carbon Cycle. The First State of the Carbon Cycle Report (SOCCR): The North American Carbon Budget and Implications for the Global Carbon Cycle. A Report by the U.S. Climate Change Science Program and the Subcommittee on Global Change Research Asheville, NC, USA*, pp. 117 – 126.
- Blake JG. 2005. Effects of prescribed burning on distribution and abundance of birds in a closed-canopy oak-dominated forest, missouri, USA. *Biol Conserv* 121(4):519-31.
- Boerner REJ, Huang J, Hart SC. 2008. Fire, thinning, and the carbon economy: Effects of fire and fire surrogate treatments on estimated carbon storage and sequestration rate. *For Ecol Manage* 255(8–9):3081-97.

- Bornemann L, Welp G, Brodowski S, Rodionov A, Amelung W. 2008. Rapid assessment of black carbon in soil organic matter using mid-infrared spectroscopy. *Org Geochem* 39(11):1537-44.
- Bowman DMJS, Balch JK, Artaxo P, Bond WJ, Carlson JM, Cochrane MA, D'Antonio CM, DeFries RS, Doyle JC, Harrison SP, et al. 2009. Fire in the earth system. *Science* 324(5926):481-4.
- Bray WL. 1904. The timber of the edwards plateau of texas; its relation to climate, water supply, and soil. USDA Bureau Forestry Bull. 49 p. .
- Briggs JM, Hoch GA, Johnson LC. 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *juniperus virginiana* forest. *Ecosystems* 5(6):578-86.
- Brooks ML. 2007. Effects of land management practices on plant invasions in wildland areas. 193:147-62.
- Brose P, Schuler T, Van Lear D, Berst J. 2001. Bringing fire back: The changing regimes of the appalachian mixed-oak forests. *J for* 99(11):30-5.
- Brown J. K. 1995. Fire regimes and their relevance to ecosystem management. Society of american foresters annual meeting.; 1995; Bethesda, MD. . 171-178 p.
- Brown RT, Agee JK, Franklin JF. 2004. Forest restoration and fire: Principles in the context of place. *Conserv Biol* 18(4):903-12.
- Buffo J, Fritschen L, Murphy J. 1972. Direct solar radiation on various slopes from 0 to 60° north latitude. USDA, Forest Service. Report nr Res. Paper PNW-142,. 74 p. .
- Burke IC, Lauenroth WK, Coffin DP. 1995. Soil organic matter recovery in semiarid grasslands: Implications for the conservation reserve program. *Ecol Appl* 5(3):pp. 793-801.
- Burton J, Hallgren S, Fuhlendorf S, Leslie D. 2011. Understory response to varying fire frequencies after 20 years of prescribed burning in an upland oak forest. *Plant Ecology* 212(9):1513-25.
- Cadet F and Offmann B. 1996. Baseline correction applied to a biological: Mid-infrared spectra collection. *Spectroscopy Letters* 29(4):591-607.
- Cairns MA, Brown S, Helmer EH, Baumgardner GA. 1997. Root biomass allocation in the world's upland forests. *Oecologia* 111(1):1-11.

- Canadell JG, Le Qu'ér'e C, Raupach MR, Field CB, Buitenhuis ET, Ciais P, Conway TJ, Gillett NP, Houghton RA, Marland G. 2007. Contributions to accelerating atmospheric CO₂ growth from economic activity, carbon intensity, and efficiency of natural sinks. *Proceedings of the National Academy of Sciences* 104(47):18866-70.
- Cannell MGR. 1982. World forest biomass and primary production data. London: Academic Press.
- Carroll J and Bright A. 2010. Integrative complexity of public beliefs toward wildfire management: Development of a scale. *J Appl Soc Psychol* 40(2):344-59.
- Carter MC and Foster CD. 2004. Prescribed burning and productivity in southern pine forests: A review. *For Ecol Manage* 191(1-3):93-109.
- Chapin FS, Matson PA, Mooney HA. 2002. - Principles of terrestrial ecosystem ecology. .
- Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR, Ni J. 2001. Measuring net primary production in forests: Concepts and field methods. *Ecol Appl* 11(2):pp. 356-370.
- Clark JS. 1991. Disturbance and tree life history on the shifting mosaic landscape. *Ecology* 72(3):1102-18.
- Clark, AI, Phillips, DR, Frederick, DJ, 1985. Weight, volume, and physical properties of major hardwood species in the Gulf and Atlantic Coastal Plain. USDA Forest Service Southeast Forest Experiment Station, Research Paper No. 250, 66 PP.
- Clark, AI, Phillips, DR, Frederick, DJ, 1986a. Weight, volume, and physical properties of major hardwood species in the upland south. USDA Forest Service Southeastern Forest Experiment Station, Research Paper SE-257, Asheville, NC, USA.
- Clark, AI, Phillips, DR, Frederick, DJ, 1986b. Weight, volume, and physical properties of major hardwood species in the Piedmont. USDA Forest Service Southeastern Forest Experiment Station, Research Paper SE-255, Asheville, NC, USA.
- Clein JS, Kwiatkowski BL, McGuire AD, Hobbie JE, Rastetter EB, Melillo JM, Kicklighter DW. 2000. Modelling carbon responses of tundra ecosystems to historical and projected climate: A comparison of a plot- and a global-scale ecosystem model to identify process-based uncertainties. *Global Change Biol* 6(S1):127-40.
- Cloudsley-Thompson, JL, 1975. Desert expansion and the adaptive problems of the inhabitants, in *Environmental Physiology of Desert Animals* (Ed. N.F.Hadley). Pennsylvania: Dowden, Hutchinson and Ross, 255-268.

