8-2020

Carbon Sequestration in a Restored West Michigan Oak Savanna: Implications for Management Practices

Jeffrey A. Heise

Grand Valley State University

Carbon Sequestration in a Restored West Michigan Oak Savanna: Implications for Management Practices

Jeffrey A. Heise

A Thesis Submitted to the Graduate Faculty of

GRAND VALLEY STATE UNIVERSITY

In

Partial Fulfillment of the Requirements

For the Degree of

Master of Science

College of Liberal Arts and Sciences

August 2020

Abstract

The savanna system is an ecosystem (i.e. a transitional ecosystem) that lies between forest and grassland ecosystems. They occur across the world in various forms, but in the North American Midwest they are specifically oak savannas: systems where the open overstory is dominated by various species of oak (*Quercus* spp.) and the understory consists of carbon-rich prairie grasses and forbs. This ecosystem is a highly degraded ecosystem and has lost almost 99% of its former range due to agriculture and fire suppression. Since savannas are fire-evolved systems, they are maintained by and require fire as a regular disturbance to clear woody encroachment and keep the canopy open for the diverse understory. This study takes place in an oak savanna in the Muskegon State Game Area (MSGA) in Muskegon, Michigan. I quantified the amount of carbon that is stored in overgrown and restored plots of oak savanna, then compared the differences in sequestered carbon to other restoration goals, including understory community composition. Since this system, once restored, can theoretically store large amounts of carbon in the roots of the diverse understory, the goal of this study was to determine if there is a relationship between carbon storage and species diversity. These results will provide land managers with information regarding the application of species diversity and carbon sequestration measurement practices.

Table of Contents:

Tables and Figures:

Table 1: Samples collected with number per site. *Not used in PCA	
Site	N=3
Temperature	N=30
% Moisture	N=30
Openness	N=30
Mean Leaf Area	N=30
Leaf Area Index	N=30
Total Site Factor	N=30
Photosynthetic Photon Flux Density	N=30
Live Carbon (Biomass)	N=30
Aboveground Herbaceous Biomass	N=30
Belowground Herbaceous Biomass	N=30
Aboveground Tree Biomass	N=3
Belowground Tree Biomass	N=3
Dead Carbon (Detritus)	N=30
Bulk Density	N=30
Soil Carbon	N=30
% C in Soil	N=30
Total Soil Carbon	N=30
Species Richness	N=30
Shannon Entropy	N=30
Shannon Diversity	N=30
Dead Tree Biomass and Carbon*	N=3

Table 2: List of species found in MSGA with abbreviations		
Common Name	**Scientific Name**	**Abbreviation**
Bracken Fern	*Pteridium spp.*	*Pteridium*
Lowbush Blueberry	*Vaccinium angustifolium*	*Vac.ang*
Pennsylvania Sedge	*Carex pensylvanica*	*Car.pen*
Wintergreen	*Gaultheria procumbens*	*Gau.pro*
Cherry	*Prunus spp.*	*Prunus*
Highbush Blueberry	*Vaccinium corybosum*	*Vac.cor*
Needlegrass	*Stipa avenacea*	*Sti.ave*
Bluejoint Grass	*Calamagrostis canadensis*	*Cal.can*
Yellow Hawkweed	*Hieracium caespitosum*	*Hie.cae*
Scribner's Panic Grass	*Dichantelium scribnerianum*	*Dic.scr*
Sweet Fern	*Comptonia peregrina*	*Com.per*
Broad-Leaf Panicgrass	*Dicanthelium boscii*	*Dic.bos*
Red Oak	*Quercus rubra*	*Que.rub*
Aspen	*Populus spp.*	*Pop.tre*
Sassafras	*Sassafras albidum*	*Sas.alb*
Coniferous Sampling	*Pinus spp.*	*Pinus*
Poison Ivy	*Toxicodendron radicans*	*Tox.rad*
St. John's Wort	*Hypericum perforatum*	*Hyp.per*
Dwarf Dandelion	*Krigia virginica*	*Kri.vir*
Flowering Spurge	*Euphorbia corollata*	*Eup.cor*
Black-Eyed Susan	*Rudbeckia herta*	*Rud.her*
Sumac	*Rhus spp.*	*Rhus*
Slender Nutsedge	*Cyperus lupulinus*	*Cyp.lup*

Table 3: Table of mean carbon measurements		
Site	Type	Carbon (tonnes)
BO3	AGB	1200.00
FECON	AGB	1130.00
Thick	AGB	830.00
BO3	BGB	470.00
FECON	BGB	380.00
Thick	BGB	280.00
BO3	Dead	71.00
FECON	Dead	175.49
Thick	Dead	129.61
BO3	Soil	25.16
FECON	Soil	22.35
Thick	Soil	15.61
BO3	TreeAGB	17037.28
FECON	TreeAGB	5921.27
Thick	TreeAGB	29592.82
BO3	TreeBGB	2525.91
FECON	TreeBGB	992.79
Thick	TreeBGB	4114.27

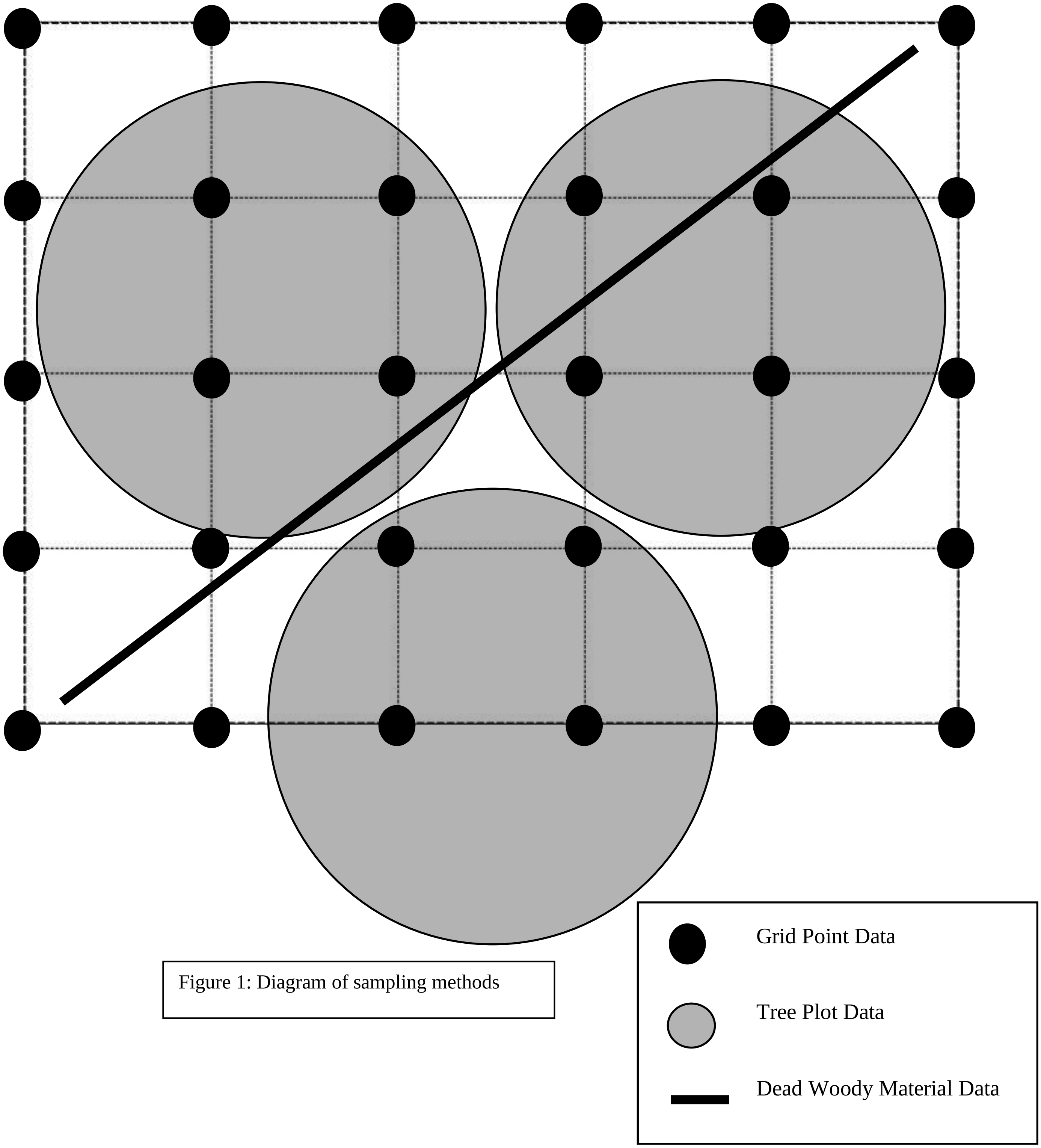

Figure 1: Diagram of sampling methods

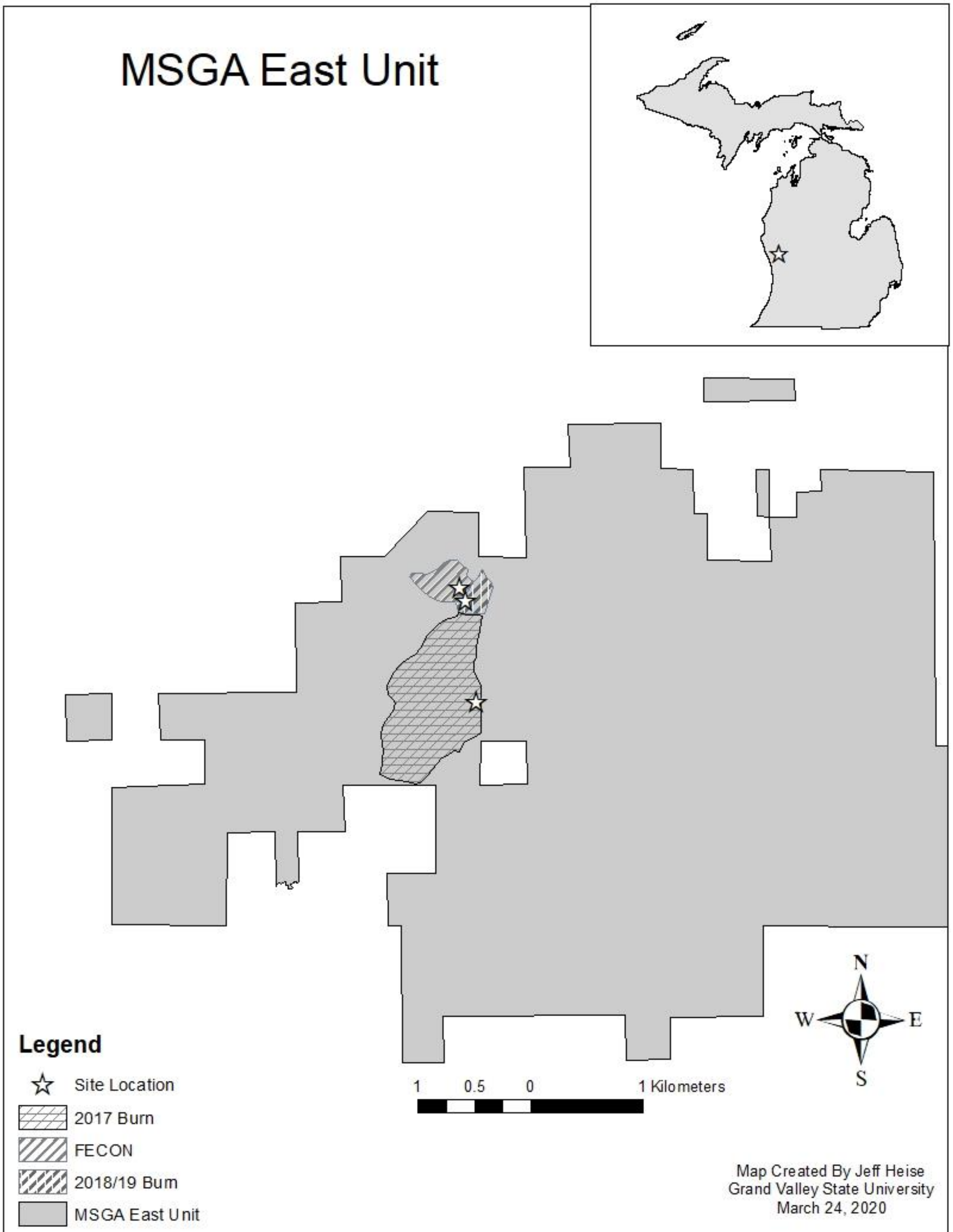

Figure 2: Map of Muskegon State Game Area (MSGA) East Unit with sample site locations.

