LAND MANAGEMENT PRACTICES ON BELOWGROUND CARBON IN THE ECOSYSTEM TRANSITIONAL ZONE IN THE SOUTHCENTRAL GREAT PLAINS

By

J HARRELL JOHNSON

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Oklahoma State University

Stillwater, Oklahoma

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Thesis Approved:

Dr. Chris Zou

Thesis Adviser

Dr. Rodney Will

Dr. Samuel Fuhlendorf

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Abstract: The mesic grasslands in the Great Plains of the USA have a great capacity to sequester atmospheric CO₂ into soil. Over 5.2 million hectares of such grasslands in the southern Great Plains are "go-back" lands; areas that were once tilled and cultivated, severely degraded and deprived of soil carbon. These grasslands are under rapid woody encroachment and potential lands for planting switchgrass (*Panicum virgatum*) for biofuel production. However, there is no systematic study of the historical and recent land-use impact on soil carbon storage and dynamics. In this study, I selected six adjacent sites representing three land uses [non-grazed prairie, grazed prairie, and eastern redcedar (Juniperus virginiana L.) woodland)] and three recent land-use changes (eastern redcedar to prairie, eastern redcedar to switchgrass, and prairie to switchgrass) in the southcentral Great Plains. I collected a total of 120 intact soil cores from the 0–30 cm depth to determine the bulk density (ρb) , percent soil organic carbon (C-content), and percent nitrogen (N-content) and calculated soil organic carbon stock (C-stock) associated with different land uses and land-use history. ρb was greater in sites with recent mechanical disturbance, whereas C-content and N-content showed the opposite trend except for Ncontent under redcedar. C-stock (mean \pm SE) was 4,671 \pm 523 g C m⁻² for the 0-30 cm soil across all sites, which was substantially lower than that reported for remnant native prairie in this region. C-stocks under prairie sites were 10 - 15% greater than the encroached redcedar woodland. Conversion of an existing prairie or redcedar woodland to a switchgrass biofuel system was associated with substantially lower of soil carbon in the upper 30 cm. Our results suggest that these "go-back" lands can be a significant carbon sink and continue sequestering carbon. The reported trend from other studies of C and N generally increasing in the mineral soil following redcedar afforestation of grasslands is not universal, particularly on sites recovering from past cultivation. Keywords: Juniperus virginiana L. (eastern redcedar); Panicum virgatum (switchgrass); restored prairie; encroachment; woody plant removal; carbon storage

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CHAPTER I

INTRODUCTION TO SOIL ORGANIC CARBON

Overview

The terrestrial carbon pool is about three times greater than the CO₂ currently in the atmosphere, with over three-quarters of this stored within the soil (Lal, 2010; Paustian et al., 2016). Rangelands account for approximately 40% of the terrestrial biosphere by cover type and store as much as 30% of terrestrial carbon, roughly equal to the amount in the atmosphere (Schuman et al., 2002; Derner et al., 2006; Lal, 2010). Understanding the rate and capacity of carbon sequestration in rangeland soils under diverse management practices is essential for climate-smart land management and implementing land-based climate mitigation strategies (Lal, 2010; Paustian et al., 2016).

1. Soil Organic Matter and Soil Organic Carbon

1.1 Soil organic matter

Soil organic matter (SOM) is biomass found within the soil. Generally, it includes both living (living roots, active soil microorganisms) and dead (decayed plant material, humic substances, charred biomass) (Baldock and Nelson, 2000). However, what is and is not constituted as SOM is not always consistent (Baldock and Nelson, 2000). Some studies exclude living biomass (MacCarthy et al., 1990; Miltner et al., 2012) and charcoal (Skjemstad et al., 1990). Organic material on the surface of the soil is generally not used for calculations of SOC (Batjes, 1996), though this can contain a relatively large amount of organic material carbon within it (Norris et al., 2001a; Smith and Johnson, 2003; Nunes Biral et al., 2019).

SOM is used as an indicator of soil quality and is critical in regulating soil properties, plant growth, and productivity (Lal, 2009). SOM increases the ability of the soil to retain water and nutrients (Stevenson, 1994; Hansen et al., 2016) and is a crucial component of soil aggregate structure (Baldock and Nelson, 2000). In addition, it is the metabolic substrate for microbial biological activity within the soil (Baldock and Nelson, 2000). This microbial action of decomposition results in a gradual nutrient release (Janzen, 2006) which provides the largest source of plant nutrients in unmanaged systems (Baldock and Nelson, 2000).

1.2 Soil organic carbon

The elemental carbon within the SOM is soil organic carbon (SOC). The general assumption is that SOC comprises approximately 58% of SOM (Tabatabai, 1996; Post et al., 2001). Although this assumption has been frequently used, real-world ratios are more varied, with SOC being closer to 40% of the SOM in deeper soils (Broadbent, 1965). It is estimated that 2,344 GT of SOC is held in the top 3 meters of soil globally, with the majority of this, 1,500 GT, in the first meter (Jobbágy and Jackson, 2000; Guo and Gifford, 2002).

In addition to SOC, which originates from atmospheric CO_2 and is transformed through biological processes, there is also soil inorganic carbon (SIC). SIC is generally found within carbonite minerals (Eswaran et al., 1995; Batjes, 1996). Many strongly weathered and well drained soils lack significant amounts of SIC, as precipitation generally dissolves these carbonites, leaching them from the soil profile (Wang et al., 2010). SIC can be common in xeric environments or where the soil is derived from calcareous rock (Batjes, 1996). In arid conditions, SIC is estimated to be able to persist for thousands of years (Schlesinger et al., 1986; Wang et al., 2010).

1.3 Origin and rate of SOC change

When plants undergo photosynthesis, light provides the energy to transform atmospheric CO₂ to glucose. This is utilized directly or in forming other organic compounds to facilitate the plant's biological processes, and are collectively known as photosynthates (Baldock and Nelson, 2000). The total amount of photosynthates created by plants in a given time is gross primary productivity (GPP). Some of these photosynthates are used by the plant for metabolic functions (autotrophic respiration), and the carbon returns to the atmosphere relatively quickly (De Deyn et al., 2008; Gough, 2012). The total gross carbon taken up by a plant as CO₂ for photosynthesis (GPP) minus the carbon compounds lost through autotrophic respiration is net primary productivity (NPP). All SOC originates, directly or indirectly, from actual vegetation NPP (Kögel-Knabner, 2002).

Most NPP is retained as plant biomass (Sanderman and Amundson, 2003) which generally ranges from 45% to 48% carbon by weight (Ma et al., 2018). Measured biomass is usually used as a proxy for NPP (Sanderman and Amundson, 2003), though NPP estimated from biomass and actual NPP are not entirely the same (Chapin and Eviner, 2003). This plant biomass makes up most of the carbon that enters the soil (Czimczik et al., 2005) though measuring changes in belowground biomass is difficult to measure directly and is often estimated (Mokany et al., 2006).

In addition to plant biomass accumulation, photosynthates are allocated to other components, such as volatile organic compounds, which are emitted into the atmosphere (Clark et al., 2001) and non-biomass components of rhizodeposits (Farrar et al., 2003; Dennis et al., 2010) such as root exudates. These non-biomass NPP products are usually much less than biomass products (Sanderman and Amundson, 2003). Volatile emissions, when measured, are generally less than 5% of NPP (Chapin and Eviner, 2007). Rhizopdeposits are estimated to make up around 11% of NPP, though this varies based on plant species, age, and health (Jones et al., 2009; Vives-Peries et al., 2020). Some rhizodeposits are quickly utilized for soil microbial respiration, which is often recorded as a component of root respiration (Chapin and Eveiner, 2007). However, while much of the carbon of rhizodeposits is lost as CO₂ due to microbial respiration, some of it is incorporated into microbial biomass (Jones et al., 2009; Angst et al., 2021).

SOC is in constant flux between photosynthetic inputs of above and belowground plant biomass and C mineralization (Baldock and Nelson, 2000; Post et al., 2001), with the respiration of soil microbiota being the most significant contributor to C mineralization (Follett, 2001). Historically, microbial life has been viewed primarily as an agent of soil carbon loss (Bradford et al., 2016). Many photosynthates are lost to microbial consumption within hours (Bradford et al., 2013), while other forms of plant-derived carbon, such as lignin, are relatively resistant to microbial consumption (Rasse et al., 2005). With 60 to 80% of the carbon from organic matter released as CO₂ during microbial decomposition (González-Pérez et al., 2004), it was assumed that the remaining carbon forms were difficult for microbes to utilize and made up much of the stable carbon within the soil. However, more recent research has shown that the microbial transformation of soil carbon is more complicated than just mineralization.

There has been a growing shift to viewing soil microbiota as a major factor in SOC stabilization. While much of the carbon utilized by microbes is released as CO_2 , the rest is used by the microorganisms themselves, such as in the formation of cell walls (Miltner and Bombach, 2012). While the carbon held within living microbial biomass is generally less than four percent of the total carbon in the soil (Sparling, 1992), the rapid growth, generation, and death of the microbiota results in the formation of microbial necromass (Miltner and Bombach, 2012). This necromass, and by extension, the initial photosynthates that allowed for its genesis, is now thought to be the source of the majority of the stable carbon within the soil (Liang and Blaser, 2011; Bradford et al., 2013). The transformation into necromass enables organic carbon to be occluded to mineral surfaces and form soil aggregates (Miltner and Bombach, 2012). Contrary to initial assumptions, carbon use efficiency of the initially deemed recalcitrant photosynthates is often inefficiently utilized by most soil microbiota (Miltner and Bombach, 2012; Bradford et al., 2013; Cotrufo et al., 2013), resulting in a greater portion of this being lost as CO₂ and not utilized within living biomass.

1.4 Soil organic carbon fluctuations: hard come, easy go

Massive losses in SOC can occur in relatively short periods through erosion of SOC-rich topsoil (Doetteral et al., 2016) or subsurface fires in peat-based soils (Santín et al., 2016).

In the first case, eroded soil is usually the SOC-rich topsoil and fine soil particles (Larney et al., 1998), with the highest SOC concentration within the soil column. In many cases, much of this SOC is laterally transported from the site and not mineralized (Doetterl et al., 2016), resulting in a local net SOC loss but more minor losses on the landscape level. Subsurface fires, while capable of significant reductions in SOC, are uncommon, and the scale of this impact is often minimal except for peat-based soils (Santín et al., 2016).

By comparison, gains in SOC stocks take much longer to accumulate and are generally not expected to be observable in less than half a decade (Lal, 2009), except in cases where erosion transports and deposits new soil and its carbon over existing soils (Chaopricha and Marín-Spiotta, 2014; Doetterl et al., 2016).

In addition, the rates of SOC sequestration decrease with time as more carbon is bound to the mineral fraction (Singh et al., 2018), eventually reaching a steady-state equilibrium of inputs and mineralization (Baldock and Nelson, 2000). One notable exception to this is for soils of peatlands and wetlands. As the SOC in peatlands and wetlands is restricted from microbial degradation by limited oxygen availability, as long as these conditions persist, SOC may increase indefinitely (Baldock and Nelson, 2000).