- Colthup NB, Daly LH, Wilberley SE. 1990. Introduction to infrared and raman spectroscopy / norman B. colthup, lawrence H. daly, stephen E. wilberley. .
- Conard SG and A. Ivanova G. 1997. Wildfire in russian boreal Forests—Potential impacts of fire regime characteristics on emissions and global carbon balance estimates. *Environmental Pollution* 98(3):305-13.
- Cook GD, Liedloff AC, Eager RW, Chen X, Williams RJ, O'Grady AP, Hutley LB. 2005. The estimation of carbon budgets of frequently burnt tree stands in savannas of northern australia, using allometric analysis and isotopic discrimination. *Aust J Bot* 53(7):621-30.
- Czimczik CI and Masiello CA. 2007. Controls on black carbon storage in soils. *Global Biogeochem Cycles* 21(3):GB3005.
- Dai X, Boutton TW, Glaser B, Ansley RJ, Zech W. 2005. Black carbon in a temperate mixed-grass savanna. *Soil Biol Biochem* 37(10):1879-81.
- Dale VH, Joyce LA, McNulty S, Neilson RP. 2000. The interplay between climate change, forests, and disturbances. *Sci Total Environ* 262(3):201-4.
- DeLuca TH and Aplet GH. 2008. Charcoal and carbon storage in forest soils of the rocky mountain west. *Frontiers in Ecology and the Environment* 6(1):18-24.
- Diamond, DD, 1997. An old-growth definition for western juniper woodlands: Texas Ashe juniper dominated or codominated communities. General Technical Report SRS-15. USDA Forest Service Southern Research Station.
- Efron B. 2004. The estimation of prediction error. *Journal of the American Statistical Association* 99(467):619-32.
- Ellenwood MS, Dilling L, Milford JB. 2012. Managing united states public lands in response to climate change: A view from the ground up. *Environ Manage* 49(5):954-67.
- Elliott KJ and Vose JM. 2005. Effects of understory prescribed burning on shortleaf pine (*pinus echinata* mill.)/mixed-hardwood forests. *J Torrey Bot Soc* 132(2):236-51.
- Faith DP, Minchin PR, Belbin L. 1987. Compositional dissimilarity as a robust measure of ecological distance. *Vegetatio* 69(1-3):57-68.
- Farquhar GD, Caemmerer S, Berry JA. 1980. A biochemical model of photosynthetic CO₂ assimilation in leaves of C₃ species. *Planta* 149(1):78-90.

- Fedoroff N, Courty MA, Thompson ML. 1990. Micromorphological evidence of paleoenvironmental change in pleistocene and holocene paleosols. In: *Developments in soil science*. Elsevier. 653 p.
- Flannigan MD, Stocks BJ, Wotton BM. 2000. Climate change and forest fires. *Sci Total Environ* 262(3):221-9.
- Flannigan MD, Krawchuk MA, De Groot WJ, Wotton BM, Gowman LM. 2009. Implications of changing climate for global wildland fire. *Int J Wildland Fire* 18(5):483-507.
- Floyd ML, Romme WH, Hanna DD. 2000. Fire history and vegetation pattern in mesa verde national park, colorado, USA. *Ecol Appl* 10(6):1666-80.
- Foster, JH, 1917. The spread of timbered areas in central Texas. *J. For.* 15, 442–445.
- Fuhlendorf SD, Smeins FE, Grant WE. 1996. Simulation of a fire-sensitive ecological threshold: A case study of ashe juniper on the edwards plateau of texas, USA. *Ecol Model* 90(3):245-55.
- Fulé PZ, Cocke AE, Heinlein TA, Covington WW. 2004. Effects of an intense prescribed forest fire: Is it ecological restoration? *Restor Ecol* 12(2):220-30.
- Gavin DG. 2003. Forest soil disturbance intervals inferred from soil charcoal radiocarbon dates. *Can J for Res* 33(12):2514-8.
- Gehlbach FR. 1988. Forests and woodlands of the northeastern balcones escarpment. *Edwards Plateau Vegetation: Plant Ecological Studies in Central Texas* :57-77.
- Geladi P and Kowalski BR. 1986. Partial least-squares regression: A tutorial. *Anal Chim Acta* 185(0):1-17.
- Glaser B and Amelung W. 2003. Pyrogenic carbon in native grassland soils along a climosequence in north america. *Global Biogeochem Cycles* 17(2):1064.
- Glaser B, Lehmann J, Zech W. 2002. Ameliorating physical and chemical properties of highly weathered soils in the tropics with charcoal - a review. *Biology and Fertility of Soils* 35(4):219-30.
- Glenn-Lewin DC. 1977. Species diversity in north american temperate forests. *Vegetatio* 33(2-3):153-62.
- Goetz SJ, Mack MC, Gurney KR, Randerson JT, Houghton RA,. 2007. Ecosystem responses to recent climate change and fire disturbance at northern high latitudes: Observations and model results contrasting northern eurasia and north america. *Environmental Research Letters* 2(4):045031.