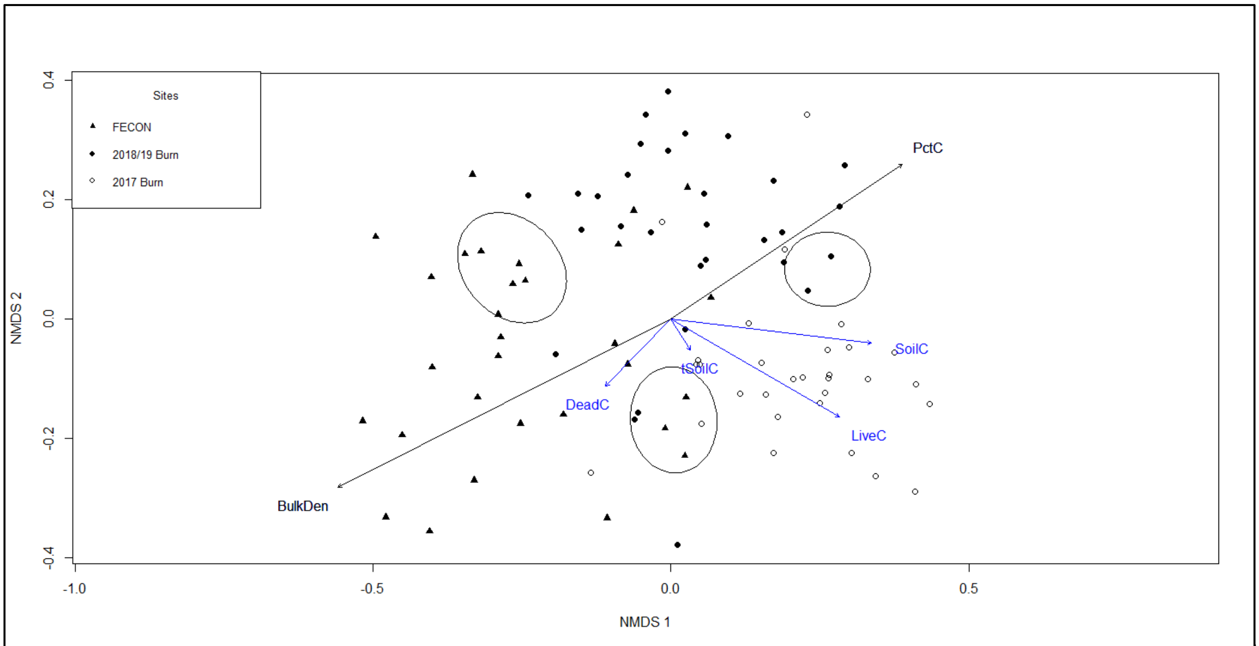

Figure 3: Non-metric multidimensional scaling (NMDS) of the Bray-Curtis similarity of MSGA vegetation community composition. Stress = 20.307. ENVFIT overlay of carbon vectors: black lines indicate significance with $p < 0.05$.

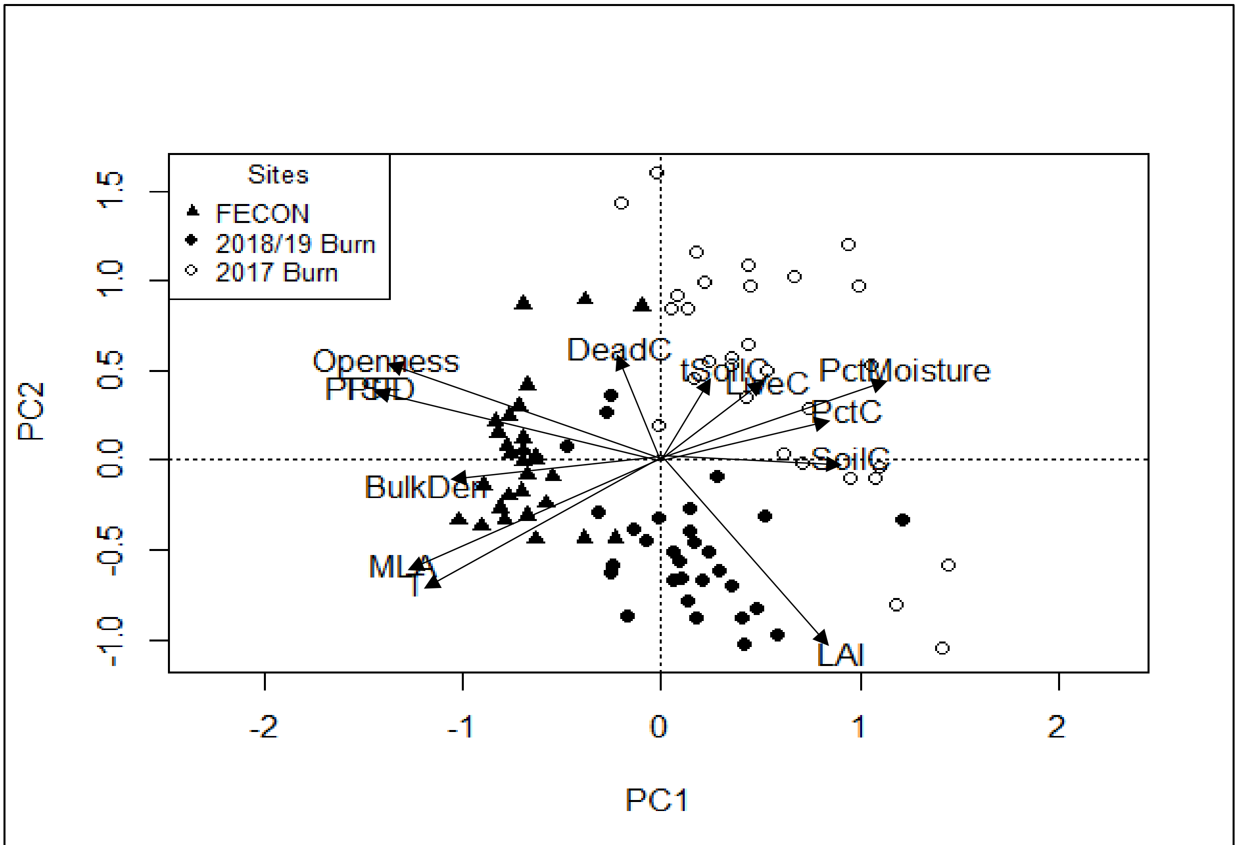

Figure 4: Principle Component Analysis (PCA) on environmental factors in three sites. PC1 = 45.12% variation, PC2 = 11.17% variation.

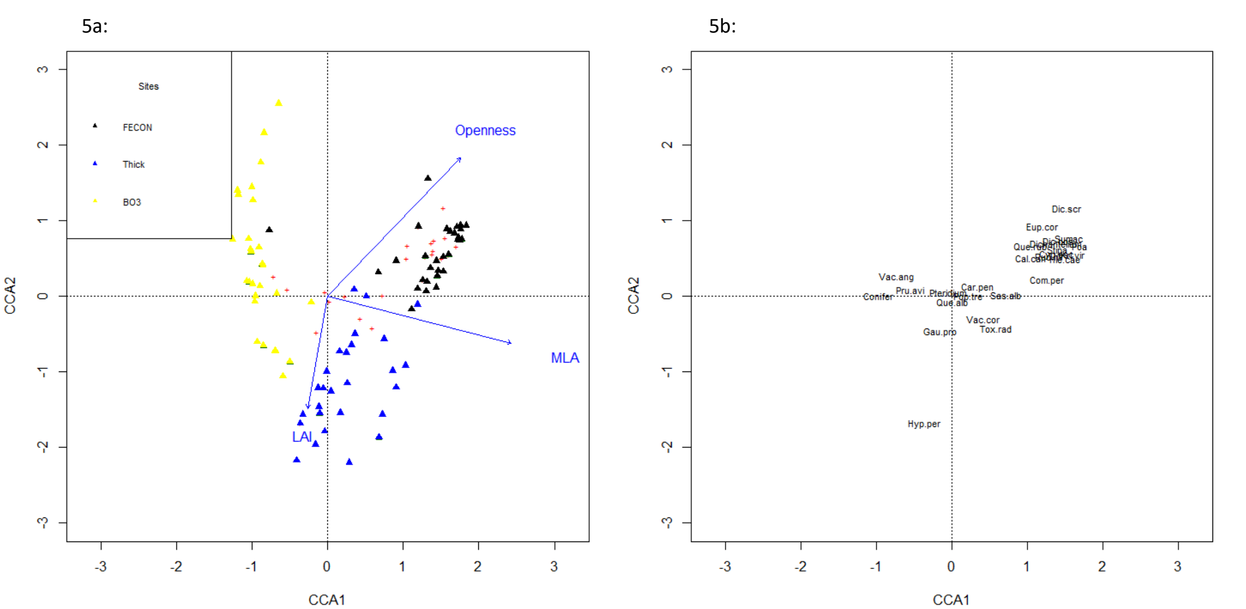

Figure 5: Canonical Correspondence Analysis (CCA) on three sites. 4a (left) shows three significant vectors and even dispersion of FECON, Thick, and BO3. 4b (right) shows species grouped by site, represented on 4a by "plus" signs. Species abbreviation are listed in the supplemental materials.

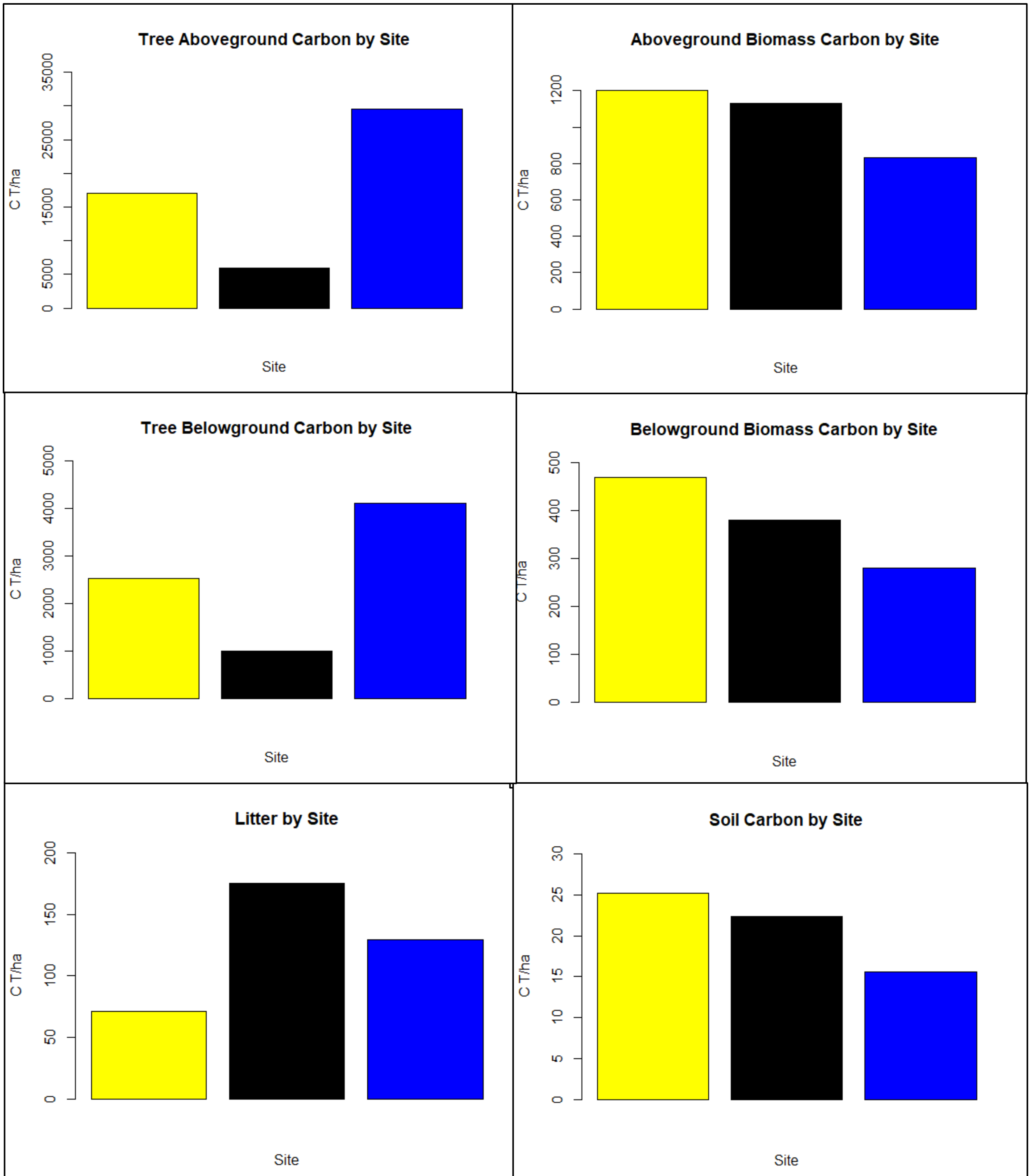

Figure 6: Carbon measurements (C T/ha) by site. Yellow = BO3, Black = FECON, Blue = Thick.