2. Measurements of Soil Organic Carbon

Soil metrics are generally measured through conventional laboratory analysis or in-field proximal soil sensing (PSS). Laboratory analysis is usually considered more accurate. However, it can prove more cost, labor, and time-intensive, especially at large scales (Rossel et al., 2015). Estimates of SOC with PSS often require data to be calibrated with relevant sampling materials and preprocessed before giving actual SOC estimates (Stenberg et al., 2010). These can further be confounded by factors such as soil moisture and vegetation. While these methods are improving, due to the need for fine-scale accuracy, many scientific studies use laboratory measurements over PSS to quantify SOC content and calculate soil organic carbon densities or stocks.

2.1 Collection of samples

Studies of land-use impact on SOC always face difficulties balancing precision and expenses (Conant et al., 2011a). Many studies have used a sampling depth of 30 cm from the top of the mineral soil, and the Intergovernmental Panel on Climate Change (IPCC) recommended this as the minimum sampling depth (Smith et al., 2019). However, this may not be sufficient to accurately quantify and estimate SOC fluctuations if significant changes occur below this depth, especially as most woody vegetation (Jobbágy and Jackson, 2000) and some crops have rooting depths that far exceed this (Chimento et al., 2016; Martani et al., 2021). As such, the Food and Agriculture Organization of the United Nations (FAO) recommends a sampling depth of 1 meter (Poeplau, 2019), though the expenses and machinery required to do so may prove prohibitive for many soil studies (Smith et al., 2019).

2.2 Accounting for soil inorganic carbon (SIC)

In most non-calcareous soils, the total soil carbon equals the SOC (Tabatabai, 1996). Where SIC is present, the gravimetric fraction of SIC is often determined and then subtracted from the total carbon in the soil. In such cases, samples are usually pretreated with acid, generally hydrochloric acid, to remove mineral carbonates with pre and posttreatment weights used to determine SIC content. This is often not seen as practical for large samples or where SIC is negligible (Sherrod et al., 2002). Additionally, acid pretreatment can react with the sample's organic carbon (Roberts et al., 1973; Wang et al., 2012), necessitating limiting acid strength and acid pre-treatment duration to mitigate the loss of soluble SOC (Roberts et al., 1973).

The pressure–calcimeter method has also been used as an alternative method of estimating SIC (Sherrod et al., 2002; Wang et al., 2012). This method uses FeCl₂ to limit reactions with SOC while still reacting with the SIC, and the gravimetric change is used to determine SIC. While its results are seen as more accurate, it requires more time and equipment than traditional gravimetric acid treatments. SIC is generally negligible in acidic and well drained soils and is usually not considered in assessing the land-use impact on SOC.

2.3 Loss on ignition

One of the most common methods for measuring SOC is loss on ignition (LOI) (Frogbrook and Oliver, 2001; Sullivan et al., 2019). In this method, a field-collected sample of soil that has been dried at 105°C to remove water (Ball, 1964) is weighed, and is then heated, generally between 450-550°C for 2.5 to 4 hours (Sun et al., 2009), though temperature ranges from between 375°C to 1025°C have been used in the past (Donkin, 1991). When the sample is heated at these higher temperatures, the carbon within the organic material combusts into CO₂ and is lost to the atmosphere. The resulting weight reduction before and after heating the sample is assumed to be equal to the weight of the carbon in the sample. This method has received criticism as it is known to overestimate SOC because of its assumptions, and values can vary more than other methods upon repeated testing (Gavlak et al., 2005; Sullivan et al., 2019). As stated previously, if SIC is present, this will also be transformed into CO₂ (Ball, 1964; Sherrod et al., 2002), resulting in a SOC overestimation. In addition, some soils have clay mineral structures that contain structural water. This is retained within the soil during regular drying but often is released during LOI tests, with higher clay contents resulting in greater potential inaccuracy (Ball 1964; Sun et al., 2009). Most structural water loss occurs between temperatures of 450°C and 600°C; combustion below this should minimize structural water loss (Ball, 1964) but may also result in incomplete combustion of SOC (Gallardo Lancho et al., 1987; Donkin 1991). Correction factors can be applied for LOI estimates in clay soils to help account for structural water loss, and they vary based on the type and proportions of clays present in the sample (Sun et al., 2009). Despite these limitations, LOI is often favored due to the relatively inexpensive cost and the ability to run large sample numbers simultaneously (Sullivan et al., 2019).

2.4 Wet oxidation

Wet oxidation via chromic acid, also known as the Walkley-Black method (Walkley and Black, 1934; Sullivan et al., 2019; FAO, 2020), is another method that is often implemented to determine SOC and is considered more accurate than LOI (Wang et al., 2012; Sullivan et al., 2019). A soil sample is treated with 0.167 M potassium dichromate in sulfuric acid to oxidize the carbon within the sample, converting this carbon into CO₂ (FAO, 2020). The amount of carbon can be calculated by changes in pre and posttreatment gravimetric weight, with the mass loss assumed to be organic carbon. Alternatively, colorimetric methods can be used to measure the amount of chromic ion (CR^{+3}) formed, with the chemical reaction resulting in the production of four chromic ions for every one molecule of carbon dioxide produced (FAO, 2020).

A limitation of the wet oxidation method is that the standard amount of reagent used may not fully oxidize the organic carbon in SOC-rich soils, resulting in underestimations. In addition, iron and chloride ions present in the soil may also undergo reactions that result in overestimating SOC, while the presence of manganese oxides may underestimate SOC (FAO, 2020). Still, this method generally generates more reproducible results than LOI (Gavlak et al., 2005).

2.5 Dry combustion

Dry combustion, also known as element analysis (Wang et al., 2012), uses a similar methodology to LOI, with the soil sample being heated to cause the sample's carbon to be combusted to form CO_2 . However, here higher temperatures are used, at least 1000°C. In addition, while LOI utilizes before and after gravimetric data to determine the carbon content of the sample, dry combustion measures the amount of CO_2 produced via infrared or conductivity detectors during combustion (Sullivan et al., 2019). This method can also detect other elements if desired due to differences in infrared or conductivity associated with different elements. This has the same limitations with SIC as previous methods with similar methods for correction. While the amount of detection is limited by the equipment, it is generally able to give results with better accuracies than other methods

and greater reproducibility (Gavlak et al., 2005), and corrections are not needed for structural water loss.

2.6 Estimating change at the filed scale through direct measurement or carbon accounting means

The most frequently employed method of detecting changes in SOC is measuring stock inventories through direct sampling. Soil samples are collected through time in Before-After (BA) studies or on sites with different land uses, Control-Impact (CI) studies, with one or several sites designated as a control. Samples are collected from these sites, analyzed via the preferred laboratory analysis method, and compared. While both designs have strengths, independently, they both make assumptions that can lead to inaccuracies (Christie et al., 2019). A combination Before-After-Control-Impact (BACI) study design can help to refine. The BACI study design helps to isolate changes from inherit variability by using both before and after data and using control to compare to noncontrols, enabling better determination of the cause of change. While more intensive and not without its criticisms (Smokowski and Randall, 2017), this methodology helps to balance the issues BA and CI studies have when done alone.

Except in cases of rapid SOC losses following disturbance, BA, CI, and BACI studies require a relatively long time between changes in management and measurements, as detectable changes in SOC are generally expected to take several years to a decade to occur (Alberti et al., 2009; Lal, 2009; Nave et al., 2013). However, more rapid estimations of SOC changes can be made indirectly through carbon budgeting means.

Net ecosystem carbon balance (NECB), also known as net ecosystem exchange (NEE), indirectly accounts for the changes in soil carbon by creating a carbon budget. Net primary productivity (NPP) equates to increments in biomass per unit of land surface and time. On an annual scale, the change in SOC and litter is assumed to equal the difference between NEE and NPP. If the change in living biomass (both aboveground and belowground) and litter is calculated, then the change in SOC can be calculated, and the rate of SOC change can be estimated by dividing SOC change by the time. Measurements of the flux of CO₂ can be done on a large scale with the eddy covariance technique (EC) via eddy flux towers with a footprint ranging from hundred meters to several kilometers (Alberti et al., 2009) or on a much smaller scale of a few meters or less with the chamber method (Hoffman et al., 2017). A range of methods can quantify changes in aboveground living biomass and litter. However, the change in belowground living biomass remains a technical challenge.

NECB methods have several limitations. Time and expense associated with the equipment used for measuring carbon in the field can be significant (Conant et al., 2011a). In addition, many locations may have topography poorly suited for eddy flux towers to measure land use change adequately. Estimating biomass production can also be an issue, necessitating either the collection of biomass samples (Skinner and Dell, 2015) or using other means to determine the change in living plant tissues, particularly belowground biomass.

These methods have strengths and weaknesses. While costs and manpower may dictate what methods can be utilized, they can be used in tandem (Leifeld et al., 2011; Skinner

and Dell, 2015). In these situations, they can provide datasets that cover more in time, detail, and scope than either direct or account measurements can in isolation.

2.7 Detecting changes: balancing time and sampling density

Minimum detectable difference (MDD), as defined by Garten and Wullschleger (1999): "is the smallest detectable difference between treatment means once the variation, significance level, statistical power, and sample size are specified." Balancing these components is often a challenge between budget, human effort, and natural variability.

Except in cases of extreme disturbances and rapid C loss, changes in SOC are relatively minor compared to the total organic carbon in the soil (Conant and Paustain, 2002; Batjes and Wesemael, 2014). A temperate grassland containing 30–80 Mg C ha⁻¹ of soil carbon may sequester carbon at an average annual rate of 0.46 Mg C ha⁻¹ (Conant et al., 2001; Conant and Paustain, 2002), with this rate decreasing as more carbon becomes sequestered and the soil reaches C saturation (Stewart et al., 2007). As such, to maintain the certainty of results, a balance between different schools of thought can be utilized to detect changes. Given that rates of change are relatively slow, when using direct sampling techniques, enough time is needed to pass between initial sampling and follow-up sampling to result in a measurable difference.

The timeframe of how soon changes can be observed depends on the magnitude of change. However, even under ideal conditions with a relatively high rate of SOC increase and low noise, the comparatively small change compared to the total SOC stock may require dozens of samples (Conant and Paustain, 2002; Conant et al., 2011a) to detect changes in less than a decade. The costs associated with analyzing these samples can be

prohibitively expensive for many researchers (Strickland et al., 2010). Such minor changes are more easily observed following more time, often several years, which may allow for effects of gradual SOC changes to accumulate.

Nave et al. (2013) suggested that 15 and 30 years were needed to detect meaningful changes in SOC following afforestation. While the establishment of high productivity perennial biofuel crops has shown some comparatively rapid results (Anderson-Teixeira et al., 2009; Guzman and Lal, 2014; Chimento et al., 2016), it should be taken with the caveat that many of these studies are on previously cultivated degraded sites and are often being compared to areas that are still undergoing traditional cultivation.

Differences in SOC across sites of the same treatment at the same layer, even under traditionally tilled conditions, can be notable (Robertson et al., 1997). Intrasite variability can sometimes be accounted for due to differences in bulk density (Davidson and Ackerman, 1993) and the landscape slope position (Zilverberg et al., 2016), though this may not account for specific unknowns of land history.