- Gonçalves CN, Dalmolin RSD, Dick DP, Knicker H, Klamt E, Kögel-Knabner I. 2003. The effect of 10% HF treatment on the resolution of CPMAS ¹³C NMR spectra and on the quality of organic matter in ferralsols. *Geoderma* 116(3–4):373-92.
- Goodale CL, Apps MJ, Birdsey RA, Field CB, Heath LS, Houghton RA, Jenkins JC, Kohlmaier GH, Kurz W, Liu S, et al. 2002. FOREST CARBON SINKS IN THE NORTHERN HEMISPHERE. *Ecol Appl* 12(3):891-9.
- Graham, RT, McCaffrey, S, Jain, TB, 2004. Science basis for changing forest structure to modify wildfire behavior and severity. USDA Forest Service General Technical Report, RMRS– 120, Rocky Mountain Research Station, Ogden, Utah, 43 p.
- Grier CG and Running SW, 1977, Leaf area of mature northwestern coniferous forests: relation to site water balance, *Ecology* , Vol. 58, No. 4, pp. 893-899
- Haaland DM and Thomas EV. 1988. Partial least-squares methods for spectral analyses. 1. relation to other quantitative calibration methods and the extraction of qualitative information. *Anal Chem* 60(11):1193-202.
- Habselka CW, Drawe, DL, Ruthven, DC, 2007. Management of South Texas Shrublands with prescribed fire. USDA Forest Service RMRS–P–47. Lubbock, TX, USA.
- Hahn, JT, 1984. Tree volume and biomass equations for the Lake States. USDA Forest Service Research Paper NC–250, North Central Forest Experiment Station, St. Paul, MN, USA.
- Haines TK, Busby RL, Cleaves DA. 2001. Prescribed burning in the south: Trends, purpose, and barriers. *South J Appl for* 25(4):149-53.
- Hammes K, Smernik RJ, Skjemstad JO, Herzog A, Vogt UF, Schmidt MWI. 2006. Synthesis and characterisation of laboratory-charred grass straw (*oryza sativa*) and chestnut wood (*castanea sativa*) as reference materials for black carbon quantification. *Org Geochem* 37(11):1629-33.
- Hammes K, Schmidt M, Ball W, Currie L, Nguyen T, Louchouart P, Fukudome M, Houel S, Gustafsson O, Rumpel C, et al. 2007. Comparison of quantification methods to measure fire-derived (black/elemental) carbon in soils and sediments using reference materials from soil, water, sediment and the atmosphere. *Global Biogeochem Cycles* 21(3):GB3016.
- Hann WJ and Bunnell DL. 2001. Fire and land management planning and implementation across multiple scales. *Int J Wildland Fire* 10(3-4):389-403.
- Harris D, Horwath WR, van Kessel C. 2001. Acid fumigation of soils to remove carbonates prior to total organic carbon or carbon-13 isotopic analysis. *Soil Sci Soc Am J* 65(6):1853-6.

- Henderson NR and Long JN. 1984. A comparison of stand structure and fire history in two black oak woodlands in northwestern indiana. *Botanical Gazette* 145(2):222-8.
- Hobbie SE. 1992. Effects of plant species on nutrient cycling. *Trends in Ecology & Evolution* 7(10):336-9.
- Hockaday WC, Grannas AM, Kim S, Hatcher PG. 2007. The transformation and mobility of charcoal in a fire-impacted watershed. *Geochim Cosmochim Acta* 71(14):3432-45.
- Hoffmann WA and Solbrig OT. 2003. The role of topkill in the differential response of savanna woody species to fire. *For Ecol Manage* 180(1-3):273-86.
- Hood SM, McHugh CW, Ryan KC, Reinhardt E, Smith SL. 2007. Evaluation of a post-fire tree mortality model for western USA conifers. *Int J Wildland Fire* 16(6):679-89.
- Houghton RA. 2005. Aboveground forest biomass and the global carbon balance. *Global Change Biol* 11(6):945-58.
- Houghton RA, Hackler JL, Lawrence KT. 1999. The U.S. carbon budget: Contributions from land-use change. *Science* 285(5427):574-8.
- Hubbard RM, Vose JM, Clinton BD, Elliott KJ, Knoepp JD. 2004. Stand restoration burning in oak-pine forests in the southern appalachians: Effects on aboveground biomass and carbon and nitrogen cycling. *For Ecol Manage* 190(2-3):311-21.
- Hurteau MD and North M. 2010. Carbon recovery rates following different wildfire risk mitigation treatments. *For Ecol Manage* 260(5):930-7.
- Hutchinson TF, Long RP, Ford RD, Sutherland EK. 2008. Fire history and the establishment of oaks and maples in second-growth forests. *Can J for Res* 38(5):1184-98.
- Inbar M, Tamir M, Wittenberg L. 1998. Runoff and erosion processes after a forest fire in mount carmel, a mediterranean area. *Geomorphology* 24(1):17-33.
- IPCC. 2007. Climate change 2007: the physical science basis. In: S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor, and H.L. Miller, Editors. Contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change (IPCC). Cambridge University Press, Cambridge, United Kingdom and New York. <http://www.ipcc.ch>.
- Jackson RB, Moore LA, Hoffmann WA, Pockman WT, Linder CR. 1999. Ecosystem rooting depth determined with caves and DNA. *Proc Natl Acad Sci U S A* 96(20):11387-92.