Oak savannas

The savanna system is an ecosystem (i.e. a transitional ecosystem) that lies between forest and grassland ecosystems. Savannas occur across the world in various forms, but in the North American Midwest they are specifically oak savannas: systems where the overstory is dominated by various species of oak (*Quercus* spp.) (Brudvig & Mabry, 2008; Cottam, 1949; Nuzzo, 1986). Midwestern oak savannas are characterized by 10 - 50% canopy cover and are dominated by oak and pine (*Pinus* spp.) trees with an understory consisting of dense prairie vegetation (Bowles & McBride, 1998; Cottam, 1949; Lettow et al., 2014; Peterson & Reich, 2008).

Oak savannas evolved in the Silurian Period (440 mya), a time when there was high oxygen content in the atmosphere and wildfires began to shape ecosystems (Bowman et al., 2009). As a result, oak savannas are considered fire adapted rather than fire sensitive, as the vegetation thrives in the presence of semi-regular fire disturbances (Bowles & McBride, 1998; Bowman et al., 2009; Nowacki & Abrams, 2008). Historically, wildfires occurred throughout the year and were started by lightning during storms or periods of intense heat (e.g. late summer). Controlled fire was used by Native Americans to control animal grazing and to protect their settlements from wildfires (Bowman et al., 2009; Nowacki & Abrams, 2008).

The oak savanna saw a decline of over 90% of its historical range after European settlement (Brudvig & Mabry, 2008; Nuzzo, 1986). This decline was due to the conversion of oak savanna into agriculture and development, while the necessary fire disturbance was suppressed (Bowman et al., 2009). Present day land managers have been attempting to re-create and restore oak savannas through the use of mechanical tree thinning and prescribed fire to limit woody encroachment as well as to stimulate nutrient flow between the plants and soil (Brudvig & Asbjornsen, 2009; Fölster et al., 2001; Lettow et al., 2014; Yuste et al., 2010).

Oak savannas, like forests, have a vertical stratification of vegetation layers. The canopy consists of the oldest oaks in the system, which have sprawling branches to maximize photosynthetic surface area (Cavender-Bares & Reich, 2012; Nuzzo, 1986; Pearson et al., 2007). The canopy provides some of the heterogeneity of the landscape by creating shaded areas for shade-tolerant species to thrive (Peterson et al., 2007). The mid-story consists of younger oaks and woody shrubs which form the future canopy. Many trees and shrubs in this layer die out during fire disturbances, leaving only the heartiest plants that grew in periods of no fire to become the next generation (Peterson & Reich, 2001). The understory resembles grassland ecosystems with its rich abundance of wildflowers and C_4 grasses; species that also evolved with fire as a regular disturbance (Bowman et al., 2009; Pearson et al., 2007; Reinhardt et al., 2017). These species have an incredibly dense and deep root system with a high belowground biomass (Johnson & Matchett, 2001; Peterson & Reich, 2001). Since this is a system with 10 - 50% open canopy that experiences high temperatures, the soil is relatively nutrient poor, apart from the carbon being fixed by plants in root tissue (Lettow et al., 2014). This high vertical stratification compared to other forest systems provides a unique and highly heterogenous ecosystem with high biomass, species richness, and density (Schetter et al., 2013).

Thinning

Thinning has been used as a management practice for various ecosystem benefits. Thinning involves harvesting trees and some of the new growth for the purpose of promoting understory growth and the regeneration of the canopy (Ma et al., 2018). This technique can either leave the cut biomass on the ground or remove it from the system which allows land managers to alter the canopy density, allowing more light and rainfall to the understory (Dijkstra et al., 2006; Ma et al., 2018). Canopy density thinning practices have been shown to increase biodiversity in the understory (Kim et al., 2018), change the rate of litter decomposition (Bravo-Oviedo et al., 2017), increase nutrient cycling (Kim et al., 2018), decrease litter production (Bravo-Oviedo et al., 2017), and increase understory carbon content (Bravo-Oviedo et al., 2017). The resulting ecosystem after thinning is highly diverse where patches of grassland are interlaced with occasional oak trees, in part due to the increased heterogeneity of the landscape (Bergès et al., 2017).

Prescribed Fire

Another common management technique used in oak savannas is fire. Grasslands and oak savannas are systems that evolved with fire as a regular disturbance (Bowman et al., 2009). In present day, fires have been "prescribed" to restoration sites. These are carefully conducted on days when weather conditions limit the spread of fire to other areas. These prescribed fires have long been used by land managers to eliminate invasive species typically not fire-adapted as well as woody growth (Rau et al., 2008), stabilize the understory phylogenetic diversity (Bergès et al., 2017), and alter primary productivity and spatial patterns of the overall plant community (Kim et al., 2018). In a Minnesota oak savanna, prescribed fire was shown to increase canopy openness and therefore understory richness and diversity (Peterson & Reich, 2001, 2008; Peterson et al., 2007; Reich, et al., 2001). In addition, these fires decrease the amount of floor litter biomass as it is lost to burning (Tester, 1989). This causes a loss of carbon and other nutrients via volatilization, temporary increased leaching and runoff, but also more nitrogen cycling in areas frequently burned (Kim et al., 2018).

Species Richness and Management

Species richness has long been a method of quantifying the quality of ecosystem restorations. This increased biodiversity yields greater stability in ecosystems (Knops et al., 1999). It is therefore often the goal of land managers and biologists alike to manage restorations to support a greater number of species represented, in hopes to create a stabilized ecosystem where minimal management is needed. I see examples of this in the classic Tilman and Knops (1999) experiments on biodiversity. They found that an increased number of species represented an increased the ability of a midwestern prairie to resist invasion and disease, as well as increased the overall biomass of the plant community (Knops et al., 1999; Lehman & Tilman, 2000). By having a greater number of species, the prairie in the study became particularly resistant to catastrophic disease outbreak. If such an outbreak were to occur, a monoculture could be easily eliminated, where a healthy and diverse system would only lose one member of a functional group, maintaining its stability (Knops et al., 1999).

Biologically diverse ecosystems have greater community biomass, but lower biomass per species. This is due to greater competition between species in similar functional groups fighting for more available resources (Lehman & Tilman, 2000). Limited belowground resources also stimulate inter- and intraguild competition among plants, causing increased diversity of primary producers (Barot & Gignoux, 2004). Historically, this has been accepted across most ecosystems, but only a weak correlation between soil organic matter (SOM) and richness has been found in oak savannas (Weiher & Howe, 2003). Weiher (2003) instead found that canopy cover and disturbances were the primary drivers behind oak savanna understory biomass and diversity.

Overall, the benefit of having greater species richness in restorations manifests itself in various forms. Apart from invasion and disease resistance, the increased diversity and biomass of primary producers lends itself to greater species richness of primary consumers, secondary consumers, and so on with bottom-up control (Ebeling, Hines, et al., 2018; Ebeling, Rzanny, et al., 2018).

Carbon Sequestration and Management

Carbon sequestration occurs when carbon dioxide (CO_2) is absorbed from the atmosphere by plants and fixed into their structures. As plants grow, more CO_2 is sequestered and converted into biomass. The plant dies, and the carbon fixed is either converted into organic material (OM) in the soil or is given off again through heterotrophic respiration, root exudates, or into the atmosphere. By sequestering carbon from the atmosphere, oak savannas limit greenhouse gas emissions across the planet (Reinhardt et al., 2017). Tree growth in forests and savannas provide high amounts of carbon sequestration in ecosystems through their biomass. This includes aboveground woody structures, leaves, and belowground coarse root material (Pearson et al., 2007). Due to the size and chemical composition of these structures, they do not break down and decompose as quickly as herbaceous material and shrubs (Tilman et al., 2000). The heterogeneity and openness of a restored or remnant oak savanna provides more opportunities for herbaceous forbs to grow, thrive, and function as a larger carbon pool than average deciduous forest. The finer root structures of the forb-heavy understory decompose quicker than dense woody debris, allowing for more rapid carbon sequestration into the soil (Chapin, III et al., 2012). This also creates the issue of microbial respiration occurring at quicker rates due to decomposition (Yuste et al., 2007).

Where trees and plants provide massive carbon pools, the carbon in soil is the largest carbon pool and primary contributor to sequestration on the planet (Lal, 2005). In deciduous forests, often modeled similarly to oak savannas, studies have shown that the carbon sequestering potential is estimated at 0.4 Pg C/year in soils and 1-3 Pg C/year total (Lal, 2005). The soil carbon pool is driven primarily through the decomposition of OM. As dead OM is broken down by soil microbes, it is converted into smaller organic molecules, some of which are further transformed into recalcitrant molecules, or those which cannot be further broken down. These recalcitrant molecules, such as lignin, are capable of storing carbon for millions of years, and are therefore the most successful at storing atmospheric carbon dioxide (Chapin, III et al., 2012). Decomposition occurs at a higher rate in moist soils, then decreases again in waterlogged soils. The loamy sand soil of Michigan oak savannas is ideal for decomposition in light of its high porosity and flow rate. Soil temperature and pH also effect decomposition, where peak soil respiration occurs between 20-30°C. On the contrary, the rate of soil organic matter decomposition in acidic soil is lower than in neutral soil (Chapin, III et al., 2012). The open canopy of oak savannas also benefits these processes by allowing more sunlight and consequently higher temperatures into the understory.

In addition to carbon sequestration, one of the primary processes that occurs during decomposition is microbial respiration. Microbial respiration occurs when microbes are actively decomposing organic matter, be it above or belowground, and can contribute a large amount of CO_2 to the atmosphere (Schmidt et al., 2011). This reaction can be driven by temperature, but is more strongly associated with rate of photosynthesis and the photosynthetic capacity of the ecosystem (Yuste et al., 2007). When managing for carbon sequestration, it is important to consider this issue in all of its aspects.