3. Environmental Impact on the Formation and Storage of Soil Organic Carbon Environmental conditions, especially temperature and water availability, greatly impact ANPP in ecosystems, which control SOC inputs. Conditions associated with high levels of ANPP, such as higher temperatures and readily available water, are also associated with larger amounts of biomass production that can enter the soil (Gough, 2012). However, conditions that favor high ANPP are often better for microbial decomposition of these products in the soil (Conant et al., 2011b).

3.1 Higher productivity in warmer temperatures but more rapid degradation

NPP generally increases with the average annual temperature (Gough, 2012). This can be seen by the general distribution of ecosystems along latitudinal gradients and their productivity. Tundra is the least productive vegetation-dominated ecosystem. NPP increases as this transitions to boreal forests and peaks with tropical rainforests in equatorial regions (De Deyn et al., 2008). This oversimplification ignores the increasing importance of available water once mean annual temperatures are less limiting. Generally, lower latitudes have greater NPP than higher ones due to increased temperatures and regular sunlight availability.

The biological activities of soil microbes are limited by temperature in patterns similar to those that plants experience (Bradford et al., 2016). As microbial activities and thus C mineralization share the same trend as NPP in relation to temperature, cold environments have low NPP but also low SOC turnover. In contrast, warm environments that are not water-limited generally have high NPP but rapid SOC turnover (De Deyn et al., 2008). Regarding carbon storage, lower latitudes are estimated to have similar C stocks in the soil as the living biomass, with the relative proportion of SOC to vegetation C increasing with increasing latitudes (Watson et al., 2000; Saugier et al., 2001). This latitudinal pattern ratio is highest in northern permafrost, which is estimated to contain 50% of global belowground SOC (1,672 Pg)(Tarnocai et al., 2009).

Previous schools of thought have held that temperature increases resulted in increased microbial activities and SOC mineralization (Baldock and Nelson, 2000; Amundson et al., 2015) which could outpace NPP, resulting in a net loss of C from the soil (Czimczik

et al.,2005; Balogh et al.,2005). This has led to concerns about a potential positive carbon-warming feedback loop in the soil (Davidson and Janssens., 2006).

However, newer studies have challenged the paradigm that temperature increases alone would significantly reduce SOC stocks in all ecosystems (Bradford et al., 2016 and sources therein). While there is a generally positive correlation with increased temperature, mean changes in SOC may not be significant, potentially being offset with increased NPP inputs (Lu et al., 2013).

There are large SOC stocks within wetlands and permafrost (Batjes, 1996) due to environmental limitations on microbial decomposition of dead biomass (Schmidt et al., 2011). Most of the SOC in these ecosystems can be readily utilized by microbial activity if conditions change (Schmidt et al., 2011). Because of the large amount of SOC stored in the permafrost in this temperature-stable state even a minor increase in the rate of C mineralization could potentially release large amounts of CO₂ and significantly decrease global SOC (Bradford et al., 2016).

3.2 Water increases productivity and soil carbon

While vegetation type is tied more closely with SOC than precipitation (Jobbágy and Jackson, 2000), the vegetation type is often dictated by precipitation (Woodward et al., 2004), indirectly tying the two together. Arid and semi-arid ecosystems are water-limited, restricting NPP (Lal, 2001). As mean annual precipitation (MAP) increases, plants are less water-limited, and NPP increases (Gough, 2012).

While aboveground NPP is often more sensitive to the timing of precipitation than to actual precipitation totals (Robinson et al., 2013), the timing of precipitation may not be as critical in ecosystems that are less limited by water stress compared to the length of the growing season or available nutrients (Knapp and Smith, 2001). Plant functional groups, and dynamics between them, can also play roles in how soil moisture impacts NPP. Woody vegetation generally has deeper rooting depths than grasses (Jobbágy and Jackson, 2000) which can be used to access water throughout more of the soil column (Ogle and Reynolds, 2004).

 C_3 plants have the CO₂ fixing enzyme Rubisco work within the mesophyll cells directly with atmospheric air via their stomata. However, Rubisco binds to both CO₂ and O₂ resulting in lower photosynthetic efficiencies (due to increased photorespiration) when the atmospheric CO₂/O₂ ratio decreases or under high temperatures where Rubisco increasingly binds to O₂ (Ehleringer and Cerling 2002). During this process, the stomata release water from the plant's cells. When photorespiration increases, this results in higher water usage to produce the same amount of photosynthetic product and thus lower water use efficiency (WUE) (Lavergne et al., 2019).

 C_4 plants have an additional step where CO_2 binds to phosphoenolpyruvate (PEP) carboxylase within mesophyll cells. PEP is then moved to interior bundle sheath cells, decarboxylated, and the C_3 pathway proceeds, but at a more consistent efficiency than that in C_3 plants due to higher CO_2 concentrations within the bundle sheath cells compared to the atmosphere. However, an additional energy cost means that the C_4 pathway is less advantageous in cooler or high CO_2 conditions (Ehleringer and Cerling, 2002). As atmospheric CO₂ concentrations are globally relatively homogenous, the temperature is the primary agent determining the NPP of C₃ and C₄ in a given environment (Paruelo and Lauenroth, 1996), with temperatures of 22°C and above being more favorable to C₄ plants under current CO₂ levels (Ehleringer et al., 1997). Greater photosynthetic efficiency of C₄ plants at higher temperatures also results in them having greater WUE, which makes them even more competitive in water-limited ecosystems, especially where the vapor pressure deficit increases the rate of water loss from the plant (Ochsner, 2019). Due to the lower WUE of C₃ plants, in ecosystems where C₃ and C₄ grasses coexist, C₃ grasses preferentially uptake water from deeper in the soil column compared to C₄ grasses (Nippert and Knapp, 2007).

Greater water in the soil also reduces the ability of oxygen to move through the soil, to the point that soils in some lentic (standing water) systems are functionally devoid of dissolved oxygen. While many riparian and aquatic plants have adaptations that enable them to thrive in these conditions, aerobic decomposition is unable to proceed without oxygen (De Deyn et al., 2008). This limits decomposition to anaerobic pathways, which are slower and less efficient at C mineralization (Davidson et al., 2006). If soil is constantly saturated with water over several years, it can result in large quantities of biomass accumulating with little decomposition (Baldock and Nelson, 2000).

Conversely, low water availability in the soil due to drought may result in rangelands becoming net carbon sources due to water limitation disproportionately impacting photosynthesis compared to total respiration (Balogh et al., 2005). Despite the general trend of increased C mineralization rates under higher soil moisture (until saturation), SOC generally increases with precipitation (Derner et al., 2006). While dry environments may have less total SOC, the residence time is often greater than in wetter environments (Lal, 2000). As precipitation and thus soil moisture increase, there is generally an increase in microbial activity and SOC mineralization (Bradford et al., 2016).

3.3 Finer texture and complex structure associated with increased soil carbon

Fine-textured soils store and retain SOC better than coarse-textured soils (Johnston et al., 2009), and the potential for increases in SOC is positively correlated with clay content (Guo and Gifford, 2002). The adsorption of the SOM to the surfaces of the fine soil particles (Singh et al., 2018) is essential in the formation of soil aggregates (Gulde et al., 2008) which protects SOC from microbial degradation (Six et al., 1998; Gulde et al., 2008). Organic carbon often forms the nucleus of these soil aggregates (Bronick and Lal, 2005). The aggregates and the physical properties of the clay particles themselves hinder microbial movement and SOC degradation (Hassink, 1992), reducing SOC mineralization (Oades, 1984). While the initial agents that bind the soil aggregates together can be ephemeral, they can still retain SOC for decades to centuries (Skjemstad et al., 1990).

Sand does not readily form aggregates and has larger pore spaces than finer soils, allowing them greater access to oxygen (Ochsner, 2019) and enabling them to be more biologically active (Jarvis, 2017), resulting in greater SOC mineralization (Chivenge et al., 2007) and reduced mean residence time (MRT) (Oades, 1984). Microbes in sandier soils have been shown to have lower carbon use efficiency in converting photosynthates to microbial biomass (Angst et al., 2021). These factors result in lower SOC stocks in coarse soils relative to finer ones (Jobbágy and Jackson, 2000; Han et al., 2016).

3.4 Soil carbon generally decreases with depth

Plant functional group composition, NPP, and its allocation largely govern SOC distribution in the soil profile (Jobbágy and Jackson, 2000), though deposition of new sediments over existing soil profiles has been proposed as an overlooked aspect in SOC at depth (Chaopricha and Spiotta, 2014). As soil depth increases, SOC generally decreases due to the reduced root density and reduced ability of surface inputs to penetrate the ground (Schmidt et al., 2011). Across soil types, approximately 40-70% of the SOC in the first meter of soil is found within the upper 30 cm (Batjes, 1996).

Increased precipitation is associated with a greater proportion of SOC in the upper 20 cm (Wang et al., 2010). However, Jobbágy and Jackson (2000) found that vegetation cover type, while often determined by precipitation (Woodward et al., 2004), was more relevant in SOC depth distribution than precipitation. In another study, Jackson et al. (1996) found that shrubs generally had the deepest average rooting depth, followed by trees, then grasses with the shallowest. Jobbágy and Jackson (2000) showed that forests had 50% of their SOC of the first meter above 20 cm, and 56% of their SOC of the first three meters was within the first meter of depth. By contrast, grasslands had a relatively deeper distribution of SOC (42% of the first meter SOC was above 20 cm; 43% of the first meter set soce above 20 cm; 77% of the first three meters within the first meter).

While shrubs have both the deepest rooting depth and deeper relative distribution of SOC, the order of this relationship between trees and grasses is flipped. Jobbágy and Jackson (2000) found that despite grasses having a rooting depth that is on average shallower than trees, more than half of the SOC of the top three meters was in the lower two-thirds under grasses. SOC under trees showed more than half of their stock was in the upper third of the top three meters. The authors attributed this to the greater aboveground biomass and productivity that trees have relative to grasses, and the greater litter production and input are responsible for the apparent discrepancy.

Deeper SOC stocks generally have a longer MRT than SOC in the upper soil (Jobbágy and Jackson, 2000). It was previously thought that this was due to the reduced ability of soil microorganisms to degrade organic material deeper in the soil. More recent work has highlighted that particulate SOM deep in the soil is degraded relatively quickly. If transformed to microbial necromass and occluded to clay particles, the carbon within this SOM will have a MRT extending centuries, much longer than that near the surface (Fontaine et al., 2007).

Several studies indicate small changes in deep SOC stocks following land-use change (Guo and Gifford, 2002). However, it should be noted that many studies do not sample the soil below 1 m in depth, leading some to be skeptical of this long-held belief (Lorenz & Lal, 2005). Some studies have shown that, while the change is less significant than near the surface, it may be non-negligible and should be considered more frequently (Pellegrini et al., 2018).

4. Soil Mechanical Disturbances Generally Reduce Soil Carbon and Land-use Impacts Vary

Mechanical disturbances such as tillage expose SOC to microbial decomposition and erosion, resulting in reductions in SOC (Davidson and Ackerman, 1993; Smith, 2008). In addition, significant amounts of SOC can be lost from sites following vegetative cover removal for development or tillage due to erosive forces (Montgomery, 2007). This disproportionally removes organic material due to its greater bouncy in water than the mineral soil and its higher density within the surface of the soil column (Polyakov and Lal, 2004). While this may result in transport elsewhere within the watershed and not atmospheric release (Doetterl et al., 2016), this still results in reductions of SOC at the local scale.