- Jackson, WD, 2000. Nutrient Stocks in Tasmanian Vegetation and Approximate Losses Due to Fire, Papers and Proceedings of the Royal Society of Tasmania, 134, 1-18.
- Janik LJ, Merry RH, Skjemstad JO. 1998. Can mid infrared diffuse reflectance analysis replace soil extractions? *Aust J Exp Agric* 38(7):681-96.
- Janik LJ and Skjemstad JO. 1995. Characterization and analysis of soils using mid-infrared partial least-squares .2. correlations with some laboratory data. *Soil Res* 33(4):637-50.
- Janik LJ, Skjemstad JO, Raven MD. 1995. Characterization and analysis of soils using mid-infrared partial least-squares .1. correlations with XRF-determined major-element composition. *Soil Res* 33(4):621-36.
- Janik LJ, Skjemstad JO, Shepherd KD, Spouncer LR. 2007. The prediction of soil carbon fractions using mid-infrared-partial least square analysis. *Aust J Soil Res* 45(2):73-81.
- Jenkins JC, Chojnacky DC, Heath LS, Birdsey RA. 2003. National-scale biomass estimators for united states tree species. *For Sci* 49(1):12-35.
- Jensen M, Goodman I, Brewer K, Frost T, Ford G, Nesser J, 1997. Biophysical environments of the basin. Chapter 2. In: Quigley, T.M., Arbelbide, S.J. (Eds.), *An Assessment of Ecosystem Components in the Interior Columbia Basin and Portions of the Klamath and Great Basins, PNW-GTR-405*, vol. 1. USDA Forest Service, Pacific Northwest Research Station, pp. 99-335.
- Jobbágy EG and Jackson RB. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol Appl* 10(2):423-36.
- Johnson DW and Curtis PS. 2001. Effects of forest management on soil C and N storage: Meta analysis. *For Ecol Manage* 140(2-3):227-38.
- Kane E, Hockaday W, Turetsky M, Masiello C, Valentine D, Finney B, Baldock J. 2010. Topographic controls on black carbon accumulation in alaskan black spruce forest soils: Implications for organic matter dynamics. *Biogeochemistry* 100(1):39-56.
- Kauffman JB, Cummings DL, Ward DE. 1994. Relationships of fire, biomass and nutrient dynamics along a vegetation gradient in the brazilian cerrado. *J Ecol* 82(3):pp. 519-531.
- Keeley JE, 2009. Fire intensity, fire severity and burn severity: a brief review and suggested usage. *International Journal of Wildland Fire*, 18, 116-126.

- Keeling CD, Piper SC, Bacastow RB, Wahlen M, Whorf TP, Heimann M, Meijer HA. 2005. Atmospheric CO₂ and ¹³CO₂ exchange with the terrestrial biosphere and oceans from 1978 to 2000: Observations and carbon cycle implications. 177:83-113.
- Knapp EE, Estes BL, Skinner CN, 2009. Ecological Effects of Prescribed Fire Season: a Literature Review and Synthesis for Managers. PSW-GTR-224. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Berkeley, CA, 80 pp
- Knicker H. 2007. How does fire affect the nature and stability of soil organic nitrogen and carbon? A review. *Biogeochemistry* 85(1):91-118.
- Knicker H and Lüdemann H-. 1995. N-15 and C-13 CPMAS and solution NMR studies of N-15 enriched plant material during 600 days of microbial degradation. *Org Geochem* 23(4):329-41.
- Knicker H. 2007. How does fire affect the nature and stability of soil organic nitrogen and carbon? A review. *Biogeochemistry* 85(1):91-118.
- Knops JMH and Tilman D. 2000. Dynamics of soil nitrogen and carbon accumulation for 61 years after agricultural abandonment. *Ecology* 81(1):88-98.
- Kroll JC. 1980. Habitat requirements of the golden-cheeked warbler: Management implications. *J Range Manage* 33(1):pp. 60-65.
- Kuhlbusch TAJ and Crutzen PJ. 1995. Toward a global estimate of black carbon in residues of vegetation fires representing a sink of atmospheric CO₂ and a source of O₂. *Global Biogeochem Cycles* 9(4):491-501.
- Kurz WA and Apps MJ. 1999. A 70-YEAR RETROSPECTIVE ANALYSIS OF CARBON FLUXES IN THE CANADIAN FOREST SECTOR. *Ecol Appl* 9(2):526-47.
- Lavoie M, Starr G, MacK MC, Martin TA, Gholz HL. 2010. Effects of a prescribed fire on understory vegetation, carbon pools, and soil nutrients in a longleaf pine-slash pine forest in florida. *Nat Areas J* 30(1):82-94.
- Law BE, Turner D, Campbell J, Sun OJ, Van Tuyl S, Ritts WD, Cohen WB. 2004. Disturbance and climate effects on carbon stocks and fluxes across western oregon USA. *Global Change Biology* 10:1429-1444.
- Lehmann J, Gaunt J, Rondon M. 2006. Bio-char sequestration in terrestrial ecosystems – A review. *Mitigation and Adaptation Strategies for Global Change* 11(2):395-419.
- Lehmann J, Rillig MC, Thies J, Masiello CA, Hockaday WC, Crowley D. 2011. Biochar effects on soil biota – A review. *Soil Biol Biochem* 43(9):1812-36.