It is the primary goal of this study to determine what may influence and be correlated with carbon storage in oak savannas. Specifically, if a link exists between understory species diversity and carbon sequestration. To do this, I measured leaf area index (LAI), photosynthetic photon flux density (PPFD), mean leaf angle (MLA), and total site factor (TSF). LAI is the total upper surface area of leaves per area on the ground, which can become a figure for the photosynthetic capacity of the canopy of the savanna. Studies have found that LAI is unrelated to carbon storage potential, and instead increases with the height of trees (Berryman et al., 2016; Frank, 2002). Combined with the hydraulic limitations of tall trees, increased LAI is correlated with less aboveground biomass and more root growth (Berryman et al., 2016; Chapin, III et al., 2012). PPFD is the measure of the amount of light penetrating the canopy to create photosynthetic potential in the understory and is traditionally correlated with canopy openness and gap fraction data (Machado & Reich, 1999). Photosynthetic potential of the understory becomes invaluable for oak savannas which rely on the open canopy for regeneration of trees and their dense herbaceous layer (Nuzzo, 1986). MLA is correlated with particle deposition, light reflectance, and convection in the system. TSF is the totaled figure for direct and diffused sun and sky light reaching the understory, which influences the available radiation to the understory. These in turn can affect evapotranspiration in the understory, which alters decomposition rates by changing the temperature and moisture of the soil (Aerts, 1997; Bailey & Mahaffee, 2017; Chapin, III et al., 2012; Jones & Vaughan, 2010; Nilson & Kuusk, 1989; Rich, 1990).

It is important to consider that biomass removal and application of prescribed fire can have direct negative impacts regarding carbon storage. Tilman et al. (2001) described decreased carbon in the overall system after prescribed fire, quite simply due to the loss of aboveground biomass. This line of thought would immediately suggest that fire suppression is the best management practice if one were to simply use carbon storage as a restoration metric. Fire suppression, however, has also been known to increase fuel load and cause higher intensity catastrophic fires that are even more detrimental to the ecosystem over time (Starfield & Bleloch, 1991). When investigating fire dynamics in a fire-adapted ecosystem, it is vital to consider the net ecosystem carbon balance and weigh the costs and benefits of using fire as a maintenance tool against carbon emissions.

Community composition, management practices, and carbon sequestration

Given the heterogeneous nature of oak savannas, the carbon pool is potentially variable across the landscape matrix. For example, patches near trees have higher soil carbon due to the density of OM from litter-fall (Hoosbeek et al., 2016). Soil carbon densities also vary as they are dependent on which species are represented in the canopy. These differences are seen commonly in oak/pine barrens as oaks have leaves that decompose quicker than pine needles, which can also alter the soil chemistry (Vittori Antisari et al., 2011). Vittori et al. takes the perspective that the increased openness of the canopy from intense management will benefit the understory plant community and encourage higher species diversity. This heterogeneity increases the forb community biomass, increasing the yearly litter and nutrient flow of easily decomposed plants and fine root systems, contributing to the recalcitrant carbon layer in the soil profile as well as the OM layer (Lehman & Tilman, 2000; Sutton et al., 2008; Vittori Antisari et al., 2011).

Purpose

The purpose of this thesis was to look at a single moment in time of a west Michigan oak savanna restoration. I specifically wanted to determine if carbon storage is a reasonable restoration metric compared to plant abundance and diversity: a more historical method. Beyond this, carbon storage data is becoming increasingly important we face the need to remove as much carbon from the atmosphere as possible due to climate change. This study seeks to answer these questions in reference to a specific oak savanna in Michigan.

Scope

Oak savannas are important in carbon storage potential due to their heterogenous landscape matrix. Whereas the effects of prescribed fire and canopy thinning has been well documented on the vegetation community level, little research has been done to understand further ecosystem benefits, particularly regarding carbon sequestration and potential climate change mitigation benefits (Bergès et al., 2017; Bowman et al., 2009; Brudvig & Asbjornsen, 2009; Cottam, 1949; Peterson & Reich, 2001). Here, I aim to understand how prescribed fire and thinning the overstory (without biomass removal) in an oak savanna (disturbance management practices) affect carbon sequestration and plant community composition.

Objective

The objective of this study is three-fold. Foremost, I am quantifying the amount of carbon that is being stored in the overall ecosystem in three differently managed areas. Next, I am measuring the quality of the restorations using classic methods, including the plant community composition. I am then comparing these two analyses to determine if there is a link between carbon storage and plant community composition in the different restoration areas.

Significance

Oak savannas are an endangered ecosystem that are actively being restored across the eastern Midwest United States. Even still, there is limited research on savannas and what specific restoration objectives should be sought after. Even fewer discuss the effects of prescribed fire and mechanical thinning as restoration tools and their impacts on carbon storage (Brudvig & Asbjornsen, 2008; Tilman et al., 2000). This study will be important to both fields of restoration ecology and climate change. Since this study is taking place on an active three year old oak savanna restoration site, the results of this study will provide additional insight to the land manager at MSGA regarding carbon storage as a restoration metric.

II. ***Carbon sequestration in a restored West Michigan oak savanna: Implications for management practices***

Abstract

The savanna system is an ecosystem (i.e. a transitional ecosystem) that lies between forest and grassland ecosystems. They occur across the world in various forms, but in the North American Midwest they are specifically oak savannas: systems where the open overstory is dominated by various species of oak (*Quercus* spp.) and the understory consists of carbon-rich prairie grasses and forbs. This ecosystem is a highly degraded ecosystem and has lost almost 99% of its former range due to agriculture and fire suppression. Since savannas are fire-evolved systems, they are maintained by and require fire as a regular disturbance to clear woody encroachment and keep the canopy open for the diverse understory. This study takes place in an oak savanna in the Muskegon State Game Area (MSGA) in Muskegon, Michigan. I quantified the amount of carbon that is stored in overgrown and restored plots of oak savanna, then compared the differences in sequestered carbon to other restoration goals, including understory community composition. Since this system, once restored, can theoretically store large amounts of carbon in the roots of the diverse understory, the goal of this study was to determine if there is a relationship between carbon storage and species diversity. These results will provide land managers with information regarding the application of species diversity and carbon sequestration measurement practices.

Introduction:

Oak savannas

The oak savanna habitat is one such endangered ecosystem that is threatened by a lack of prescribed fire. Oak savannas evolved during the Silurian Period, approximately 400 million years ago, which was characterized by a period of high oxygen content in the atmosphere (Bowman et al., 2009). This high oxygen content allowed wildfires to run more rampant and limit woody encroachment in grassland areas, creating an ecosystem, between forests and grasslands (Bowman et al., 2009; Nuzzo, 1986). Presently, managed oak savanna regions are primarily maintained by the application of prescribed fire to replicate the wildfires that helped establish these systems. Without disturbance, oak savannas are subject to overgrowth of saplings that limit the canopy cover, which reduces the density of rich understory biomass in oak savannas (Bowman et al., 2009; Nuzzo, 1986).

Midwestern oak savannas are characterized by their limited canopy cover, few trees, and species rich understory (Cottam, 1949; Nuzzo, 1986). This open canopy allows for high amounts of sunlight to reach the understory, which increases the net primary productivity (NPP). The scattered trees primarily consist of white oak (*Quercus alba),* red oak (*Quercus rubrum*), and the occasional white pine (*Pinus strobus*), and provide small shaded areas for less sun tolerant herbaceous species (Cottam, 1949; Nuzzo, 1986). The herbaceous species that are characteristic of both grasslands and oak savannas are also known to have large and dense root systems, which add to the overall high biomass of the system (Koteen et al., 2015; Tilman et al., 2000). Given its proximity to the eastern forests and the Great Plains, the eastern edge of the North American Midwest is home to many oak savanna habitats. These exist as ecotones between dense forest and prairie ecosystems in areas historically burned by wildfire, as early as 5,000 years ago (Nuzzo, 1986).

The heterogenous nature of these ecotones present a unique opportunity to carry traits of both neighboring ecosystems, including the carbon storage potential. Grassland ecosystems have high carbon storage rates during the growing season due to their dense root systems, similar to forests and their tree carbon storage (Fan et al., 1998; Frank, 2002; Koteen et al., 2015; Tilman et al., 2000). Both of these methods of carbon sequestration store atmospheric carbon dioxide for many years, but eventually most tree carbon is returned to the atmosphere through above-ground decomposition (Chapin, III et al., 2012). Herbaceous carbon sequestration, although more volatile and subject to fire, occurs at a quicker rate due to their fine root biomass (Chapin, III et al., 2012; Tilman et al., 2000). As decomposition occurs, some fine root biomass and other soil organic matter (SOM) are transformed into mineralized organic compounds that are resistant to further breakdown, or recalcitrant. Much of this material also contributes to CO_2 additions to the atmosphere through microbial respiration (Yuste et al., 2007). These recalcitrant belowground carbon molecules become a method of storing atmospheric carbon in the soil long term, compared to the respiration-heavy decomposition occurring in aboveground detritus (Schmidt et al., 2011). This belowground process provides an opportunity for savannas to be an ecosystem of high productivity and aid in terms of atmospheric carbon sequestration.

Gap of Knowledge

Where studies on land management and restoration of endangered ecosystems with the goal of species preservation are abundant, observations of shifting carbon balances in restorations are limited (Tilman et al., 2000). In this study I aim to combine these two restoration goals and determine if there is a link between them. I hypothesized that: (1) the plant community will show an increase in diversity and abundance in areas with more intense management. This will (2) in turn cause an increase in sequestered carbon in the restored oak savanna area. Further,

(3) a relationship will exist where the increased diversity in the plant community will increase the amount of carbon sequestered in the oak savanna system.

Methodology

Study area:

I collaborated with the Muskegon State Game Area (MSGA) in Muskegon, Michigan, for this project and sampled on their newly restored oak savanna sites in the east unit. The MSGA is part of the southern-most portion of the Huron-Manistee National Forest, which is 978,906 acres **(Figure 2)**. The study site in the MSGA was historically an oak savanna with Plainfield sandy loam soil (Soil Survey Staff et al., n.d.), but was fire suppressed for 26 years. The previous wildfire was not recorded. As a result, remnant savanna areas had become overgrown by quaking aspen and bracken fern, which prevented sunlight from reaching the overgrown forest floor. Restoration sites were selected for intense management in 2015 by locating areas with *Quercus alba* and high abundance of *Carex pensylvanica*, indicator species for oak savannas in western Michigan (Brudvig & Asbjornsen, 2008). I selected three areas within these sites that were at different stages of restoration: site “BO” which was burned in 2017; “Thick” which was burned in 2018 and 2019; and “FECON” which underwent mechanical thinning, selective cut surface Glypro herbicide application, and prescribed fire in 2018 and 2019. The herbicide was applied using a “wet blade” method where trees that were not wanted were cut down with a chainsaw that had herbicide applied to the cutting chain. Over 90% of aspen (*Populus spp.*) saplings were mechanically and chemically removed from this site, as well.

I collected samples in late July 2019, at the height of the Michigan savanna growing season. At each site, I established a 40m x 50m grid that contained 5 x 6 individual equally spaced points. The grid points were used to collect the species data, soil carbon, understory carbon, and environmental metrics listed below. I further followed USDA guidelines to quantify tree and dead wood carbon by establishing three 20m radius tree plots per site, and a 100m transect that ran through the site to collect dead wood carbon measurements **(Figure 1)**. I chose the large radius tree plots due to the abundance of trees that were of 50 d.b.h. or higher. These methods followed USDA guidelines (Pearson et al., 2007) for measuring carbon.

Data collection: Environmental variables, carbon measurements, and vegetation survey

At each grid point, I used the Olympus TG-4 camera with a hemispheric lens to collect gap fraction, canopy openness, leaf area index (LAI), total site factor (TSF), mean leaf angle (MLA), and total photosynthetic photon flux density (PPFD). LAI was collected as LAI 2000, a conversion from leaf area index units to percent of pen sky covered by leaves. These data were analyzed with the WynScanopy analysis software (Regent Instruments Inc. 2020). I used a Dr.Meter multimeter to measure soil temperature and pH, and a Fieldscout TDR 300 Soil Moisture Meter to measure soil moisture. I used a 1 m^2 quadrat and stem density estimations to count the overall percent coverage of plant species at each point. Following USDA carbon stock guidelines, I collected live understory biomass within a 0.25 m^2 quadrat as well as all dead organic matter from point locations. I additionally collected soil cores at each grid point using a 70.36 cm^3 soil auger (CV) (Pearson et al., 2007). I followed USDA carbon stock guidelines to measure tree carbon within the established tree plots. I marked each tree (d.b.h. > 5cm) within the plot and recorded species and d.b.h. For each dead wood transect, I recorded the length, d.b.h., and quality of wood (rotten, intermediate, or sound) of every piece of fallen dead wood that intercepted the transect (Pearson et al., 2007).