The impacts of aboveground disturbances that do not physically disturb the mineral soil, such as surface fires, grazing, or removal of aboveground biomass for human use, can vary depending on the intensity of the disturbance, the vegetation type, and soil properties. However, fire and grazing are natural parts of the environment, and their impacts are more complicated when they are not extremely intense. Indeed, similarities between fire and grazing have been drawn to view fire as a 'global herbivore' (Bond and Keeley, 2005). Like grazing, its presence on the landscape can change plant species composition (Barger et al., 2011), which can drive changes in SOC stocks.

4.1 Fire may transform some carbon into stable forms, but appears to be a net carbon source

Fire results in the immediate volatilization of aboveground vegetation and litter (Neary et al., 1999), releasing carbon sequestered in aboveground biomass, potentially for centuries

depending on the lifespan of the vegetation and its dead biomass (Levine et al., 1995). The direct impacts of surface fire on SOC are often limited to the upper few centimeters (Hartford and Frandsen, 1992). The most obvious effect is the loss via combustion of surface litter, reducing soil carbon (Neary et al., 1999), or an increase in SOC due to previously living biomass falling to the ground (González-Pérez et al., 2004). Heat transfer from the burning of aboveground biomass to the mineral soil may also occur (DeBano et al., 1998), modifying the properties of the SOC.

Following a fire, the integration of carbon that was not completely combusted, pyrogenic carbon (PyC) can result in an increase in SOC. In addition, following a fire, sites often experience increased NPP due to a reduction in standing biomass that can shade out new plant growth (Knapp and Seastedt, 1986), as well as a release of the nutrients in this standing biomass into the soil (González-Pérez et al., 2004). This increased productivity extends to both the above and belowground components (Johnson and Matchet, 2001), with the potential to increase SOC (Pellegrini et al., 2020).

However, this nutrient release and belowground growth also coincide with increased soil respiration (Rashid, 1987; Fernández et al., 1997). This is likely attributable to a combination of the degradation of liable PyC (Bird et al., 2015), increased autotrophic respiration by new root growth (Johnson and Matchett, 2001), increased soil microbe densities (Grasso and Ripabelli, 1996), and subsequently increased mineralization of non-pyrolyzed carbon due to other nutrients no longer being limiting agents (González-Pérez et al., 2004), increased soil temperatures following removal of sunlight interception from

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the previous canopy (Knapp and Seastedt, 1986), and reduced precipitation interception resulting in greater water availability (Gilliam et al., 1987).

The intensity and duration of fire play a significant role in the fire's impact, which are, in turn, influenced by the soil moisture and the type of vegetative material being burned (Hartford and Frandsen, 1992; González-Pérez et al., 2004). Loss of SOC begins between 100 °C and 200 °C (Giovannini and Lucchesi, 1997). A faster fire front reduces the time the soil is exposed to high temperatures, and this heat transmission is limited by depth. Soil temperatures can remain below 100 °C even when surface fire temperatures go over 500 °C (Hartford and Frandsen, 1992), and the increase in soil temperature fades quickly (Humphreys and Craig, 1981) as the soil itself acts as an insulator (DeBano et al., 1998). Smoldering ground fires, where fires burn slowly and close to the mineral surface, have a larger impact on ecosystems and SOC. While these fires have a much lower maximum temperature (Neary et al., 1999), they attain this much closer to the mineral surface and, due to the slow rate of spread, can maintain this temperature for several hours (Hartford and Frandsen, 1992).

Soil nutrients, especially N, start to volatilize between 200 °C and 400 °C (Neary et al., 1999). Intense fires may have a sterilization effect which, combined with nutrient loss (Johnson and Matchett, 2001), can slow or stop autotrophic and heterotrophic biological activities (González-Pérez et al., 2004). Lacking new vegetative cover, and with the old cover lost, the soil may form soil surface crusts that prevent water infiltration and reduce new growth (Stoof et al., 2011) or cause soil erosion (González-Pérez et al., 2004), resulting in losses of carbon from the site.

Combustion of plant material to CO₂ is usually incomplete (Barger et al., 2011); some of it is chemically transformed into pyrogenic carbon (PyC) (Bird et al., 2015). Charcoal holds a large amount of the PyC after fires (residual PyC), though smaller amounts exist in smoke and aromatic molecules (atmospheric PyC) (Jones et al., 2019). Global annual residual PyC production is estimated to be 56-123 Tg (Bird et al., 2015).

Most PyC is more biologically resistant than before being burned (Almendros et al., 1988; Schmidt et al., 2011), though it still experiences degradation over time (Bird et al., 1999). The MRT of PyC is determined primarily by the temperature of the fire that pyrolyzed the carbon. Bird et al. (2015) proposed a model of three PyC MRT pools: a short-lived liable pool without aromatic rings and a half-life less than a year; a semiliable pool with aromatic rings with a half-life stretching from years to centuries; and a stable pool with aromatic rings with a half-life extending from centuries to millennia. Under the model proposed by Bird et al. (2015), fires below 400 °C will result in predominantly semi-liable PyC, while fires above 600 °C will have largely stable PyC. However, the authors point out that environmental conditions ultimately dictate the fate of PyC. Warm and wet conditions can reduce PyC MRT to less than a century (Bird et al., 1999), whereas stable low oxygen conditions can retain PyC for thousands of years (Masiello and Druffel, 1998).

More significant amounts of PyC are produced in forest fires than in grassland fires (Stocks and Kauffman, 1997) because woody biomass can generate more PyC per unit of unburnt C than other common biomass fuels (Jones et al., 2019) due to its high volume to surface area ratio preventing complete combustion due to oxygen limitation during burning (Santín et al., 2015). Wood-derived PyC also has a longer MRT and is more recalcitrant than PyC from other sources (Hilscher et al., 2009). This partly explains why grassland fires resulted in more significant SOC losses than temperate and boreal conifer forests in the Pellegrini et al. (2018) model.

Estimates of PyC in the soil vary significantly (Bird et al., 2015); 1-6% (González-Pérez et al., 2004), 1-35% (Forbes et al., 2006), 5-15% (Hockaday et al., 2007), 14% (Reisser et al., 2016) and ranges between (>1-60%) for other estimates (Preston and Schmidt, 2006). Its rate of production is contentious as well. Santín et al. (2016) suggested that the production of PyC was around 116-385 Tg C yr⁻¹, comprising around 0.2-0.6% of global terrestrial NPP. This estimate was refined in Jones et al. (2019), calculating a slightly narrower annual PyC generation range of 196-340 Tg C yr⁻¹, though a wider estimate of 188-424 Tg C yr⁻¹ was given by Bowring et al. (2022).

Fire also increases the presence of hydrophobic compounds on the surface of the soil and potentially increases the instability of soil aggregates (Lal, 2001; Shakesby and Doerr, 2006). This, in addition to the loss of surface vegetation and litter that protects the mineral soil and assists in infiltration (Baldock and Nelson, 2000) and similar functions lost as a result of fire degradation of soil aggregate stability (Neary et al., 1999) can result in the formation of soil surface crusts which prevent infiltration (Stoof et al., 2011) or result in soil erosion (González-Pérez et al., 2004) which can reduce later NPP. PyC on the soil's surface is frequently subject to these erosive forces, with oceans estimated to accumulate 8-27% of total pyrolyzed carbon annually (Santín et al., 2016). While this

PyC can sequester C for several millennia (Masiello and Druffel, 1998), this is a loss of potential SOC from the initial site where in situ production occurred.

Despite the ability of fire to transform carbon into forms resistant to degradation and the increased productivity following standing biomass removal (Knapp and Seastedt, 1986), fire is generally negatively related to SOC. Pellgrini et al. (2018) showed that burned sites had over a third less SOC than those protected from fire in a global analysis. This study also separately modeled changes in NPP following nitrogen losses due to fire, estimating that post-fire NPP reductions were 20% greater than the carbon released by burning, with the greatest impacts in broadleaf forests and grasslands. This goes against other shorter-scale analyses, which had suggested that the net effect of non-land use change burning was near zero due to increased NPP following fire (Shakesby and Matthews, 2016) and the buffering of C losses by PyC (Jones et al., 2019). Other subsequent reviews have supported this conclusion (Li et al., 2021, Wu et al., 2022; Zhou et al., 2022).

In contrast, a separate study by Pellegrini et al. (2020) examined how fire frequency related to SOC in oak savannas. Increased fire frequency led to decreases in root biomass. However, the relationship was different with SOC. Intermediate fire return intervals (~0.30 fires/yr) resulted in higher SOC totals than unburned sites containing greater SOC stocks than sites with frequent fire return intervals (~0.75 fires/yr).

The science behind fire and SOC is still being developed. As Pellegrini et al. (2020) highlight, fire interval may significantly affect the direction of changes. The fate of SOC, particularly that which has been partially pyrolyzed, is also an area of future interest

(Pellegrini et al., 2021). Despite acknowledging that reduced fire has led to greater SOC sequestration, Zhou et al. (2022) noted that the ecological costs associated with a lack of fire must be balanced against these relatively modest gains. In addition, Li et al. (2021) noted that SOC might have the potential to recover to pre-burn levels if given enough time, with a greater proportion of SOC being more degradation-resistant PyC.

4.2 Grazing: complex relationships dependent on multiple factors

Fire and grazing have some similar impacts on ecosystems, to the point some have deliberately drawn parallels between them (Bond and Keely, 2005). Grazing and fire both remove standing biomass, which can stimulate NPP (Knapp and Seastedt, 1986). However, unlike fire which is generally a temporarily limited event that can volatilize nutrients in standing biomass, the grazing is a continuous pressure, and many of the nutrients in the removed biomass are returned to the soil in a plant-accessible form (Johnson and Matchett, 2001). As with fire, grazing can lead to changes in the vegetational composition, which in turn has the potential to drive SOC changes (Derner and Schuman 2007).

The net impact of grazing on SOC stocks is variable and often depends on local conditions, management, and livestock species composition (McSherry and Ritchie, 2013). In some cases, high grazing intensity could lead to rangelands becoming net sources of CO_2 (Janzen, 2006; Powlson et al., 2011). Concerns about the net impact of grazing on SOC have led to suggestions that a reduction of grazers, including limiting grazing wildlife, may benefit SOC stocks (Tanentzap and Coomes, 2012).

Grazing accelerates nutrient cycling from plant biomass to the soil (Chapin et al., 1986). Herbivores preferentially consume vegetation that has not yet senesced and reabsorbed its nutrients (Chapin et al., 1986), and the process of digestion chemically and mechanically breaks down plant biomass (Schuman et al., 1999). The nutrients that were previously locked within biomass are then returned to the soil in readily accessible forms in urine or feces (Johnson and Matchett, 2001). Due to this rapid cycling of nutrients under grazing, plants can reduce their root growth and allocate more NPP to their shoots (Johnson and Matchett, 2001). However, grazing can lead to decreases in vegetative cover and increases in bulk density (Pluhar et al., 1987), reducing NPP.