- Lloret F, Pausas JG, Vilà M. 2003. Responses of mediterranean plant species to different fire frequencies in garraf natural park (catalonia, spain): Field observations and modelling predictions. *Plant Ecol* 167(2):223-35.
- Loomis JB, 1993. Integrated Public Lands Management. Columbia Univ. Press, New York.
- Lutes DC, Keane RE, Caratti JF, Key CH, Benson NC, Sutherland S, Gangi LJ, 2006. FIREMON: The fire effects monitoring and inventory system. USDA For. Serv. Gen. Tech. Rep. RMRS-164-CD.
- Lynch JA, Clark JS, Stocks BJ. 2004. Charcoal production, dispersal, and deposition from the fort providence experimental fire: Interpreting fire regimes from charcoal records in boreal forests. *Can J for Res* 34(8):1642-56.
- MacKenzie MD, McIntire EJB, Quideau SA, Graham RC. 2008. Charcoal distribution affects carbon and nitrogen contents in forest soils of california. *Soil Sci Soc Am J* 72(6):1774-85.
- Malhi Y, Baker TR, Phillips OL, Almeida S, Alvarez E, Arroyo L, Chave J, Czimczik CI, Di Fiore A, Higuchi N, et al. 2004. The above-ground coarse wood productivity of 104 neotropical forest plots. *Global Change Biol* 10(5):563-91.
- Masiello CA. 2004. New directions in black carbon organic geochemistry. *Mar Chem* 92(1-4):201-13.
- Matyssek R. 1986. Carbon, water and nitrogen relations in evergreen and deciduous conifers. *Tree Physiol* 2(1_2_3):177-87.
- McCune B and Grace JB. 2002. Analysis of ecological communities. MjM Software, Gleneden Beach, Oregon, USA .
- McDermott CL, Noah E, Cashore B. 2008. Differences that 'matter'? A framework for comparing environmental certification standards and government policies. *Journal of Environmental Policy and Planning* 10(1):47-70.
- McEwan RW, Hutchinson TF, Long RP, Ford DR, McCarthy BC. 2007. Temporal and spatial patterns in fire occurrence during the establishment of mixed-oak forests in eastern north america. *Journal of Vegetation Science* 18(5):655-64.
- McLemore C, Kroh GC, Pinder III JE. 2004. *Juniperus ashei* (cupressaceae): Physiognomy and age structure in three mature texas stands. *SIDA, Contributions to Botany* 21(2):1107-20.
- Merrill LB, Young VA, 1959. Effect of drought on woody plants. *Texas Agriculture Progress* 3,9-10.

- Monteith JL and Unsworth MH. 2008. Principles of environmental physics
. Third ed. Academic Press.
- Morgan P, - Hardy CC, - Swetnam TW, - Rollins MG, - Long DG. 2001. Mapping fire regimes across time and space: Understanding coarse and fine-scale fire patterns. *Int J Wildland Fire* (4):329-342.
- Morrison DA and Renwick JA. 2000. Effects of variation in fire intensity on regeneration of co-occurring species of small trees in the Sydney region. *Aust J Bot* 48(1):71-9.
- Murray DB, White JD, 2012 (*in review*). Loss of Neighbors, Fire, and Climate Effects on Texas Red Oak Growth in a Juniper-dominated Woodland Ecosystem. *American Midland Naturalist*.
- NCDC, 2001a. Climate data online, National Climate Data Center, National Oceanic and Atmospheric Administration, Asheville, NC, USA. <http://www.ncdc.noaa.gov/cdo-web/search#t=firstTabLink>.
- NCDC, 2011b. Historical Palmer Drought Indices, National Climate Data Center, National Oceanic and Atmospheric Administration, Asheville, NC, USA. <http://www.ncdc.noaa.gov/temp-and-precip/drought/historical-palmers.php>.
- NCSS, 2010. National Cooperative Soil Survey Characterization Laboratory Pedon Database. National Soil Survey Center, Lincoln, NE. <http://soils.usda.gov/survey/nscd/>.
- Nelson E, Mendoza G, Regetz J, Polasky S, Tallis H, Cameron DR, Chan KMA, Daily GC, Goldstein J, Kareiva PM, et al. 2009. Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. *Frontiers in Ecology and the Environment* 7(1):4-11.
- Nelson PN, Baldock A, Oades JM, Churchman GJ, Clarke P. 1999. Dispersed clay and organic matter in soil: Their nature and associations. *Soil Res* 37(2):289-316.
- Nelson PN and Baldock JA. 2005a. Estimating the molecular composition of a diverse range of natural organic materials from solid-state ^{13}C NMR and elemental analyses. *Biogeochemistry* 72(1):1-34.
- Nelson PN and Baldock JA. 2005b. Estimating the molecular composition of a diverse range of natural organic materials from solid-state ^{13}C NMR and elemental analyses. *Biogeochemistry* 72(1):pp. 1-34.
- Nguyen TH, Brown RA, Ball WP. 2004. An evaluation of thermal resistance as a measure of black carbon content in diesel soot, wood char, and sediment. *Org Geochem* 35(3):217-34.

- Nocentini C, Certini G, Knicker H, Francioso O, Rumpel C. 2010. Nature and reactivity of charcoal produced and added to soil during wildfire are particle-size dependent. *Org Geochem* 41(7):682-9.
- Oguntunde PG, Abiodun BJ, Ajayi AE, van de Giesen N. 2008. Effects of charcoal production on soil physical properties in Ghana. *Journal of Plant Nutrition and Soil Science* 171(4):591-6.
- Olschewski R and Benítez PC. 2005. Secondary forests as temporary carbon sinks? the economic impact of accounting methods on reforestation projects in the tropics. *Ecol Econ* 55(3):380-94.
- Paine RT, Tegner MJ, Johnson EA. 1998. Compounded perturbations yield ecological surprises: Everything else is business as usual. *Ecosystems* 1:535-545.
- Palmer WC, 1965. Meteorological drought, research paper 45. U.S. Department of Commerce, Weather Bureau, Washington, DC.
- Peterken GF. 1981. Woodland conservation and management. London, United Kingdoms: Chapman & Hall.
- Piccolo A, Pietramellara G, Mbagwu JSC. 1997. Use of humic substances as soil conditioners to increase aggregate stability. *Geoderma* 75(3-4):267-77.
- Pickett STA, & White PS, 1985, *The Ecology of Natural Disturbance as Patch Dynamics*. New York: Academic Press.
- Pregitzer KS and Euskirchen ES. 2004. Carbon cycling and storage in world forests: Biome patterns related to forest age. *Global Change Biol* 10(12):2052-77.
- Pregitzer KS, 2007. North American forests. In: King, A.W., Dilling, L., Zimmerman, G.P., Fairman, D.M., Houghton, R.A., Marland, G., Rose, A.Z., Wilbanks, T.J. (Eds.), *The First State of the Carbon Cycle Report (SOCCR): The North American Carbon Budget and Implications for the Global Carbon Cycle. The First State of the Carbon Cycle Report (SOCCR): The North American Carbon Budget and Implications for the Global Carbon Cycle. A Report by the U.S. Climate Change Science Program and the Subcommittee on Global Change Research Asheville, NC, USA*, pp. 117 - 126.
- Preston CM and Schmidt MWI. 2006. Black (pyrogenic) carbon: A synthesis of current knowledge and uncertainties with special consideration of boreal regions. *Biogeosciences* 3(4):397-420.
- Preston CM, Schnitzer M, Ripmeester JA. 1989. A spectroscopic and chemical investigation on the de-ashing of a humin. *Soil Sci Soc Am J* 53(5):1442-7.