All collected soil and organic matter samples were brought back to the lab and massed. They were then dried in a drying oven at 80°C for two weeks and massed again to determine AGB of non-tree vegetation. To calculate below-ground biomass (BGB), I used the regression formula for temperate forest BGB from Pearson et al., (2007). These were multiplied by 0.5 to quantify t/ha of carbon (Pearson et al., 2007). For dead biomass (t/ha) (DOM), I used the Pearson regression formula that accounts for forest-floor oven-dry weight and the size of the sampling frame area. DOM measured in the dead wood plots were first converted to volume (m^3/ha) then converted to biomass stock. To convert the volume of dead wood into biomass (biomass stock), I used regression formulas using the density and quality of wood (Pearson et al., 2007). Tree biomass (Tree AGB) was determined by regression formulas specific to the density of different tree clades. The conversion formula from herbaceous AGB to herbaceous BGB was used again to convert tree AGB to tree BGB. These were all multiplied by 0.5 to convert to t C/ha (Pearson et al., 2007).

Each soil auger was used for a different measurement. The first auger at each point was used to calculate the bulk density of soil, the second was used to measure total soil carbon. Each core was collected and weighed wet, then dried at 80°C for seven days. The oven-dry sample was weighed for an additional soil moisture measurement. The bulk density sample was then filtered with a 2mm sieve to separate the oven-dry fine soil fraction from the oven-dry coarse fragments. Both soil orders were massed and used to calculate bulk density using Pearson regression formulas. Density of rock fragments was assumed to be 2.65 g/cm^3 (Pearson et al., 2007). Percent carbon was determined by homogenizing the second soil core and filtering through (0.7 mm) sieve. The fine material was massed to 4g in a warm crucible and heated at 500°C for 8 hours, or until all carbon had been burned off. The remaining difference divided by the original mass yielded percent carbon (%C). Total carbon in the mineral soil (C t/ha) was calculated using Pearson's regression formulas (Pearson et al., 2007). For a list of formulas used, please refer to the extended methodology.

Herbaceous vegetation percent cover was estimated at each grid point using a $1m^2$ quadrat according to (Wilhelm & Rericha, 2017). I recorded 26 different herbaceous species across the three sites.

Data analysis

I had two primary data sets, the grid point data (n=30) and the pooled total carbon data per site (n=1). The grid point data units were standardized using z-scores to remove the effect of units. I also log10 transformed pH, percent moisture, and vegetation carbon data. I analyzed the grid point environmental data using principal component analysis (PCA) of the standardized correlation matrix to determine the percent of variation explained by each variable (List of variables found in Extended Methodology). Variables with eigenvalues of less than 0.70 (Soil C, % C in Soil, Total Soil Carbon, Shannon Richness, Shannon Entropy and Shannon Diversity) were eliminated from the PCA. This left temperature, percent moisture, gap fraction, openness, MLA, LAI, TSF, PPFD, aboveground herbaceous carbon, and belowground fine root carbon as primary variables.

Species data were analyzed with non-metric multidimensional scaling (NMDS) with a Bray-Curtis similarity matrix in the vegan package in R to provide a graphical representation of plant community similarities (Clarke, 1993; Okansen et al., 2019; R Core Team, 2017). I used ANOSIM post-hoc with SIMPER to determine the if management significantly influenced plant communities and if so, what specific species drove those changes in (R Core Team 2017). I used the ENVFIT function to overlay carbon-specific vectors over the species data to investigate a potential link between understory species diversity and carbon storage. Species data and environmental factors were additionally analyzed using a canonical correspondence analysis (CCA) to determine potential links between understory communities and potential environmental explanatory variables. The CCA plot originally contained all variables included in the PCA, but after testing with ANOVA only three were found to be significant in the best model.

Results

Restoration and carbon, considering environmental factors

The first three PCs of the environmental PCA accounted for 66.45% of variation in the environmental data **(Figure 4)**. The first PC (45.12%) described variation from high temperature, openness, PPFD, MLA, bulk density, and TSF, to high percent carbon, soil carbon, live herbaceous carbon, and percent moisture. The FECON site was characterized by high temperature sites, and the thick and BO3 sites were characterized by higher percent moisture. PC2 (11.17%) describes high levels of carbon found in living herbaceous biomass.

Restoration and species

The CCA **(Figure 5)** was split into two ordinations, the first detailing site differences and the three significant vectors (openness, MLA, LAI). The second ordination includes the species recorded and the community composition. When these two ordinations are overlaid, they present a complete picture of the research site. The species portion of the CCA **(Figure 5b)** showed higher clustering of more species in the FECON site, including several unique and rare species (*Krigia virginica, Comptonia peregrina, Stipa avenacea, Calamagrostis canadensis*) of grass that serve as indicators of a budding oak savanna. The more common species (*Carex penn.*, *Pteridium spp.*, *Vaccinium angustifolium*, *Quercus alba*, *Populus tremuloides*) were found in greater abundance and regularity in the 2017 Burn and 2018/19 Burn sites. The 2018/19 Burn site had the densest tree biomass, but a relatively open canopy regardless **(Figure 5a)**. There were a few more species observed there, but they were more common species. I used a CCA ANOVA with a global pseudo F test which indicated model significance ($p < 0.001$). The first two axes were also significant (Axis 1: $p < 0.001$, Axis 2: $p < 0.01$). The NMDS showed similar relationships (Stress = 20, $p < 0.001$) **(Figure 3)**.

Restoration with species and carbon

The second portion of the split CCA ordination includes the species recorded and the community composition. When these two ordinations are considered together, they present a complete picture of the research site. There are three distinct groups among the sites with minimal overlap. The FECON site had the highest diversity and most uniform communities with rare species being represented at a much higher rate than the other two sites. Additionally, the Openness vector is strongly correlated with the FECON site. BO3 and Thick were characterized by *Pteridium*, wintergreen, cherry, quaking aspen, blueberry, and high LAI. Thick and FECON share high MLA. The global pseudo F test indicated the model was significant ($p < 0.001$). The first two axes were also significant (Axis 1: $p < 0.001$, Axis 2: $p < 0.01$). The three significant variables in the CCA were: openness (VIF = 2.067655), LAI (VIF = 2.765016), and MLA (VIF = 1.500692). I also used the ENVFIT function to look at this relationship only using carbon vectors and species diversity data. We found that there was higher overall percent carbon in the 2017 Burn and the 2018/19 Burn sites which additionally had lower bulk density. I also found higher soil carbon in the 2017 Burn site which had lower plant diversity **(Figure 3)**.

Discussion

Restoration and carbon

The FECON site showed the lowest amount of soil carbon, with most being in the 2017 Burn site (**Figure 6)**. These results were expected due to the higher moisture, organic matter presence, and low soil compaction making it ripe for decomposition to take place (Chapin, III et al., 2012). These observations in the West Michigan oak savanna were directly contrary to the results of a study conducted in a grassland which showed higher amounts of carbon sequestration in areas of higher biodiversity (Yang et al., 2019). Another study looking at microbial activity, microbial functional diversity, and soil organic carbon content in similar management areas found no differences in similarly aged restoration (Giai & Boerner, 2007). It should be noted that the MSGA is still a relatively young restoration site and is still in the process of recovery from being overrun. Our findings rejected our hypothesis that the most intense management would lead to more carbon sequestration. However, it is important to see where most of the carbon is being stored. The 2017 Burn site had the most understory biomass and soil carbon. These findings support the idea that areas with denser understory sequester more carbon for greater periods of time (Chapin, III et al., 2012).

Restoration and species

The effects of intense management in the MSGA oak savanna compared to lesser managed sites are most apparent in the FECON site, where I found greater diversity in plant species, including some species that were found nowhere else in our survey and are considered rare indicator/target species. The increase in diversity in the herbaceous vegetation community in the FECON site is a direct function of the increased solar radiation and openness of the canopy and is a primary characteristic of midwestern oak savannas (Cottam, 1949; Nuzzo, 1986). Conversely, the increased bulk density in the FECON site from the lesser managed sites should also be noted and may be a result of the machinery used. Bulk density directly limits root growth by influencing the porosity of the soil and limiting root growth (Kimble et al., 2001; Tracy et al., 2011). The effects of bulk density on soil are something that should be considered in the future management of this site and others.

Restoration with species and carbon

The open canopy and high amounts of solar radiation in the FECON site have increased with community composition, increasing the diversity and allowing the seed bank to begin re-establishing. The higher soil temperature and lower soil moisture that resulted from the solar radiation may have slowed decomposition, thus limiting the type of SOC stored in the soil. The driver of carbon sequestration in oak savanna is almost entirely a function of soil bulk density, where areas that have higher bulk density have lower percent carbon in the soil. The link between species diversity and carbon sequestration was not abundantly clear but is more of an effect of bulk density influencing both carbon sequestration and plant abundance. Additionally, sites with higher moisture had higher percent carbon. The FECON site had higher bulk density as well, which may have affected the carbon storage potential in the roots of the understory plants. The species that exist in this site do not have the deep root systems of the larger prairie plants that can store more recalcitrant carbon with their massive belowground biomass. I calculated the belowground biomass using regression formulas based off of plants in deciduous forests (Pearson et al., 2007), which were primarily what I encountered in the study.

I further believe that the higher compaction that has occurred in the FECON site is limiting root biomass and growth (Tracy et al., 2011). Although many different species are represented in the site, none of them (trees notwithstanding) were very large in stature. The effect of the young perennials is represented in the total aboveground biomass calculated which is used to calculate belowground root biomass. It must also be noted that the methods and regression formulas described by Pearson *et al.* are linear functions that may not be representative of prairie plants that have abnormally deep root systems. A future study that has the capacity for more destructive methods may reveal more about the exact root to shoot ratios of the plants growing in this particular ecosystem and their carbon storage potential.

Management Recommendations

If managing for greater diversity and rare species, FECON is an effective tool in oak savannas to quickly open the canopy. However, the compaction of soil is of concern and should be weighed when developing management plans. If managing for carbon storage, there is greater carbon stock in sites that remain forested but are managed with prescribed fire. In this study, minimal management in heavily forested sites as seen in the 2018/19 Burn site is also not beneficial in either diversity or carbon sequestration.

I believe the link between carbon, species diversity, and restoration in this oak savanna to be a function of canopy openness and understory biomass. This pattern is seen in other studies and is well accepted in the literature when describing the effect of sunlight on biomass (Araújo et al., 2017; Brudvig & Asbjornsen, 2009). Regarding our hypotheses, carbon sequestration is not directly linked to intense management practices. It is instead related to opening the canopy, which provides more solar energy for understory biomass growth. Species richness is also related to canopy openness, but requires more intense management to limit the overrunning capabilities of *Pteridium spp.* This species alone limited diversity in the 2017 Burn site. The link, being as weak as it is in this ecosystem, requires a careful balance in management with no broad and sweeping prescription to restore endangered ecosystems.

Acknowledgements

I warmly thank GVSU for the support and funding of this research and thesis, Greg Hochstetler and the MSGA staff for use of their land and thoughts, Drs. Meg Woller-Skar, Priscilla Nyamai, and Ali Locher for their advising and care throughout this process. Additionally I would like to thank Chris Rocha, Afafia Herweyer, and Aaron Christiansen for help in the field; my amazing wife, the Biology Department, fellow graduate students, and my family for keeping me going through this whole process. I will also be eternally thankful to Dr. Holly Jones and all members of her lab for beginning my journey into academia.