McSherry and Ritchie (2013) found that high-intensity grazing increased SOC in C₄ and C₃-C₄ mixed grasslands and in grasslands where MAP is lower than 600 mm. This same study found that SOC decreased in more mesic and C₃-dominated grasslands. This is likely driven by the competitive advantage of C₄ plants over C₃ plants in hot and dry ecosystems as explained in the soil moisture and precipitation section.

In an analysis by Abdalla et al. (2018), the authors attempted to standardize grazing intensity and associated SOC data. Grazing as a whole was associated with reduced SOC but varied based on climate. All grazing intensities increased SOC under moist (MAP >500mm) and warm (tropic and subtropic) conditions and reduced them under moist, cool conditions. Under dry, warm and dry, cool conditions, only lower grazing intensities resulted in increases in SOC. Grazing intensities can impact the relative abundance of C_3 and C_4 plants on rangelands, which is likely a significant contributing factor for changes in SOC with livestock stocking rates, with grazing often appearing to favor C_4 grasses in cases where SOC increased following grazing (Frank et al., 1995; Derner et al., 2006; Derner and Schuman, 2007; McSherry and Ritchie 2013). In addition, many of these same studies found that high grazing intensity increased SOC in C₄-dominated systems but reduced them in C₃-dominated grasslands.

Adding legumes and fertilizers is often associated with increased SOC (Conant et al., 2017). However, these practices are not typical nor economically feasible for many management plans.

4.3 Traditional cultivation results in losses, newer methodologies may cause reversals Agricultural sites subjected to heavy and repeated cultivation are associated with low SOC, which reduces their productivity (Amundson et al., 2015). Soil disruption can increase microbial activity and mineralization of long sequestered carbon (Guo and Gifford., 2002). SOC losses as a result of conventional agriculture can be up to 50% (Stockmann et al., 2013).

Conservation agriculture (CA) aims to sustain cropping systems production by maintaining SOC and minimizing the use of chemical fertilizers. The main principles behind CA include retention of plant materials on the soil, cover cropping, and integrated nutrient management, which reduces the reliance on chemical fertilizers with natural ones and eliminates soil disturbances (Lal, 2015a,b,c). If properly implemented, this reduces the carbon loss from mechanical preparation (Lal, 2004) and the nutrient loss from soil erosion. Retention of plant residues and cover cropping is done to protect the soil's surface. Due to interrelated factors, soil aggregate stability is generally lower when the ground has no cover than under vegetation or litter (López-Bermudez et al., 1996). Soil with less cover has less resistance to wind and water erosion (Lal, 2000). Losses in soil aggregates lead to surface crust formation, followed by subsequent reduction in precipitation infiltration, soil available water, and ultimately plant biomass production (Lal, 2001).

Tillage is used as preparation for the seedbed for crops. All forms of mechanical till operations and seed placement result in direct emissions due to fuel consumption, which increases with plow depth and clay content (Lal, 2004). More relevant to soil carbon is that tillage breaks up soil aggregates and enables the breakdown of SOC into CO₂ where it would otherwise be protected. In a US-based meta-analysis, Nunes et al. (2020) found that most soil health indicators increased under no-till compared to tillage. Even under some tillage, benefits can be seen if the intensity is reduced. Reduced tillage has been shown to result in higher SOC (Chivenge et al., 2007), carbon use efficiency of the soil microbiota on SOC inputs, and a reduced priming effect compared to traditionally tilled fields (Sauvadet et al., 2018).

Some studies have found that under full inversion tillage (i.e., the topsoil is inverted to move the carbon-dense surface soil to the bottom of the plow layer), the amount of SOC at the bottom of this plow layer increased. However, in a meta-analysis of studies directly comparing no-till to full inversion tillage by Anger and Eriksen-Hamel (2008), the authors found that while SOC was often significantly greater under full inversion tillage

compared to no-till just below the average deepest plow depth, this did not offset the overall higher SOC stocks under no-till.

4.4 Biofuel production on cultivated soils may increase soil carbon, but results mixed The impact of haying and biomass removal, such as the use of land to produce biofuels, depends strongly on the initial SOC stock and management techniques. Agricultural sites subjected to heavy cultivation lose many of their original properties, which often reduces their productivity (Amundson et al., 2015), and soil disruption can increase microbial activity and mineralization of long sequestered carbon (Guo and Gifford., 2002). SOC losses as a result of conventional agriculture can be up to 50% (Stockmann et al., 2013). However, due to this lowered SOC state, the potential exists for previously degraded sites to take up new soil carbon (Lal, 2009; Amundson et al., 2015; Signh et al., 2018). One proposed strategy is to use these areas to grow perennial crops to produce biofuels (Anderson-Teixeira et al., 2009; Guzman and Lal, 2014; Chimento et al., 2016).

Currently, the vast majority of ethanol production is derived from corn (*Zeya mays* L.) grain. However, with land, fertilization, and water costs associated with corn production, there are interests in the production of biofuels from cellulosic (non-grain) sources, be it either from existing crop residues (Downing et al., 2011) or through the planting of perennial grasses (Guzman and Lal, 2014). Anderson-Teixeria et al. (2009) found that removing non-grain (residue) biomass from a corn field led to reductions in SOC, with every 1% increase in residue removed resulting in approximately 0.2% reduction in SOC. Their modeling suggested that this management would always have a net negative impact on SOC.

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While corn grain is currently the primary feedstock for biofuel production, interest has been raised in the utilization of designated perennial biofuel crops with relatively high productivity and low input requirements (Lewandowski et al., 2003; Chimento et al., 2016). Poplar (*Populus* spp.), black locust (*Robina pseudoacacia*), willow (*Salix* spp.), giant reed (*Arundo donax*), miscanthus (*Miscanthus* x gigantus), and switchgrass (*Panicum virgatum*) (Chimento et al., 2016; Martani et al., 2021) and others have all been considered as potential candidates due to both their high aboveground productivity for feedstock production and belowground productivity for potential SOC sequestration.

Switchgrass is of particular interest in the great plains of North America. It is native C₄ grass in the region and was used in range grass mixtures for livestock forage and erosion mitigation (Lewandowski et al., 2003; Parrish and Fike, 2005). The low nutrient requirements allow it to be grown on marginal land (Guzman and Lal, 2014) using little water (Schmidt et al., 2021). Adding N can result in increased productivity, and N can recycle back to belowground after senescence (Parrish and Fike, 2005). In addition, its deep roots enable it to reach soil N at depths inaccessible to most crops (Huang et al., 1996). Most of the plant's biomass is found within the roots and crown tissue (Frank et al., 2004), and per unit area has denser coarse roots (Garten and Wullschleger, 1999) and often greater aboveground NPP than native grass assemblages (Schmidt et al., 2021).

However, the promising productivity and root densities of switchgrass seem to have comparatively delayed responses to SOC. In a review paper, Anderson-Teixeria et al. (2009) projected net SOC gains under the management of switchgrass on previously cultivated sites. Other studies have had more tempered responses. Despite the deep rooting depth, Chimento et al. (2016) found that compared to adjacent arable land, SOC only increased in the top 10 centimeters, with reductions in SOC below this resulting in no overall statistical change in SOC, with similar results found by Martani et al. (2021). Indeed, the authors found that when compared to other perennial biofuel crops, switchgrass had a negative correlation between fine root stock and SOC content in the top 10 centimeters 11 years after switchgrass establishment. Martani et al. (2021) proposed that the high root production of switchgrass may have induced a priming effect on existing SOC stocks, whereby additions of new carbon that are relatively degradable enable microbial life to metabolize and mineralize older, more resistant forms of soil carbon (Hopkins et al., 2014)

Another concern related to biomass production is the removal of nutrients from the site, also known as nutrient mining (Jones et al., 2013). As plant material is removed from where it was grown, it takes with it the nutrients. If this loss is not balanced with inputs, gradually, these nutrient pools are depleted, resulting in lower NPP and SOC inputs.

The impact of this loss of soil nutrients is more pronounced in older and weathered soils (Jones et al., 2013) which often have lower initial nutrient stocks. While younger soils are more resistant to the effects of nutrient mining, they can become exhausted (Tiessen et al., 1983). While atmospheric sources can replace soil nitrogen, either naturally via microbial fixation or artificially using the Haber-Bosch process, this cannot be done with other nutrients (Amundson et al., 2015) and requires off-site inputs to offset. This loss of nutrients can lead to reductions in NPP (Chapin et al., 1986; Jones et al., 2013) and carbon inputs into the soil, as well as a reduction in litter quality (Vitousek, 1982). This

could result in reduced C turnover of this litter but may prevent the cycling of nutrients, further reducing NPP (Norris et al., 2001a,b).

4.5. Woody plant encroachment globally trends to increase soil organic carbon, but specifics vary

Encroachment of woody vegetation, or more specifically, afforestation of areas where woody vegetation was not historically the primary vegetation type, is a worldwide phenomenon. At both the global scale (Eldridge et al., 2011) and within North America (Barger et al., 2011), studies appear to support a general trend of SOC increasing following afforestation in most ecosystems. Woody vegetation often has much greater leaf surface area and thus frequently has greater potential NPP than many herbaceous systems they replace (Norris et al., 2001a,b; Hessler-White et al., 2008). In addition, the average rooting depth of woody vegetation is also greater than that of most herbaceous vegetation (Jackson et al., 1996). Despite this, Barger et al. (2011) found that changes in SOC following afforestation were often not tightly correlated with ANPP. Indeed, while ANPP following woody encroachment was positively correlated with MAP, SOC was negatively related to MAP when trees were encroaching, and a non-significant relationship with shrubs.

The diversity of different encroaching species' life traits, encroached habitats, and local scale factors limits the applicability of global generalizations in all instances (Archer et al., 2001; Ratajczak et al., 2012). In the United States, three genera are of particular concern within rangelands: *Prosopis, Juniperus*, and *Pinus* though other woody species are increasing or of more localized concern (Barger et al., 2011). *Prosopis* species are resprouting leguminous deciduous woody encroachers, whereas *Juniperus* and *Pinus*

species are evergreen with some species resprouting. Due to its ability to fix N_{2} , *Prosopis* can increase soil fertility, increasing NPP and SOC accumulation (Hibbard et al., 2001).

Studies of *Juniperus*, specifically *J. virginiana*, have generally shown that SOC increases following encroachment of native grasslands (Norris et al., 2001a; McKinely and Blair, 2008) or finding no statistical change (Smith and Johnson, 2003). However, these are on remnant prairie sites, and Smith and Johnson (2003) acknowledge that these systems may have already achieved soil carbon saturation. Notably, these sites also have relatively high MAP, which would predict that, based on the modeling by Jackson et al. (2002), woody encroachment would decrease SOC in these systems.

5. Research Need

While there seems to be a general trend in SOC following redcedar establishment in the Great Plains of North America, there are important caveats. Most rangelands in the United States are not in their native state and either experienced cultivation in the past or some form of heavy degradation, with remnant pockets largely being areas that were deemed unsuitable for the plow (Smith and Johnson, 2003). In addition, redcedar has been shown to have significant impacts on the hydrology of the landscape (Zou et al., 2014), which may have implications for NPP and SOC throughout the watershed.