- Pulich WM, 1976. The golden-cheeked warbler, a bioecological study. Texas Parks and Wildlife Department, Austin, TX, USA.
- Pyne SJ, 1997. Fire in America: Cultural History of Wildland and Rural Fire. University of Washington Press, Seattle, WA.
- Raupach MR, Marland G, Ciais P, Le Quéré C, Canadell JG, Klepper G, Field CB. 2007. Global and regional drivers of accelerating CO₂ emissions. *Proceedings of the National Academy of Sciences* 104(24):10288-93.
- Reemts CM and Hansen LL. 2008. Slow recolonization of burned oak-juniper woodlands by ashe juniper (*juniperus ashei*): Ten years of succession after crown fire. *For Ecol Manage* 255(3-4):1057-66.
- Reeves JB, McCarty GW, Rutherford DW, Wershaw RL. 2008. Mid-infrared diffuse reflectance spectroscopic examination of charred pine wood, bark, cellulose, and lignin: Implications for the quantitative determination of charcoal in soils. *Appl Spectrosc* 62(2):182-9.
- Richards SA, Possingham HP, Tizard J. 1999. Optimal fire management for maintaining community diversity. *Ecol Appl* 9(3):880-92.
- Roberts C and Jones JA. 2000. Soil patchiness in juniper-sagebrush-grass communities of central oregon. *Plant Soil* 223(1-2):45-61.
- Rodionov A, Amelung W, Peinemann N, Haumaier L, Zhang X, Kleber M, Glaser B, Urusevskaya I, Zech W. 2010. Black carbon in grassland ecosystems of the world. *Global Biogeochem Cycles* 24(3):GB3013.
- Ropelewski CF, Halpert MS, 1986: North American Precipitation and Temperature Patterns Associated with the El Niño/Southern Oscillation (ENSO). *Monthly Weather Review*, 114, 2352–2362.
- Rumpel C, Ba A, Darboux F, Chaplot V, Planchon O. 2009. Erosion budget and process selectivity of black carbon at meter scale. *Geoderma* 154(1–2):131-7.
- Rumpel C, Alexis M, Chabbi A, Chaplot V, Rasse DP, Valentin C, Mariotti A. 2006. Black carbon contribution to soil organic matter composition in tropical sloping land under slash and burn agriculture. *Geoderma* 130(1–2):35-46.
- Running SW. 2008. CLIMATE CHANGE: Ecosystem disturbance, carbon, and climate. *Science* 321(5889):652-3.
- Russell FL and Fowler NL. 2004. Effects of white-tailed deer on the population dynamics of acorns, seedlings and small saplings of *quercus buckleyi*. *Plant Ecol* 173(1):59-72.

- Russell FL and Fowler NL. 2002. Failure of adult recruitment in *quercus buckleyi* populations on the eastern edwards plateau, texas. *Am Midl Nat* 148(2):201-17.
- Ruess RW, Ronald LH, Andrew JB, Kurt SP, Bjartmar S, Michael FA, and Gregory EM. 2003. Coupling fine root dynamics with ecosystem carbon cycling in Black Spruce forest of interior Alaska. *Ecological Monographs* 73:643–662.
- Ruthven III DC and Synatzske DR. 2002. Response of herbaceous vegetation to summer fire in the western south texas plains. *Tex J Sci* 54(3):195-210.
- Schenk HJ. 2006. Root competition: Beyond resource depletion. *J Ecol* 94(4):725-39.
- Schenk HJ and Jackson RB. 2002. Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *J Ecol* 90(3):480-94.
- Schnell RL, 1976. Biomass estimates of eastern redcedar tree components. Tennessee Valley Authority, Division of Forestry, Fisheries and Wildlife Development Technical Note No. B15, Norris, TN, USA.
- Schlesinger WH. 1986. Changes in soil carbon storage and associated properties with disturbance and recovery. In: *The changing carbon cycle. A global analysis.* Trabalka JR and Reichle DE, editors. New York, New York, USA.: Springer Verlag. 194 p.
- Schmidt MWI, Knicker H, Hatcher PG, Kogel-Knabner I. 1997. Improvement of ¹³C and ¹⁵N CPMAS NMR spectra of bulk soils, particle size fractions and organic material by treatment with 10% hydrofluoric acid. *Eur J Soil Sci* 48(2):319-28.
- Schulze ED. 1982. Plant life forms and their carbon, water and nutrient relations. *Physiological Plant Ecology II. Water Relations and Carbon Assimilation.* Springer-Verlag, Berlin, Germany :616-76.
- Sellards EH, 1933. The geology of Texas. *The University of Texas Bulletin* 3232.
- Simpson MJ and Hatcher PG. 2004. Determination of black carbon in natural organic matter by chemical oxidation and solid-state ¹³C nuclear magnetic resonance spectroscopy. *Org Geochem* 35(8):923-35.
- Skjernstad JO, Taylor JA, Smernik RJ. 1999. Estimation of charcoal (char) in soils. *Commun Soil Sci Plant Anal* 30(15-16):2283-98.
- Smernik RJ and Oades JM. 2003. Spin accounting and RESTORE ? two new methods to improve quantitation in solid-state ¹³C NMR analysis of soil organic matter. *Eur J Soil Sci* 54(1):103-16.