III. Extended Review of Literature and Extended Methodology

Extended Review of Literature

Oak Savannas

Oak savannas occur across the Midwest and exist as a product of active ecosystem succession between grasslands and forests. (Brudvig & Mabry, 2008; Cottam, 1949; Nuzzo, 1986). They are characterized by 10 - 50% canopy cover and are dominated by oak and pine species, and an understory consisting of dense prairie vegetation (Bowles & McBride, 1998; Cottam, 1949; Lettow et al., 2014; Peterson & Reich, 2008). This system evolved with fire as a regular disturbance in a time when there was high oxygen content in the atmosphere, as a result, oak savannas are fire adapted rather than fire sensitive and thrive in the presence of fire (Bowles & McBride, 1998; Bowman et al., 2009; Nowacki & Abrams, 2008). Historically, wildfires occurred throughout the year in these systems and were started by lighting during storms or periods of intense heat. As humans settled on the land, they began to use prescribed fires to control animal grazing and to protect their settlements from wildfires (Bowman et al., 2009; Nowacki & Abrams, 2008). Time passed, and European settlers converted oak savanna into agriculture and suppressed wildfires, causing the oak savanna to decline by over 90% of its historical range (Brudvig & Mabry, 2008; Nuzzo, 1986). As land managers have been attempting to re-create and restore these ecosystems, they have used prescribed fire as a management technique to limit woody encroachment as well as to stimulate nutrient flow between the plants and soil (Brudvig & Asbjornsen, 2009; Fölster et al., 2001; Lettow et al., 2014; Yuste et al., 2010).

Oak savannas are inherently heterogeneous systems. This heterogeneity is derived from vertical stratification of the vegetation biomass. The relatively limited canopy provides shaded areas for forest understory species, where the most open areas have more available sunlight and solar radiation to support the growth of dense prairie vegetation (Cavender-Bares & Reich, 2012;

Nuzzo, 1986; Peterson et al., 2007). Savanna understories contain a mixture of grassland and forest understory species, such as *Pteridium spp., Carex pennsylvanica,* and *Monarda fistulosa.* (Bowman et al., 2009; Pearson et al., 2007; Reinhardt et al., 2017). Since this is a system with a primarily open canopy that can experience high temperatures, the soil is relatively nutrient poor, apart from the carbon being fixed by plants (Lettow et al., 2014). Prairie and grassland vegetation is known for having deep and dense root systems, an additional contributor to high recalcitrant soil carbon (Johnson & Matchett, 2001; Peterson & Reich, 2001). This high vertical stratification compared to other forest systems provides a unique and highly heterogenous ecosystem with high biomass, species richness, and density (Schetter et al., 2013). Heterogeneity in grassland and savanna ecosystems also increases plant biomass and soil mixing. Minute differences in plant height, soil depth, and nutrient requirements allows for inter-species competition to take place, which maximizes the resources that are being used (Lehman & Tilman, 2000).

This system is particularly important due to its impact on climate change, given its high vertical stratification. Foremost, the dense belowground biomass of the prairie understory can store atmospheric carbon dioxide (CO_2) in a process known as carbon sequestration (Nelson et al., 2008). As plants fix CO_2 from the atmosphere during photosynthesis, the CO_2 is converted into sugars, which become the biomass of the plant both above and in the soil (von Haden & Dornbush, 2017). When the plant dies or loses biomass, the carbon and other nutrients in the biomass decompose and become part of the organic layer in the soil, thus sequestering atmospheric carbon in the soil (Nelson et al., 2008; Pearson et al., 2007). Another benefit to this system regarding its high vertical stratification is the low reflective capacity of the ecosystem, or its albedo. Systems with less stratification absorb less sunlight than savannas and reflect more, increasing latent heat (Hollinger et al., 2010). From a land manager's perspective, it would benefit the planet as a whole to manage these ecosystems not only for ecosystem recovery, but also for maximum carbon storage (Lal, 2005; Nelson et al., 2008). As I attempt to mitigate climate change, heterogenous systems with high vertical stratification and dense biomass that have adapted to high temperatures and wildfires will be imperative (Lal, 2005; Nelson et al., 2008; Wang et al., n.d.).

Management practices

Prescribed Fire

Oak savannas evolved with fire as a regular disturbance, and current management strategies commonly use prescribed fire for land management (Bowman et al., 2009; Cottam, 1949; Lettow et al., 2014; Peterson et al., 2007). Many studies have also been conducted on the more specific effects of prescribed fire in this system. The most well-known and cited use of prescribed fire is the limitation of woody undergrowth. This applies to both savannas and prairies, as they are both fire-adapted systems that cannot tolerate woody encroachment (Bergès et al., 2017; Bowman et al., 2009; Brudvig & Asbjornsen, 2009; Cottam, 1949; Peterson & Reich, 2001). The benefit of limiting the woody mid-story is limiting future canopy cover. Many savanna species are shade-intolerant and thrive in areas with high sunlight. This comes into play when prescribed fires eliminate woody growth and limit the canopy cover in the system (Bellow & Nair, 2003; Bergès et al., 2017; Brudvig & Asbjornsen, 2009; Cottam, 1949; Henneron et al., 2017). This increased light availability increases overall biomass, species richness, total abundance, allows for more available rainwater in the system, and is the primary driver of litter decomposition rates (Bravo-Oviedo et al., 2017; Cavender-Bares & Reich, 2012; Henneron et al., 2017; Peterson et al., 2007; Peterson & Reich, 2008; Schetter et al., 2013). Other studies have been conducted on canopy cover and fire frequency and their effects on oak savanna composition. Overall, these studies found that an increase in fire frequency decreased tree density and basal area while increasing tree mortality rate (Cavender-Bares & Reich, 2012; Frelich et al., 2017). This is to be expected for tree species, but the interesting findings are in the understory species. Studies conducted on Minnesota oak savanna restoration found that C_4 grass (adapted for high temperature environments) abundance increased with fire frequency while decreasing with canopy cover. C_3 grasses (common species) preferred 40-60% canopy cover, and forbs (wildflowers) peaked at 4-7 fires per decade (Peterson et al., 2007; Peterson & Reich, 2001). Overall, these studies found that the ideal average canopy cover for highest species richness is approximately 30% with fires every 2-5 years (Peterson et al., 2007; Peterson & Reich, 2001). Fire also alters primary productivity in the understory causing a loss of nutrients via volatilization (Arocena & Opio, 2003). Nutrient volatilization occurs when the fire intensity is high enough that nutrients (especially nitrogen) are burned off and become part of the atmosphere (Arocena & Opio, 2003). The same study also examined the relationship between the vegetation composition and found increased nitrogen cycling in systems that were frequently burned (1-3 years) (Dijkstra et al., 2006). It should be noted that fire is a variable disturbance depending on site topography, soil type, and intensity; this can lead to varying quantified effects if the environmental conditions surrounding the fire are not recorded (Dey & Kabrick, n.d.).

Prescribed fire also has a large effect on sequestering carbon in savannas; plant decomposition creates the organic matter layer in the soil, which is comprised primarily of carbon. Prescribed fire and its effects have been described to initially decrease the carbon content in aboveground biomass, but eventually increase the total understory and soil carbon content (Kim et al., 2018; Peterson & Reich, 2001). Apart from the prairie-style dynamics in the system, it is still true that much carbon is stored in trees and in soil near trees, as they individually carry high biomass and provide protection from runoff and erosion (Hoosbeek et al., 2016; Koteen et al., 2015). This being said, soil carbon remains the largest carbon pool on the planet, and the largest contributor to carbon sequestration (Kim et al., 2018). A study estimating carbon storage in various systems estimated that savannas are responsible for the sequestering of 1-3 petagrams (Pg) of carbon per year (Lal, 2005).

Thinning/harvest

Fire suppression in oak savanna systems leads to the overdevelopment of the understory and mid-story, which increases canopy cover and eventually transforms the system into a dense forest (Brudvig & Asbjornsen, 2009). As a last resort method for the restoration of savanna sites, land managers have used machinery to manually thin the canopy and woody encroachment. This process, which began as a method of agricultural harvest in an attempt to preserve the forest and regenerate it as soon as possible for a successional harvest, has since been used to restore the available light gradient that defines oak savannas and provides many of its ecosystem benefits (Baker, 1934; Hawley, 1921; Pearson et al., 2007; Peterson & Reich, 2001). Among various methods for the removal of woody encroachment, this study examines sites that have been heavily thinned (>90%) (Ma et al., 2018) by FECON harvesting technology. FECON units use grinding tools to cut down and mulch the aboveground biomass of trees, allowing the biomass to decompose with limited soil disturbance, aside from compaction.

Studies have shown that the benefits of thinning as a method of oak savanna restoration are based on decreasing canopy cover. Similar to what occurs after prescribed fire, canopy cover has been shown to be the primary driver of changes in litter decomposition rates by allowing more rainfall to reach the soil (Bravo-Oviedo et al., 2017; Reich et al., 2001). In addition to this, root fraction and fine root biomass increase with canopy openness, leading to a decrease in canopy mass and nitrogen mineralization (Reich et al., 2001). Further, areas that still have trees are found to show greater losses in nitrogen, but higher available soil nitrogen (Dijkstra et al., 2006). The increase in soil nitrogen could be explained by the correlation of thinning to increased soil microbial biodiversity, which increases soil nutrient availability (Henneron et al., 2017). The trends noticed after the application of thinning are similar to those seen after prescribed fire. This is due to thinning being an extension of the effects of fire, just on a larger scale. The main difference between the two is that thinning does not cause a volatilization of nutrients as biomass combusts (Bravo-Oviedo et al., 2017; Peterson et al., 2007).

Please note: our study was originally going to contain four separate variables: control (no treatment), prescribed fire, thinning, and both treatments. The land manager at the field site then decided to burn the sites that had been thinned to avoid invasion by exotic species and woody encroachment, as is suggested by literature (Asbjornsen et al., 2007). As a result, thinning treatment will be coupled with prescribed fire as it is unreasonable to thin without burning in a practical oak savanna restoration. As is common with thinning treatments, carefully applied herbicide was also used on tree stumps to permanently eliminate them.

Study Site:

Our study's field site is located in the Muskegon State Game Area (MSGA, Muskegon, Michigan, USA) and is owned by the Michigan Department of Natural Resources (MDNR). The current land manager began thinning the ecosystem in the spring of 2017 by using a FECON mulching head to heavily clear oak and pine saplings, making way for the future generation of the oak savanna. Other studies have discussed the effects of varying intensity of thinning, but that is not the goal of this study (Ma et al., 2018). The FECON method does not remove the dead biomass from the system: instead, the grinding head mulches the trees stumps and returns the biomass to the soil. Removing the thinned biomass from the system could result in total carbon loss from the system, which would counteract the results. This patch of oak savanna is unique in that its young sapling population is about 50 years old, but with a low diameter at breast height (dbh), which is estimated at four centimeters. This is in part due to fire suppression and lack of management since the mid-1980s. The thinning left the current generation of ancient canopy trees and several of the low dbh “saplings” to take their place in the future.

<u>Research Questions and Hypotheses:</u>

Where the ecosystem benefits of management practices have been well-documented (Brudvig & Asbjornsen, 2009; Lettow et al., 2014), the combined effects of prescribed fire and thinning on carbon sequestration in the relatively understudied oak savanna system are not well-described. I will ask how the application of prescribed fire and overstory thinning (perturbation management practices) affect:

- Abundance, community composition, and diversity of the plant community
- Amount of carbon that is being sequestered in the canopy, mid-story, understory, belowground biomass, and soil

These questions will help us determine how biodiversity, oak savanna restoration and sequestered carbon are related at MSGA. I hypothesize that applying management practices such as prescribed fire and FECON thinning will increase biodiversity and species abundance in the understory, while further restoring the seedbank of the historical system. Beyond this, I hypothesize that while there will be an initial decrease in carbon sequestered due to the use of fire and FECON thinning, the restoration of the understory will lead to increased carbon in the belowground biomass and soil. This study is novel in that it is beginning to take an ecosystem-specific approach towards sequestering CO_2 emissions and mitigating the effects of climate change. Broader studies have been done that classify the overall carbon being sequestered by the planet, but few have been done on how specific management practices alter the landscape for these specific benefits (Hoosbeek et al., 2016; Lal, 2005; von Haden & Dornbush, 2017).