The rate and capacity for rangeland carbon sequestration vary significantly among biomes, land use, and prior land-use history (Jobbágy and Jackson, 2000). In rangelands of the North American Great Plains, both the rate of sequestration and the capacity of soil to store organic carbon were reported to increase with annual precipitation (Jobbágy and Jackson, 2000; Schuman et al., 2002; Poeplau, 2011). The mesic grasslands at the central and eastern parts of the Great Plains have a large capacity to sequester atmospheric CO₂ into biomass due to their high net primary productivity (NPP). Many of these grasslands were once tilled and severely degraded and deprived of soil fertility, then converted to production for livestock forage or abandoned, occasionally called "go-back" lands (Owensby and Anderson, 1965). Based on USDA data (USDA Economic Research Service) about 5.2 million hectares of such lands existed in Kansas, Oklahoma, and Texas in 2012. While these sites lost much of their pre-agricultural soil organic carbon (SOC) due to cultivation (Davidson and Ackerman, 1993; Amundson et al., 2015; Lal, 2018). Given their current diminished SOC status, they have a high capacity to sequester future ANPP into stable humic substances and secondary carbonates, particularly when cultivation ceases (Gebhart et al., 1994; Conant et al., 2017; Lal et al., 2018).

Many of these "go-back" grasslands are managed as pasture (Bigelow and Borchers, 2017), while some of these lands with pronounced soil erosion are enrolled under Conservation Protection Program (CRP) and are excluded from direct agricultural usage. The CRP was initially implemented to move easily degraded lands out of agricultural production to reduce surplus and mitigate the adverse effects of cultivation on their soils, such as soil erosion (Heimlich and Kula, 1991; Dunn et al., 1993; Tanner and Fuhlendorf, 2018). Gebhart et al. (1994) estimated that CRP lands gained an average of 1.12 Mg C ha⁻¹ yr⁻¹, while Conant et al. (2017) estimated conversion from cultivation led to an average of 0.87 Mg C ha⁻¹ yr⁻¹. These "go-back" lands have the highest rate of woody encroachment in the world (Barger et al., 2011), primarily by an evergreen juniper species (*Juniperus virginiana* L., henceforth, redcedar). Redcedar is native, fire-intolerant woody species and was historically kept in check in grasslands under pre-European fire

regimes (Ansley and Rasmussen, 2005). However, due to changes in land management practices and fire exclusion, it has become a prolific encroaching species in the southern and northcentral Great Plains ranging from Texas to Nebraska. If unmanaged, redcedar can reach canopy closure within half a century, drastically reducing the presence and diversity of herbaceous species (Bragg and Hulbert, 1976; Briggs et al., 2002; Limb et al., 2010). However, redcedar woodlands often have aboveground net primary productivity (ANPP) significantly greater than the grasslands they usurp (Norris et al., 2001b; Schmidt et al., 2021) and can hold 10 to 20-fold greater C in aboveground biomass than grasslands (Norris et al., 2001a; Norris et al., 2001b). Indeed, afforestation of rangelands has been proposed as a strategy to sequester atmospheric carbon (Lal, 2018). Despite the apparent benefit of rapid carbon accrual into aboveground woody biomass and litter, the effect of high productivity on belowground soil carbon accrual is inconclusive, especially in "go-back" lands with annual precipitation exceeding 800 mm (Barger et al., 2011).

Scientific literature recommends the use of prescribed fire to curtail redcedar expansion to protect forage productivity and biodiversity (Bragg and Hulbert, 1976; Briggs et al., 2002; Limb et al., 2010), as well as rangeland watershed function and water resources (Zou et al., 2014; Zou et al., 2018; Zhong et al., 2020). For dense redcedar woodlands in which the application of fire is not safe or feasible, mechanical removal is recommended to re-establish herbaceous dominance. However, the associated costs of mechanical removal may dissuade landowners from pursuing it (Ansley and Rassmusssen, 2005; Ortmann et al., 1998), and the long-term benefits of such practices may be minimal or unrealized (Archer and Predick, 2014), and the long-term benefits of such practices may

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be minimal or unrealized (Archer and Predick, 2014). Planting perennial grass feedstock for cellulosic ethanol production is a potential alternate land use for sites post-redcedar removal (Guzman and Lal, 2014). Specifically, many of these "go-back" lands are identified as suitable locations for the native biofuel crop switchgrass (Panicum virgatum). Switchgrass has a high ANPP capacity exceeding that of redcedar in northcentral Oklahoma (Schmidt et al., 2021) and has a neutral or even positive impact on water yield (Zhong et al., 2020).

Soil organic carbon originates as a byproduct of photosynthesis. While it is easy to perceive as simply the remains of "dead stuff", the importance it plays to the soil's function cannot be overstated. How components of the soil organic carbon cycle have been viewed has changed significantly over the past few decades, especially regarding its long-term stabilization. While the onset of agriculture has led to significant carbon reductions within the soil, it has also offered a large potential sink to help mitigate greenhouse gas emissions if managed correctly.

With the increasing demand for climate-smart range management and the potential role previously cultivated mesic grasslands could play, it is becoming urgent to understand the impact of the prevailing land uses and possible land-use alternatives on soil carbon sequestration in those "go-back" lands.

CHAPTER II

RESPONSE OF SOIL CARBON TO HISTORICAL AND RECENT LAND USE IN MESIC GRASSLANDS IN THE SOUTHCENTRAL GREAT PLAINS, USA

1. Introduction

The terrestrial carbon pool is about three times greater than the CO₂ currently in the atmosphere, with over three-quarters of this stored within the soil (Lal, 2010; Paustian et al., 2016). Rangelands account for approximately 40% of the terrestrial biosphere by cover type and store as much as 30% of terrestrial carbon, roughly equal to the amount in the atmosphere (Schuman et al., 2002; Derner et al., 2006; Lal, 2010). Understanding the rate and capacity of carbon sequestration in rangeland soils under diverse management practices is essential for climate-smart land management and implementing land-based climate mitigation strategies (Lal, 2010; Paustian et al., 2016).

The rate and capacity for rangeland carbon sequestration vary significantly among biomes, land use, and prior land-use history (Jobbágy and Jackson, 2000). In rangelands of the North American Great Plains, both the rate of sequestration and the capacity of soil to store organic carbon were reported to increase with annual precipitation (Jobbágy and Jackson, 2000; Schuman et al., 2002; Poeplau, 2019). The mesic grasslands at the central and eastern parts of the Great Plains have a large capacity to sequester atmospheric CO₂ into biomass due to their high net primary productivity (NPP). Many of these grasslands were once tilled and severely degraded and deprived of soil fertility, then converted to production for livestock forage or abandoned, occasionally called "go-back" lands (Owensby and Anderson, 1965). Based on USDA data (USDA Economic Research Service), around 5.2 million hectares of such lands existed in Kansas, Oklahoma, and Texas in 2012. These lands lost much of their pre-agricultural soil organic carbon (SOC) due to cultivation (Davidson and Ackerman, 1993; Amundson et al., 2015; Lal, 2018). Given their current diminished SOC status, they have a high capacity to sequester future ANPP into stable humic substances and secondary carbonates, particularly when cultivation ceases (Gebhart et al., 1994; Conant et al., 2017; Lal et al., 2018).

Many of these "go-back" grasslands are managed as pasture (Bigelow and Borchers, 2017), while some of these lands with pronounced soil erosion are enrolled under Conservation Protection Program (CRP) and are excluded from direct agricultural usage. The CRP was initially implemented to move easily degraded lands out of agricultural production to reduce surplus and mitigate the adverse effects of cultivation on their soils, such as soil erosion (Heimlich and Kula, 1991; Dunn et al., 1993; Tanner and Fuhlendorf, 2018). Gebhart et al. (1994) estimated that CRP lands gained an average of 1.12 Mg C ha⁻¹ yr⁻¹, while Conant et al. (2017) estimated conversion from cultivation led to an average of 0.87 Mg C ha⁻¹ yr⁻¹. These "go-back" lands have the highest rate of woody encroachment in the world (Barger et al., 2011), primarily by an evergreen juniper species (*Juniperus virginiana* L., henceforth, redcedar). Redcedar is native, fire-intolerant woody species and was historically kept in check in grasslands under pre-European fire regimes (Ansley and Rasmussen, 2005). However, due to changes in land management

practices and fire exclusion, it has become a prolific encroaching species in the southern and northcentral Great Plains ranging from Texas to Nebraska. If unmanaged, redcedar can reach canopy closure within half a century, drastically reducing the presence and diversity of herbaceous species (Bragg and Hulbert, 1976; Briggs et al., 2002; Limb et al., 2010). However, redcedar woodlands often have aboveground net primary productivity (ANPP) significantly greater than the grasslands they usurp (Norris et al., 2001b; Schmidt et al., 2021) and can hold 10 to 20-fold greater C in aboveground biomass than grasslands (Norris et al., 2001a; Norris et al., 2001b). Indeed, afforestation of rangelands has been proposed as a strategy to sequester atmospheric carbon (Lal, 2018). Despite the apparent benefit of rapid carbon accrual into aboveground woody biomass and litter, the effect of high productivity on belowground soil carbon accrual is inconclusive, especially in "go-back" lands with annual precipitation exceeding 800 mm (Barger et al., 2011).

While aboveground carbon storage of redcedar woodland far exceeds that of grasslands on the same land area, they are more vulnerable to fire than belowground carbon storage. Fire can rapidly release much of the carbon stored in aboveground biomass and surface litter into the atmosphere, especially if crown fires occur (Neary et al., 1999). In contrast, the impacts of fire on SOC mineralization are often limited to the upper soil (Hartford and Frandsen, 1992). As such, SOC is considered more stable than that stored in aboveground biomass in terms of natural surface disturbances, with possible residence times stretching several centuries (Fontaine et al., 2007).

Scientific literature recommends the use of prescribed fire to curtail redcedar expansion to protect forage productivity and biodiversity (Bragg and Hulbert, 1976; Briggs et al., 2002; Limb et al., 2010), as well as rangeland watershed function and water resources (Zou et al., 2014; Zou et al., 2018; Zhong et al., 2020). For dense redcedar woodlands in which the application of fire is not safe or feasible, mechanical removal is recommended to re-establish herbaceous dominance. However, the associated costs of mechanical removal may dissuade landowners from pursuing it (Ansley and Rassmusssen, 2005; Ortmann et al., 1998), and the long-term benefits of such practices may be minimal or unrealized (Archer and Predick, 2014). Planting perennial grass feedstock for cellulosic ethanol production is a potential alternate land use for sites post-redcedar removal (Guzman and Lal, 2014). Specifically, many of these "go-back" lands are identified as suitable locations for the native biofuel crop switchgrass (*Panicum virgatum*). Switchgrass has a high ANPP capacity exceeding that of redcedar in northcentral Oklahoma (Schmidt et al., 2021) and has a neutral or even positive impact on water yield (Zhong et al., 2020).