- Smernik RJ and Oades JM. 2000. The use of spin counting for determining quantitation in solid state ^{13}C NMR spectra of natural organic matter: 1. model systems and the effects of paramagnetic impurities. *Geoderma* 96(1–2):101-29.
- Smernik RJ, Baldock JA, Oades JM, Whittaker AK. 2002. Determination of $T_1\rho\text{H}$ relaxation rates in charred and uncharred wood and consequences for NMR quantitation. *Solid State Nucl Magn Reson* 22(1):50-70.
- Stambaugh MC, Guyette RP, Godfrey R, McMurry ER, Marschall JM. 2009. Fire, drought, and human history near the western terminus of the cross timbers, wichita mountains, oklahoma, USA. *Fire Ecology* 5(2):51-65.
- Sterl A, Severijns C, Dijkstra H, Hazeleger W, van Oldenborgh GJ, van den Broeke M, Burgers G, van den Hurk B, van Leeuwen PJ, van Velthoven P. 2008. When can we expect extremely high surface temperatures? *Geophys Res Lett* 35(14).
- Stocks BJ and Kauffman JB. 1997. Biomass consumption and behavior to wildland fires in boreal, temperate, and tropical ecosystems: Parameters necessary to interpret historic fire regimes and future fire scenarios. in: Clark JS, cachier H, goldammer JG, stocks B, editors. . In: *Sediment records of biomass burning and global change*. Clark JS, cachier h, goldammer JG, et al, editors. NATO ASI Series. Series I, Global Environmental Change, vol. 51 ed. Berlin, Germany: Springer. 169 p.
- Stroup WW and Stubbendieck J. 1983. Multivariate statistical methods to determine changes in botanical composition. *J Range Manage* 36(2):pp. 208-212.
- Tans P. and Keeling R, 2012, *NOAA/ESRL* online data, www.esrl.noaa.gov/gmd/ccgg/trends/
- Tharp BC, 1939. The vegetation of Texas. The Anson Jones Press, Houston, TX, USA.
- Theobald DM and Romme WH. 2007. Expansion of the US wildland-urban interface. *Landscape Urban Plann* 83(4):340-54.
- Thornton PE, 2010, Theoretical framework of Biome-BGC version 4.2, available from <http://www.ntsg.umt.edu>.
- Thornton PE, Law BE, Gholz HL, Clark KL, Falge E, Ellsworth DS, Goldstein AH, Monson RK, Hollinger D, Falk M, et al. 2002. Modeling and measuring the effects of disturbance history and climate on carbon and water budgets in evergreen needleleaf forests. *Agric for Meteorol* 113(1–4):185-222.
- Thornton PE and Running SW, 1999. An improved algorithm for estimating incident daily solar radiation from measurements of temperature, humidity, and precipitation. *Agricultural and Forest Meteorology*, 93:211-228.

- Thornton PE. 1998. Description of a numerical simulation model for predicting the dynamics of energy, water, carbon, and nitrogen in a terrestrial ecosystem. .
- Tiedemann AR and Klemmedson JO. 1995. The influence of western juniper development on soil nutrient availability. *Northwest Sci* 69(1):1-8.
- Tiedemann AR, O. Klemmedson J, Bull EL. 2000. Solution of forest health problems with prescribed fire: Are forest productivity and wildlife at risk? *For Ecol Manage* 127(1-3):1-18.
- Tiedemann AR and Klemmedson JO. 1995. The influence of western juniper development on soil nutrient availability. .
- Tromp-van Meerveld HJ and McDonnell JJ. 2006. On the interrelations between topography, soil depth, soil moisture, transpiration rates and species distribution at the hillslope scale. *Adv Water Resour* 29(2):293-310.
- Tryon EH. 1948. Effect of charcoal on certain physical, chemical, and biological properties of forest soils. *Ecol Monogr* 18(1):pp. 81-115.
- Turner DP, Ritts WD, Yang Z, Kennedy RE, Cohen WB, Duane MV, Thornton PE, Law BE. 2011. Decadal trends in net ecosystem production and net ecosystem carbon balance for a regional socioecological system. *For Ecol Manage* 262(7):1318-25.
- USDA, 1974. Soil survey of Travis County, Texas, USDA soil conservation service in cooperation with Texas Agricultural Experiment Station, USA.
- USDA, 2011. Soil Survey Staff , Natural Resources Conservation Service, United States Department of Agriculture. Soil Survey Geographic (SSURGO) Database for [BCNWR, TX]. Available online at <http://soildatamart.nrcs.usda.gov>. Accessed [11/01/2011].
- USFWS, 1992. Golden-cheeked Warbler (*Dendroica chrysoparia*) recovery plan. U.S. Fish and Wildlife Service region 2, Albuquerque, NM, USA.
- Van Auken OW, Jackson JT, Jurena PN. 2005. Survival and growth of juniperus seedlings in juniperus woodlands. *Plant Ecology* 175(2):245-57.
- Van Auken OW, 2008. Western North American juniperus communities: a dynamic vegetation type. Springer, New York, NY, USA.
- van Mantgem PJ, Stephenson NL, Knapp E, Battles J, Keeley JE. 2011. Long-term effects of prescribed fire on mixed conifer forest structure in the sierra nevada, california. *For Ecol Manage* 261(6):989-94.