Extended Methodology

At each grid point, I used the Olympus TG-4 camera with a hemispheric lens to collect gap fraction, canopy openness, leaf area index (LAI), total site factor (TSF), mean leaf angle (MLA), and total photosynthetic photon flux density (PPFD). LAI was collected as LAI 2000, a conversion from leaf area index units to percent of pen sky covered by leaves. These data were analyzed with the WynScanopy analysis software (Cite). I measured soil pH and temperature using a Dr.Meter multimeter, and a Fieldscout TDR 300 Soil Moisture Meter to measure soil moisture. I used a 1 m^2 quadrat and stem density counts to estimate the overall percent coverage of plant species at each point. Following carbon stock guidelines, I collected live understory biomass within a 0.25 m^2 quadrat as well as all dead organic matter from point locations. I additionally collected soil cores using a 70.36 cm^3 soil auger (CV). I followed carbon stock guidelines to measure tree carbon within the established tree plots. I marked each tree (d.b.h. > 5cm) within the plot and recorded species and d.b.h. For each dead wood transect, I recorded the length, d.b.h., and quality of wood (rotten, intermediate, or sound) of every piece of fallen dead wood that intercepted the transect (Pearson et al., 2007).

All collected samples were brought back to the GVSU soil processing lab and massed individually. They were then dried in a drying oven at 80°C for two weeks and massed again to determine AGB of non-tree vegetation. To calculate below-ground biomass (BGB), I used the regression formula for temperate forest BGB from Pearson et al., (2007):

$$BGB = e^{(-1.0587 + 0.8836 * \ln(AGB) + 0.2840)} \text{ (t/ha)}$$

These were also multiplied by 0.5 to quantify t/ha of carbon (Pearson et al., 2007). For dead biomass (t/ha) (DOM), I used the formula:

$$DOM = (\text{forest-floor oven-dry weight (g) / sampling frame area } (cm^2)) * 100$$

Dead wood measured in the dead wood plots were first converted to volume (m^3/ha):

$$V = \pi^2 * [(d_1^2 + d_2^2 + \ldots + d_n^2)/800]$$

To convert the volume of dead wood into biomass (biomass stock), I used regression formulas using the density and quality of wood. (Sound density: 0.43 t/m^3, Intermediate: 0.34 t/m^3, Rotten: 0.19 t/m^3)

$$\text{Biomass stock t/ha} = \Sigma(V_{sound})* 0.43) + \Sigma(V_{intermediate})* 0.34) + \Sigma(V_{rotten})* 0.19)$$

Tree biomass (Tree AGB) was determined by regression formulas specific to the density of different tree clades:

$$\text{Tree AGB} = e^{(\beta 0 + \beta 1 \text{ Ln } x)}$$

Where β_0 and β_1 are clade specific parameters and x = tree d.b.h. (cm). The conversion formula from AGB to BGB was used again to convert tree AGB to tree BGB. These were all multiplied by 0.5 to convert to t C/ha (Pearson et al., 2007).

Each soil auger was used for a different measurement. The first auger at each point was used to calculate the bulk density of soil, the second was used to measure total carbon. Each core was collected and weighed wet, then dried at 80°C. The oven-dry sample was weighed for an additional soil moisture measurement. The bulk density sample was then filtered with a 2mm sieve to separate the oven-dry fine soil fraction (ODW) from the oven-dry coarse fragments (RF). Both soil orders(?) were massed and used to calculate bulk density (ρ_b) using this formula:

$$\rho_b \text{ (g/cm}^3\text{)} = \text{ODW} / [\text{CV} - (\text{RF} / \text{PD})]$$

Density of rock fragments (PD) is assumed to be 2.65 g/cm^3 (Pearson et al., 2007). Percent carbon was determined by homogenizing the second soil core and filtering through (0.7 mm) sieve. The fine material was massed to 4g in a crucible and heated at 500°C for 8 hours, or until all carbon had been burned off. The remaining difference divided by the original mass yielded percent carbon (%C). Total carbon in the mineral soil (C t/ha) was calculated using this formula:

$$\text{C (t/ha)} = (\rho_b * \text{soil depth (cm)} * \text{\%C})*100$$

Herbaceous vegetation percent cover was estimated at each grid point using a 1m^2 quadrat. I recorded 26 different species across the three sites.

References

Aerts, R. (1997). Climate, leaf litter chemistry and leaf litter decomposition in terrestrial ecosystems: A triangular relationship. *Oikos*, *79*(3), 439–449. https://doi.org/10.2307/3546886

Araújo, F. D. C., Tng, D. Y. P., Apgaua, D. M. G., Coelho, P. A., Pereira, D. G. S., & Santos, R. M. (2017). Post-fire plant regeneration across a closed forest-savanna vegetation transition. *Forest Ecology and Management*, *400*, 77–84. https://doi.org/10.1016/j.foreco.2017.05.058

Arocena, J. M., & Opio, C. (2003). Prescribed fire-induced changes in properties of sub-boreal forest soils. *Geoderma*, *113*(1), 1–16. https://doi.org/10.1016/S0016-7061(02)00312-9

Asbjornsen, H., Tomer, M. D., Gomez-Cardenas, M., Brudvig, L. A., Greenan, C. M., & Schilling, K. (2007). Tree and stand transpiration in a Midwestern bur oak savanna after elm encroachment and restoration thinning. *Forest Ecology and Management*, *247*(1), 209–219. https://doi.org/10.1016/j.foreco.2007.04.043

Bailey, B. N., & Mahaffee, W. F. (2017). Rapid measurement of the three-dimensional distribution of leaf orientation and the leaf angle probability density function using terrestrial LiDAR scanning. *Remote Sensing of Environment*, *194*, 63–76. https://doi.org/10.1016/j.rse.2017.03.011

Baker, F. (1934). Theory & practice of silviculture. McGraw-Hill Book Company, Inc.

Barot, S., & Gignoux, J. (2004). Mechanisms promoting plant coexistence: Can all the proposed processes be reconciled? *Oikos*, *106*(1), 185–192. JSTOR.

Bellow, J. G., & Nair, P. K. R. (2003). Comparing common methods for assessing understorey light availability in shaded-perennial agroforestry systems. *Agricultural and Forest Meteorology*, *114*(3–4), 197–211. https://doi.org/10.1016/S0168-1923(02)00173-9

Bergès, L., Feiss, T., Avon, C., Martin, H., Rochel, X., Dauffy-Richard, E., Cordonnier, T., & Dupouey, J. L. (2017). Response of understory plant communities and traits to past land use and coniferous plantation. *Applied Vegetation Science*, *20*(3), 468–481. https://doi.org/10.1111/avsc.12296

Berryman, E., Ryan, M. G., Bradford, J. B., Hawbaker, T. J., & Birdsey, R. (2016). Total belowground carbon flux in subalpine forests is related to leaf area index, soil nitrogen, and tree height. *Ecosphere*, *7*(8), e01418. https://doi.org/10.1002/ecs2.1418

Bowles, M. L., & McBride, J. L. (1998). Vegetation composition, structure, and chronological change in a decadent Midwestern North American savanna remnant. *Natural Areas Journal*, *18*(1), 14–27.

Bowman, D. M. J. S., Balch, J. K., Artaxo, P., Bond, W. J., Carlson, J. M., Cochrane, M. A., D’Antonio, C. M., DeFries, R. S., Doyle, J. C., Harrison, S. P., Johnston, F. H., Keeley, J. E., Krawchuk, M. A., Kull, C. A., Marston, J. B., Moritz, M. A., Prentice, I. C., Roos, C. I., Scott, A. C., … Pyne, S. J. (2009). Fire in the earth system. *Science*, *324*(5926), 481–484. https://doi.org/10.1126/science.1163886

Bravo-Oviedo, A., Ruiz-Peinado, R., Onrubia, R., & del Río, M. (2017). Thinning alters the early-decomposition rate and nutrient immobilization-release pattern of foliar litter in Mediterranean oak-pine mixed stands. *Forest Ecology and Management*, *391*, 309–320. https://doi.org/10.1016/j.foreco.2017.02.032

Brudvig, L. A., & Asbjornsen, H. (2008). Patterns of oak regeneration in a Midwestern savanna restoration experiment. *Forest Ecology and Management*, *255*(7), 3019–3025. https://doi.org/10.1016/j.foreco.2007.11.017

Brudvig, L. A., & Asbjornsen, H. (2009). The removal of woody encroachment restores biophysical gradients in Midwestern oak savannas. *Journal of Applied Ecology*, *46*(1), 231–240.

Brudvig, L. A., & Mabry, C. M. (2008). Trait-based filtering of the regional species pool to guide understory plant reintroductions in Midwestern oak savannas, U.S.A. *Restoration Ecology*, *16*(2), 290–304. https://doi.org/10.1111/j.1526-100X.2007.00317.x

Cavender-Bares, J., & Reich, P. B. (2012). Shocks to the system: Community assembly of the oak savanna in a 40-year fire frequency experiment. *Ecology*, *93*(8), S52–S69.

Chapin, III, F. S., Matson, P. A., & Vitousek, P. M. (2012). *Principles of Terrestrial Ecosystem Ecology* (2nd ed.). Springer Science+Business Media.

Clarke, K. R. (1993). Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology*, *18*, 117–143.

Cottam, G. (1949). The phytosocioloy of an oak woods in Southwestern Wisconsin. *Ecology*, *30*(3), 271–287. https://doi.org/10.2307/1932609

Dey, D. C., & Kabrick, J. M. (n.d.). Restoration of Midwestern oak woodlands and savannas. *Restoration of Boreal and Temperate Forests*, 28.

Dijkstra, F. A., Wrage, K., Hobbie, S. E., & Reich, P. B. (2006). Tree patches show greater N losses but maintain higher soil N availability than grassland patches in a frequently burned oak savanna. *Ecosystems*, *9*(3), 441–452.

Ebeling, A., Hines, J., Hertzog, L. R., Lange, M., Meyer, S. T., Simons, N. K., & Weisser, W. W. (2018). Plant diversity effects on arthropods and arthropod-dependent ecosystem functions in a biodiversity experiment. *Basic and Applied Ecology*, *26*, 50–63. https://doi.org/10.1016/j.baae.2017.09.014

Ebeling, A., Rzanny, M., Lange, M., Eisenhauer, N., Hertzog, L. R., Meyer, S. T., & Weisser, W. W. (2018). Plant diversity induces shifts in the functional structure and diversity across trophic levels. *Oikos, 127*(2), 208–219. https://doi.org/10.1111/oik.04210

Fan, S., Gloor, M., Mahlman, J., Pacala, S., Sarmiento, J., Takahashi, T., & Tans, P. (1998). A large terrestrial carbon sink in North America implied by atmospheric and oceanic carbon dioxide data and models. *Science*, *282*(5388), 442–446. JSTOR.

Fölster, H., Dezzeo, N., & Priess, J. A. (2001). Soil–vegetation relationship in base-deficient premontane moist forest–savanna mosaics of the Venezuelan Guayana. *Geoderma*, *104*(1–2), 95–113. https://doi.org/10.1016/S0016-7061(01)00058-1

Frank, A. B. (2002). Carbon dioxide fluxes over a grazed prairie and seeded pasture in the Northern Great Plains. *Environmental Pollution*, *116*(3), 397–403. https://doi.org/10.1016/S0269-7491(01)00216-0

Frelich, L. E., Reich, P. B., & Peterson, D. W. (2017). The changing role of fire in mediating the relationships among oaks, grasslands, mesic temperate forests, and boreal forests in the Lake States. *Journal of Sustainable Forestry*, *36*(5), 421–432. https://doi.org/10.1080/10549811.2017.1296777

Giai, C., & Boerner, R. E. J. (2007). Effects of ecological restoration on microbial activity, microbial functional diversity, and soil organic matter in mixed-oak forests of southern Ohio, USA. *Applied Soil Ecology*, *35*(2), 281–290. https://doi.org/10.1016/j.apsoil.2006.08.003

Hawley, R. C. (1921). *The practice of silviculture, with particular reference to its application in the United States*. John Wiley & Sons Incorporated.