With the increasing demand for climate-smart range management and the potential role previously cultivated mesic grasslands could play, it is becoming urgent to understand the impact of the prevailing land uses and possible land-use alternatives on soil carbon sequestration in those "go-back" lands. Soil texture and vegetation prior to cultivation may confound the impact of land use since cultivation. This study aimed to confine the effect of soil texture and legacy effect from pre-cultivation to assess the soil carbon dynamics in "go-back" lands under different vegetation cover (prairie vs. redcedar woodland) and recent site management practices (redcedar removal and establishment of

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prairie or biofuel production system). Our specific objectives were to (1) quantify the change in soil bulk density (ρb g cm⁻³) among the different land uses; (2) determine the soil organic carbon content (C–Content, %), nitrogen content (N–Content, %), C/N ratio (%), and organic carbon densities (C–density, mg cm⁻³) in the 0-2, 2-10, 10-20, and 20-30 cm depths and their interactions with land uses; (3) compare the soil organic carbon pool by focusing on the soil carbon stock (C–stock, g C m⁻²) in the top 30 cm soil, and (4) assess the impact of soil texture and potential legacy effect from vegetation prior to the cultivation. This is the first study to systematically analyze soil carbon dynamics and soil carbon pool on "go-back" lands with multiple historical land uses and recent land-use changes in one study area.

2. Material and methods

2.1 Study location

The study was conducted at the Oklahoma State University Range Research Range (OSU-RRS), located 15 km southwest of Stillwater, Oklahoma, USA (36°3'46.73" N, 97°11'3.33" W). The site is in the western part of the crosstimbers ecoregion: naturally a patchwork of prairie, open savannas, and oak forests in the transition between the mesic eastern forests of the eastern United States and the drier grasslands on the central Great Plains (Hoagland et al., 1999). The sites in our study were plowed to grow cotton in the 1930s (Fig. 1A), which caused severe soil erosion, prompting the construction of terraces (Fig. 1B). The cultivated agricultural fields were later abandoned and allowed to revegetate as grasslands in the 1950s naturally. The vegetation on the prairie sites consisted mainly of C4 grasses such as little bluestem (*Schizachyrium scoparium* [Michx.] Nash), big bluestem (*Andropogon gerardii* Vitman), Indiangrass (*Sorghastrum*

nutans [L.] Nash), switchgrass (*Panicum virgatum* L.), and tall dropseed (*Sporobolus asper* [Michx.] Kunth) (Limb et al., 2010). Redcedar trees appeared scattered in the study area in the 1970s (Fig. 1C). Prescribed fire of three-year return interval was introduced in 1983, which kept the majority of the western portion of the study area open (Fig. 1D). However, the entire area has been in the same grazing unit with a low stocking rate (17 acres/head/year) (Philippe, 2022). During the last half-century, the land to the east has been continuously encroached by redcedar with an estimated woody canopy cover of ~75% based on a survey in 2011 (Fig. 1D). In the redcedar woodland sites, redcedar made up the vast majority of the aboveground biomass, and comprised 99% of the tree biomass (Schmidt et al., 2021) with pockets of grasses often being found in larger intercanopy spaces. Pockets of blackberries (*Rubus sp.* [L.]) could be found, with higher densities in grass-dominated sites.

2.2 Land use and sampling site

Experimental watersheds were constructed in 2009 to study the impact of conversion from grassland to redcedar woodland on water balance (Zou et al., 2014; Qiao et al., 2017). In this study, six watersheds were used as study sites to represent a unique land use or cover type (Fig. 1). In July 2015, redcedar on F3 and F4 was cut via a skid steer with a Marshall tree saw. Fallen trees were left on site to dry until February 2016, when they were mulched and removed. One of the sites F4 was left to revegetate naturally following the removal of fallen trees. Two sites,F3 and G2 were both treated with the herbicide glyphosate in March 2016. In April 2017, these two sites were seeded with the switchgrass cultivar "Alamo" to a depth of 0.64 cm at a rate of 7.8 kg ha⁻¹ via Truax nodrill machine and converted to switchgrass production. Sites converted to switchgrass were harvested annually at a 10 cm height, baled, and removed each November following the first frost (Zhong et al., 2020; Schmidt et al., 2021; Phillippe, 2022; Zhong et al., 2022). All watersheds except for F2 and G3 were fenced to exclude cattle, preventing site grazing since June 2017. As a result, it created a combination of six different land-use scenarios – eastern redcedar (ERC), eastern redcedar to switchgrass (ERC \rightarrow SWG), eastern redcedar to restored prairie (ERC \rightarrow P), non-grazed prairie (NGP), prairie to switchgrass (P \rightarrow SWG), and grazed prairie (GP) (Fig. 1).

The soils of the six watersheds included 10 different soil series or complexes (USDA Web Soil Survey; NRCS OSDs). The Stephenville (fine-loamy, siliceous, active, thermic Ultic Haplustalfs) -Darnell (loamy, siliceous, active, thermic, shallow Udic Haplustepts) complex (StDD) was the most common soil type and occurred in all watersheds, occupying 22.4% to 75.4% percent of the total area of each watershed (Table 1). Coyle loam (CoyB and Coy)(fine-loamy, siliceous, active, thermic Udic Argiustolls), Harrah (fine-loamy, siliceous, active, thermic Ultic Paleustalfs)-Pulaski (coarse-loamy, mixed, superactive, nonacid, thermic Udic Ustifluvents) complex (HaPE), and Zaneis (fineloamy, siliceous, active, thermic Udic Argiustolls.)-Huska (fine, mixed, superactive, thermic Mollic Natrustalfs) complex (ZaHC) were only present in grassland watersheds, while Renfrow (fine, mixed, superactive, thermic Udertic Paleustolls) and Grainola (fine, mixed, active, thermic Udertic Haplustalfs) soils (ReGr), Coyle- Zaneis complex (CoyZ), Grainola-Lucien (loamy, mixed, superactive, thermic, shallow Udic Haplustolls) complex (GrLE), Stephenville fine sandy loam (StSl) and Coyle-Lucien complex (CoLC) only occurred in encroached watersheds. Except for ReGr and GrLE which contain a silty clay texture deeper than 10 cm, all other soil types have a loam texture throughout the first meter. Fine sandy loam soil was the main soil texture class for the upper thirty

centimeters across both vegetation cover types, followed by loam, clay loam, silty clay, sandy clay loam, and silt loam. All sites are well drained.

2.3 Soil sampling and analysis

Soil samples were collected from July to November 2020. Twenty previously established random points were used for representing each land use (Fig. 1). Points were located with a handheld GPS (Garmin Etrex Vista). At each point, leaf litter and O-horizon were removed if present, and herbaceous vegetation was clipped to the mineral soil, and three soil cores were collected. Two soil cores of 5.71 cm in diameter and 15 cm in depth were sequentially extracted to provide a soil core from 0-30 cm in depth. All soil cores remained in plastic sleeves to keep them intact for further analysis. Additionally, a core of 6.67 cm in diameter was carefully excavated to a depth of 2 cm using a steel ring and rubber mallet for separated determination of bulk density of the 0-2 cm depth.

Soil cores were measured from the top of the extracted soil column and cut within the plastic sleeves at 2, 10, and 20 cm depths with a hacksaw. After cutting, a soil core was divided into four sections (0-2, 2-10, 10-20, and 20-30 cm), and each section was remeasured to verify length and recorded to calculate volume. The soil was then separated from plastic sleeves, broken up, and passed through a 2 mm sieve. Soil that passed through the sieve was then dried at 105°C for 24 hours and weighed to collect dry weight. Rocks and roots that failed to pass through the sieve were weighed and removed. Bulk density was calculated with the weight of the sample, divided by the volume calculated from the diameter and height of the cylinder segment, with corrections to both made for the removed debris. Sieved samples were dried at 105°C for at least 24 hours and weighed to determine bulk density.

Sub-samples were selected from the sieved and oven-dried sample and sent to the Soil Water and Forage Analytical Laboratory (SWFAL) to determine the C–Content (%) and N–Content (%). C–density (mg cm⁻³) was calculated from C–Content and ρb (Davidson and Ackerman, 1993). C–stock (g C m⁻²) was calculated for the 0–30 cm soil depth by summing the C–stock for 0-2, 2-10, 10-20, and 20-30 cm to assess land use impact on SOC following the FAO guidelines for rangeland (Poeplau, 2019).

2.3 Statistic analysis

All analyses were conducted using Proc Mixed (SAS 9.2), assuming site, i.e., watershed and soil depth as fixed factors and sampling points as random. The analysis tested the effects of site and soil depth (0–2, 2–10, and 10–30 cm) on ρb , C–content, N–content, C/N ratio, C–density, and C–stock using a split-plot analysis with site as the whole-plot factor, soil depth as the split-plot factor, and points serving as the experimental units. Given that the variance was much larger for the 0–2 cm depth, data for all metric except for C-stock was log-transformed when depth was included.

3. Results

3.1 Statistic Results

Bulk Density (ρb), C–content, C/N ratio, and C–density were significantly different among site (P<0.0001) and depths (P<0.0001) and also had interactions between site and depth (P<0.04) (Table 2). N–nitrogen and C–stock were significantly affected by site (P<0.0001) and depth (P<0.0001), but the interaction between site and depth was not significant (P>0.05) (Table 2). The majority of interactions occurred because of differences among sites in the 0-2 cm depth interval that were not consistent with differences below 2 cm and because the range among site means tended to decrease with soil depth. For this reason, the main effects were emphasized below.

3.2 Soil Bulk Density

Bulk density (ρb) (mean ± SE) differed among sites (Table 3, Figure 2). The switchgrass site converted from redcedar (ERC \rightarrow SWG) was statically greater than all other sites. ρb of the switchgrass site converted from prairie (P \rightarrow SWG) was higher than redcedar (ERC) and non-grazed prairie (UGP) but was not statistically different from grazed prairie (GP) and redcedar to prairie (ERC \rightarrow P). There were no significant differences among GP, ERC \rightarrow P, ERC, and UGP. ρb increased with soil depth (Figure 2), with the 0–2 cm depth interval having a significantly lower ρb and the 20-30 cm depth interval having a significantly higher ρb than the other depths. ρb for 2-10 cm and 10-20 cm was not significantly different.

The interaction between site and depth occurred because although ERC (1.38 ±0.03 g cm⁻³) and NGP (1.35 ±0.02 g cm⁻³) had the lowest overall pb, ERC \rightarrow P (1.29 ± 0.64 g cm⁻³) and GP (1.12 ± 0.03 g cm⁻³) had the lowest pb in the 0-2 cm depth interval. ERC and UGP did have the lowest pb in the deeper soil depths, i.e., 2-10, 10-20, and 20-30 cm (Figure 2).

3.3 C-content

C-content varied by site (Table 3; Figure 2). The grazed prairie (GP) and non-grazed prairie (NGP) had the greatest C-content values. Switchgrass sites (ERC \rightarrow SWG and P \rightarrow SWG) and the redcedar to prairie site (ERC \rightarrow P) had the lowest C-content values. The C-content in the redcedar site (ERC) was greater than the sites that followed a recent land

use change (ERC \rightarrow SWG, P \rightarrow SWG, ERC \rightarrow P), but lower than the two prairies that did not undergo recent land use change.

C-content decreased with depth (Table 3; Figure 2), with the values for each depth interval being statistically different from each other. The greatest change of C-content occurred in the top 10 cm, with the C-content at 0-2 cm being over twofold greater than that at 2-10 cm. However, the change of C-content between 10 -20 cm and 20-30 cm was relatively small despite its statistical difference. The interaction between site and depth occurred primarily because the C-content of the ERC \rightarrow P site was intermediate in the 0-2 cm soil interval but the lowest for the deeper depths (Figure 3).