- Varner III JM, Gordon DR, Putz FE, Kevin Hiers J. 2005. Restoring fire to long-unburned pinus palustris ecosystems: Novel fire effects and consequences for long-unburned ecosystems. *Restor Ecol* 13(3):536-44.
- Viscarra Rossel RA, Walvoort DJJ, McBratney AB, Janik LJ, Skjemstad JO. 2006. Visible, near infrared, mid infrared or combined diffuse reflectance spectroscopy for simultaneous assessment of various soil properties. *Geoderma* 131(1-2):59-75.
- Wade D, Lunsford JD, 1989. A guide for prescribed fire in Southern forests. USDA Forest Service Technical Publication R8-TP 11.
- Wan S, Hui D, Luo Y. 2001a. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: A meta-analysis. *Ecol Appl* 11(5):1349-65.
- Wan S, Hui D, Luo Y. 2001b. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: A meta-analysis. *Ecol Appl* 11(5):1349-65.
- Weatherspoon PC, Skinner CN, 2002. An ecological comparison of fire and fire surrogates for reducing wildfire hazard and improving forest health. Association of Fire Ecological Miscellaneous Publication, 1 pp. 239-245.
- Weiler M and McDonnell JJ. 2006. Testing nutrient flushing hypotheses at the hillslope scale: A virtual experiment approach. *Journal of Hydrology* 319(1-4):339-56.
- West LT, Waltman SW, Wills S, Reinsch TG, Benham EC, Smith CS, Ferguson R, 2010, Soil carbon stocks in the US: current data and future inventories, Proceedings of International Workshop on Evaluation and Sustainable Management of Soil Carbon Sequestration in Asian Countries. Bogor, Indonesia.
- Whelan RJ, 1995. The ecology of fire. Cambridge Studies in Ecology, Landon, UK
- White J, Oakley J, Anderson M, Bonazza R. 2010. Experimental measurements of the nonlinear rayleigh-taylor instability using a magnetorheological fluid. *Physical Review E - Statistical, Nonlinear, and Soft Matter Physics* 81(2).
- White JD and Moore BR. 2010. Carbon accumulation in a humid temperate prairie pasture following abandonment and afforestation. *Journal of Agricultural Science and Technology* 4(5):1-9.
- White MA, Thornton PE, Running SW, Nemani RR. 2000. Parameterization and sensitivity analysis of the BIOME-BGC terrestrial ecosystem model: Net primary production controls. *Earth Interact* 4(3):1-85.
- Wiant HJ, Castaneda F, Sheetz C, Colaninno A, Demoss J, 1977. Equations for predicting weights of some Appalachian hardwoods. West Virginia University. Agriculture and Forestry Experiment Station Bulletin 659T.

- Wiedinmyer C and Hurteau MD. 2010. Prescribed fire as a means of reducing forest carbon emissions in the western united states. *Environmental Science and Technology* 44(6):1926-32.
- Williams RA and McClenahan JR. 1984. Biomass prediction equations for seedlings, sprouts, and saplings of ten central hardwood species. *For Sci* 30(2):523-7.
- Wood SW, Murphy BP, Bowman DMJS. 2011. Firescape ecology: How topography determines the contrasting distribution of fire and rain forest in the south-west of the tasmanian wilderness world heritage area. *J Biogeogr* 38(9):1807-20.
- Wood S and Bowman D. 2012. Alternative stable states and the role of fire–vegetation–soil feedbacks in the temperate wilderness of southwest tasmania. *Landscape Ecology* 27(1):13-28.
- Woodward FI. 1987. Climate and plant distribution. Cambridge studies in ecology. Cambridge, United Kingdom: Cambridge University Press.
- Yao J, Murray DB, Adhikari A, White JD. 2012. Fire in a sub-humid woodland: The balance of carbon sequestration and habitat conservation. *For Ecol Manage* 280(0):40-51.
- Yong EL, Richards B, 1996. Big Game Research and Surveys: White-Tailed Deer Population Trends. Texas Parks and Wildlife Department, Austin, TX, USA
- Zackrisson O, Nilsson MC, Wardle DA. 1996a. Key ecological function of charcoal from wildfire in the boreal forest. *Oikos* 77(1):10-9.
- Zackrisson O, Nilsson MC, Wardle DA. 1996b. Key ecological function of charcoal from wildfire in the boreal forest. *Oikos* 77(1):10-9.
- Zheng D, Hunt Jr. ER, Running SW. 1996. Comparison of available soil water capacity estimated from topography and soil series information. *Landscape Ecol* 11(1):3-14.
- Zinke P, Sabhasri S, Kunstadter P. 1978. Soil fertility aspects of the lua' forest fallow system of shifting cultivation. In: *Farmers in the forest*. Kunststadter P, Chapman EC, Sabhasri S, editors. Honolulu, Hawaii, USA.: University Press of Hawaii,. 134-159 p.
- Zou X and Bashkin M. 1998. Soil carbon accretion and earthworm recovery following revegetation in abandoned sugarcane fields. *Soil Biol Biochem* 30(6):825-30.