Henneron, L., Aubert, M., Archaux, F., Bureau, F., Dumas, Y., Ningre, F., Richter, C., Balandier, P., & Chauvat, M. (2017). Forest plant community as a driver of soil biodiversity: Experimental evidence from collembolan assemblages through large-scale and long-term removal of oak canopy trees Quercus petraea. *Oikos*, *126*(3), 420–434. https://doi.org/10.1111/oik.03677

Hollinger, D. Y., Ollinger, S. V., Richardson, A. D., Meyers, T. P., Dail, D. B., Martin, M. E., Scott, N. A., Arkebauer, T. J., Baldocchi, D. D., Clark, K. L., Curtis, P. S., Davis, K. J., Desai, A. R., Dragoni, D., Goulden, M. L., Gu, L., Katul, G. G., Pallardy, S. G., U, K. T. P., … Verma, S. B. (2010). Albedo estimates for land surface models and support for a new paradigm based on foliage nitrogen concentration. *Global Change Biology*, *16*(2), 696–710. https://doi.org/10.1111/j.1365-2486.2009.02028.x

Hoosbeek, M. R., Remme, R. P., & Rusch, G. M. (2016). Trees enhance soil carbon sequestration and nutrient cycling in a silvopastoral system in south-western Nicaragua. *Agroforestry Systems*. https://doi.org/10.1007/s10457-016-0049-2

Johnson, L., & Matchett, J. (2001). Grazing regulates belowground processes in tallgrass prairie. *Ecology*, *82*(August 2000), 3377–3389. https://doi.org/10.1890/0012-9658(2001)082[3377:FAGRBP]2.0.CO;2

Jones, H. G., & Vaughan, R. A. (2010). *Remote Sensing of Vegetation: Principles, Techniques, and Applications*. OUP Oxford.

Kim, S., Kim, C., Han, S. H., Lee, S.-T., & Son, Y. (2018). A multi-site approach toward assessing the effect of thinning on soil carbon contents across temperate pine, oak, and larch forests. *Forest Ecology and Management*, *424*, 62–70. https://doi.org/10.1016/j.foreco.2018.04.040

Kimble, J. M., Follett, R. F., & Lal, R. (2001). *Assessment Methods for Soil Carbon*. Lewis Publishers.

Knops, J. M. H., Tilman, D., Haddad, N. M., Naeem, S., Mitchell, C. E., Haarstad, J., Ritchie, M. E., Howe, K. M., Reich, P. B., Siemann, E., & Groth, J. (1999). Effects of plant species richness on invasion dynamics, disease outbreaks, insect abundances and diversity. *Ecology Letters*, *2*(5), 286–293. https://doi.org/10.1046/j.1461-0248.1999.00083.x

Koteen, L. E., Raz-Yaseef, N., & Baldocchi, D. D. (2015). Spatial heterogeneity of fine root biomass and soil carbon in a California oak savanna illuminates plant functional strategy across periods of high and low resource supply. *Ecohydrology*, *8*(2), 294–308. https://doi.org/10.1002/eco.1508

Lal, R. (2005). Forest soils and carbon sequestration. *Forest Ecology and Management*, *220*(1), 242–258. https://doi.org/10.1016/j.foreco.2005.08.015

Lehman, C. L., & Tilman, D. (2000). Biodiversity, stability, and productivity in competitive communities. *The American Naturalist*, *156*(5), 534–552. https://doi.org/10.1086/303402

Lettow, M. C., Brudvig, L. A., Bahlai, C. A., & Landis, D. A. (2014). Oak savanna management strategies and their differential effects on vegetative structure, understory light, and flowering forbs. *Forest Ecology and Management*, *329*, 89–98. https://doi.org/10.1016/j.foreco.2014.06.019

Ma, J., Kang, F., Cheng, X., & Han, H. (2018). Moderate thinning increases soil organic carbon in Larix principis-rupprechtii (Pinaceae) plantations. *Geoderma*, *329*(September 2017), 118–128. https://doi.org/10.1016/j.geoderma.2018.05.021

Machado, J.-L., & Reich, P. B. (1999). *Evaluation of several measures of canopy openness as predictors of photosynthetic photon flux density in deeply shaded conifer-dominated forest understory*. *29*, 7.

Nelson, E., Polasky, S., Lewis, D. J., Plantinga, A. J., Lonsdorf, E., White, D., Bael, D., & Lawler, J. J. (2008). Efficiency of incentives to jointly increase carbon sequestration and species conservation on a landscape. *Proceedings of the National Academy of Sciences of the United States of America*, *105*(28), 9471–9476.

Nilson, T., & Kuusk, A. (1989). A reflectance model for the homogeneous plant canopy and its inversion. *Remote Sensing of Environment*, *27*(2), 157–167. https://doi.org/10.1016/0034-4257(89)90015-1

Nowacki, G. J., & Abrams, M. D. (2008). The demise of fire and "mesophication" of forests in the Eastern United States. *BioScience*, *58*(2), 123–138. https://doi.org/10.1641/B580207

Nuzzo, V. A. (1986). Extent and Status of Midwest Oak Savanna: Presettlement and 1985. *Natural Areas Journal*, *6*(2), 6–36.

Okansen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2019). *Vegan: Community ecology package* (Version R package version 2.5-4) [Computer software]. https://CRAN.R-project.org/package=vegan

Pearson, T. R. H., Brown, S. L., & Birdsey, R. a. (2007). Measurement guidelines for the sequestration of forest carbon. *General Technical Report NRS-18. Delaware: United States Department of Agriculture - Forest Service*, *18*(1), 42. https://doi.org/10.1089/hum.2005.16.57

Peterson, D. W., & Reich, P. B. (2001). Prescribed fire in oak savanna: Fire frequency effects on stand structure and dynamics. *Ecological Applications*, *11*(3), 914–927. https://doi.org/10.2307/3061125

Peterson, D. W., & Reich, P. B. (2008). Fire frequency and tree canopy structure influence plant species diversity in a forest-grassland ecosystem. *Plant Ecology*, *194*(1), 5–16.

Peterson, D. W., Reich, P. B., & Wrage, K. J. (2007). Plant functional group responses to fire frequency and tree canopy cover gradients in oak savannas and woodlands. *Journal of Vegetation Science*, *18*(1), 3–12.

R Core Team. (2017). *R: A lauguage and environment for statistical computing*. R Foundation for Statistical Computing. https://www.R-project.org/

Rau, B. M., Chambers, J. C., Blank, R. R., & Johnson, D. W. (2008). Prescribed fire, soil, and plants: Burn effects and interactions in the central Great Basin. *Rangeland Ecology and Management*, *61*(2), 169–181. https://doi.org/10.2111/07-037.1

Reich, P. B., Peterson, D. W., Wedin, D. A., & Wrage, K. (2001). Fire and vegetation effects on productivity and nitrogen cycling across a forest–grassland continuum. *Ecology*, *82*(6), 1703–1719. https://doi.org/10.1890/0012-9658(2001)082[1703:FAVEOP]2.0.CO;2

Reinhardt, J. R., Nagel, L. M., Keough, H., & Swanston, C. (2017). Michigan oak savanna restoration: A comparison of mechanical thinning approaches in the context of prescribed fire and native seeding. *Forest Science*, *63*(4), 420–431. https://doi.org/10.5849/FS-2016-043R1

Rich, P. M. (1990). Characterizing plant canopies with hemispherical photographs. *Remote Sensing Reviews*, *5*(1), 13–29. https://doi.org/10.1080/02757259009532119

Schetter, T. A., Walters, T. L., & Root, K. V. (2013). A multi-scale spatial analysis of native and exotic plant species richness within a mixed-disturbance oak savanna landscape. *Environmental Management*, *52*(3), 581–594. https://doi.org/10.1007/s00267-013-0120-y

Schmidt, M. W. I., Torn, M. S., Abiven, S., Dittmar, T., Guggenberger, G., Janssens, I. A., Kleber, M., Kögel-Knabner, I., Lehmann, J., Manning, D. A. C., Nannipieri, P., Rasse, D. P., Weiner, S., & Trumbore, S. E. (2011). Persistence of soil organic matter as an ecosystem property. *Nature*, *478*(7367), 49–56. https://doi.org/10.1038/nature10386

Soil Survey Staff, Natural Resources Conservation Service, & United States Department of Agriculture. (2019). *Web soil survey*. Retrieved May 25, 2019, from http://websoilsurvey.sc.egov.usda.gov/

Starfield, A. M., & Bleloch, A. L. (1991). *Building models for conservation and wildlife management* (2nd ed.). Burgess International Group.

Sutton, M. A., Simpson, D., Levy, P. E., Smith, R. I., Reis, S., van Oijen, M., & de Vries, W. (2008). Uncertainties in the relationship between atmospheric nitrogen deposition and forest carbon sequestration. *Global Change Biology*, *14*(9), 2057–2063. https://doi.org/10.1111/j.1365-2486.2008.01636.x

Tester, J. R. (1989). Effects of fire frequency on oak savanna in East-Central Minnesota. *Bulletin of the Torrey Botanical Club*, *116*(2), 134–144. JSTOR. https://doi.org/10.2307/2997196

Tilman, D., Reich, P., Phillips, H., Menton, M., Patel, A., Vos, E., Peterson, D., & Knops, J. (2000). Fire suppression and ecosystem carbon storage. *Ecology*, *81*(10), 2680–2685. https://doi.org/10.2307/177333

Tracy, S. R., Black, C. R., Roberts, J. A., & Mooney, S. J. (2011). Soil compaction: A review of past and present techniques for investigating effects on root growth. *Journal of the Science of Food and Agriculture*, *91*(9), 1528–1537. https://doi.org/10.1002/jsfa.4424

USDA. (2003). *What is an oak savanna*. 6.

Vittori Antisari, L., Marinari, S., Dell'Abate, M. T., Baffi, C., & Vianello, G. (2011). Plant cover and epipedon SOM stability as factors affecting brown soil profile development and microbial activity. *Geoderma*, *161*(3), 212–224. https://doi.org/10.1016/j.geoderma.2010.12.021

von Haden, A. C., & Dornbush, M. E. (2017). Ecosystem carbon pools, fluxes, and balances within mature tallgrass prairie restorations. *Restoration Ecology*, *25*(4), 549–558. https://doi.org/10.1111/rec.12461

Wang, L., Tian, F., Wang, Y., Wu, Z., Schurgers, G., & Fensholt, R. (n.d.). Acceleration of global vegetation greenup from combined effects of climate change and human land management. *Global Change Biology*, *0*(0). https://doi.org/10.1111/gcb.14369

Weiher, E., & Howe, A. (2003). Scale-dependence of environmental effects on species richness in oak savannas. *Journal of Vegetation Science*, *14*(6), 917–920. JSTOR.

Wilhelm, G., & Rericha, L. (2017). *Flora of the Chicago Region: A Floristic and Eclogical Synthesis*. Indiana Academy of Science; Updated and Revised edition (2017).

Yang, Y., Tilman, D., Furey, G., & Lehman, C. (2019). Soil carbon sequestration accelerated by restoration of grassland biodiversity. *Nature Communications*, *10*(1), 1–7. https://doi.org/10.1038/s41467-019-08636-w

Yuste, J. C., Baldocchi, D. D., Gershenson, A., Goldstein, A., Misson, L., & Wong, S. (2007). Microbial soil respiration and its dependency on carbon inputs, soil temperature and moisture. *Global Change Biology*, *13*(9), 2018–2035. https://doi.org/10.1111/j.1365-2486.2007.01415.x

Yuste, J. C., Ma, S., & Baldocchi, D. D. (2010). Plant-soil interactions and acclimation to temperature of microbial-mediated soil respiration may affect predictions of soil CO_2 efflux. *Biogeochemistry*, *98*(1/3), 127–138.

Regent Instruments Inc. (2020). WinSCANOPY™: Canopy structure and solar radiation. Regent Instruments Inc., Quebec, Canada.