GP had the highest C-content values in the top 20 cm (Figure 2). The lower C-content from the switchgrass sites was most pronounced in the top 10 cm.

3.3 N-content

N-content differed significantly among sites (Table 3; Figure 2). Grazed prairie (GP) had the greatest N-content. N-content in the non-grazed prairie (NGP) was less than in the grazed prairie but was statistically greater than all other sites. Differences between other sites were not statistically different.

N-content decreased by depth across all sites (Table 3; Figure 2), and the effects of site were consistent among depths, i.e., no interaction (Table 2). N-content at the surface soil (0-2 cm) was more than twice that at the 2-10 cm depth. N-content of 10-20 cm depth was about 30% lower than 2-10 cm depth, but there was no significant difference between 10-20 cm and 20-30 cm depths.

3.4 C/N ratio

C/N ratio varied by site (Table 3; Figure 2). Redcedar (ERC) had the highest C/N ratio and grazed prairie (GP) had the lowest C/N ratio. No significant differences in C/N ratios were detected from all remaining sites.

C/N ratio decreased with depth (Table 10), and there was a site and depth interaction (Table 2). Although the C/N ratio at 0-2 cm was significantly greater than that below it, the C/N ratio decreased most prominently from 20 to 30 cm in depth.

The interaction occurred because redcedar (ERC) had the greatest C/N ratio in 0-2 cm and 2-10 cm, while $P \rightarrow SWG$ had significantly lower C/N ratios in the soil below 2 cm. Intrasite variability of C/N ratios was greater with increasing depth (Figure 12).

3.5 C–density

C-density varied by site (Table 3; Figure 2). C-density was greatest in the grazed prairie (GP), followed by non-grazed prairie (NGP). C-density was the lowest in the restored prairie (ERC \rightarrow P) and switchgrass converted from prairie (P \rightarrow SWG). C-density was not significantly different between redcedar (ERC) and redcedar to switchgrass (ERC \rightarrow SWG). C-density between the two switchgrass sites (ERC \rightarrow SWG and P \rightarrow SWG) was not significantly different.

C-density decreased significantly across all depth intervals (Table 3; Figure 2). The greatest decrease was between the 0-2 cm and 2-10 cm depth intervals. Beyond 10 cm, the differences in C-density with depth becomes less pronounced.

3.6 C-stock

C-stock of the top 30 cm varied by site (Table 3, Figure 3). The prairie sites which did not have recent land use change had relatively high C-stock (5,152.56±208.96 g C m⁻² for NGP and 5,769.19±185.59 g C m⁻² for GP). All other sites, including the intact redcedar site, had significantly lower carbon stock (4,560.61±274.35 C m⁻² for ERC, 4,506.97± 274 C m⁻² for ERC→SWG, and 3,986.68 ± 150.75 C m⁻² for ERC→P). Notably, the non-grazed prairie site had approximately 10% greater C-stock than the intact redcedar site (ERC). Five years after redcedar removal, detected C-stock was substantially lower in the redcedar to prairie site (ERC→P) compared with the redcedar site (ERC) as well in the prairie to switchgrass site (P→SWG) compared with the intact prairie site (NGP).

3.7 Soil texture and prior to cultivation vegetation impact on soil carbon

There were a total of 10 soil series present in our study area (USDA web soil survey, Table 1, Figure 1D). All sampling points were categorized by soil texture class in the upper 30 cm. Historically, oak woodlands are strongly associated with the StDD (Stephenville-Darnell complex), HaPE (Harrah-Pulaski complex), and 51 soil series, characterized by sandy loam texture. Points associated with those three soil series were further categorized as "forest soils" and the remaining points as "prairie soils". Testing for effects of soil texture and potential pre-cultivation vegetation cover history found no significant impacts on C–content, ρb , and C–density.

4. Discussion

4.1 Mechanical vegetation removal increases ρb

 ρb has not always been collected in soil carbon studies, or only a few ρb samples were collected due to time and equipment constraints (Schlesinger, 1985). As such, land use impact on soil organic carbon dynamic was frequently assessed using C–content, assuming the negligible change in ρb . However, failing to account for changes in ρb and rock components could result in an over- or under-estimate of soil organic pool, particularly when soil compaction is associated with certain land uses or disturbances (Schlesinger, 1985).

For our study depth and area, the presence of rock was minor, averaging 0.006% by volume, and was similar across different soil series. Reported ρb was mineral soil without rock. It was used to calculate C– density and C– stock assuming the rock space was replaced by similar mineral soil.

Grazing and machine use are associated with increased ρb (Smith and Dickson, 1990; Daniel et al., 2002). To accurately assess the land use impact on organic carbon sequestration in soil, it is critical to account for the concurrent ρb change. In our study, the two sites managed for switchgrass production (ERC \rightarrow SWG, P \rightarrow SWG) and thus experiencing annual machine harvest had the highest ρb . Meanwhile, redcedar (ERC) and non-grazed prairie (NGP) did not experience any recent disturbances and had the lowest ρb . These differences in ρb under different managements emphasize the need to consider the effect of compaction when assessing land use on C– stock. ρb of the switchgrass site averaged 1.5 g cm^{-3,} which was approximately 10% greater than the prairie site at 1.35 g cm⁻³. A 10% increase in ρb would increase C– stock by 10% even if the C– content remains unchanged.

The change in ρb was most pronounced at the top of the soil, with this being responsible for the highest overall ρb for ERC \rightarrow SWG and P \rightarrow SWG. As the surface soil has the highest C-content (Baldock and Nelson, 2000), detailed measurement of ρb at this depth is essential to capture land use impact on soil carbon. Our results showed that the variation of ρb decreases substantially below the top two centimeters. This may suggest that effort might be concentrated on quantifying ρb of the top 5 or 10 cm to characterize the soil compaction if ρb measurement for subsoils is cost-prohibited.

Opposite to our expectation, the redcedar site (ERC) had a relatively high ρb at the 0-2 cm depth interval compared to the prairie sites. In addition, the mean ρb values from the 0-2cm depth and 2-10 cm depth were closer for ERC than for any other site. Despite this, ERC ranked overall as having the second-lowest ρb values for the entire 0-30 cm soil column. This pattern in bulk density might be associated with the co-existence of the canopy and intercanopy spaces within the woodland. Interspaces were likely disproportionally compacted due to animal traffic or erosion processes. The redcedar site was accessible by cattle, and evidence of trampling was observed with cattle trails in the intercanopy spaces. In addition, a lack of herbaceous vegetation or litter cover in some intercanopy spaces was observed, as well as the formation of small headcuts and rills in the mineral soil. This was likely responsible for high sediment losses from the site following intense rainfall (Zhong et al., 2022). This could also be seen on the site

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indirectly through small-scale depositions of litter and mineral soil which were likely eroded topsoil. This suggests that the sampling scheme is critically important to characterize any belowground properties including soil carbon.

4.2 Impacts of mechanical disturbance outweigh short-term management impacts on C-content

C-content in the three sites that did not have a recent site disturbance (GP, NGP, and ERC) were significantly greater than those with recent land use change ($P \rightarrow SWG$, ERC \rightarrow SWG, and ERC \rightarrow P), in line with the trend of soil disturbance resulting in reductions of soil organic carbon (Schlesinger, 1986; Davidson and Ackerman, 1993; Guo and Gifford, 2002). The herbicide application on a prairie site ($P \rightarrow SWG$) and mechanical removal of redcedar (ERC \rightarrow SWG and ERC \rightarrow P) both exposed topsoil to direct radiation and kinetic energy of rainfall for an extended period, which might have increased photonic organic matter decomposition, high amounts of mineralization, and also a disproportional organic material efflux to water erosion (Austin and Vivanco, 2006). Prior to the removal of redcedar, Zhong et al. (2022) measured an average annual sediment yield from the redcedar sites of <0.10 t ha⁻¹. This increased to 0.28 t ha⁻¹ yr⁻¹ after the redcedar trees were cut and skeletons remained on site. After the removal of redcedar skeletons the following year, sediment yield from the ERC \rightarrow P site was 1.14 t ha⁻¹ yr⁻¹, and for the ERC \rightarrow SWG site, it was 13.29 t ha⁻¹ yr⁻¹. While sediment loads in the third and fourth years decreased to levels below the ERC site, the impact on soil carbon due to erosion was still measurable four years later. Agroecosystems are estimated to contain a 1/4 to 3/4 less SOC when compared to their natural condition (Lal 2018). Several studies found this impact long-lasting, with restored prairie established from

cultivated sites not attaining C-content levels of uncultivated sites even 50 years postrestoration (Dormaar and Smoliak, 1985; Burke et al., 1995; Fuhlendorf et al., 2002). The lack of statistical difference in C-content between the sites that underwent a recent mechanical disturbance indicates that this can greatly reshape soil organic carbon processes and obfuscate the near-term impact of land use change on soil organic carbon accrual, particularly at the surface. Compared with the land use prior to disturbance, the C-content in the topsoil (0-2 cm) was significantly reduced (P \rightarrow SWG vs. UGP, ERC \rightarrow SWG vs. ERC, ERC \rightarrow P vs. ERC). It appears that the reduction in ERC \rightarrow SWG was substantially greater than ERC \rightarrow P; this might be explained by the substantial loss of soil immediately after the application of herbicide in ERC \rightarrow SWG (Zhong et al., 2022). P \rightarrow SWG was treated with herbicide for switchgrass planting as well, but there was no significant soil erosion observed, potentially due to the more established herbaceous roots and dead vegetation biomass that remained in place after vegetation mortality.

The impact of land use appears to have primarily impacted the surface soil, as evidenced by the significant C-content and depth interaction between the 0-2 cm to 2-10 cm depth interval for both ERC \rightarrow SWG and P \rightarrow SWG (Figure 2), which is expected (Conant et al., 2017).

The C-content in redcedar (ERC) was not significantly greater than either grazed or nongrazed prairie. Another study on the same property near this study showed greater Ccontent under isolated redcedar trees than in adjacent grass-dominated areas (Nunes Biral et al., 2019). Likewise, a few studies from Kansas reported a general increase in Ccontent after remnant prairie was encroached by redcedar, especially under the redcedar canopy (Briggs et al., 2002; Smith and Johnson, 2003). It is likely that studies on the remnant prairie have reached an equilibrium state (Smith and Johnson, 2003) and that carbon dynamics on previously degraded sites may not follow the same pattern even several decades post cultivation.

4.3 Impacts of disturbance outweigh short-term management impacts on soil N

Our results showed that the prairie soils without recent land use change (GP and NGP) had greater soil N content, followed by the redcedar site that was not converted (ERC). The reduced soil N associated with all sites with recent disturbance suggests an impact on soil N dynamics. GP was the only site under continuous grazing for the three sites without recent disturbance and had the highest soil N. Some research showed an increase in soil nitrogen with grazing (Fuhlendorf et al., 2002; Abdalla et al., 2018), while others reported little change (Derner et al., 2006) or a decrease (Frank et al., 1995; Xiong et al., 2016) with grazing.

Our study found that soil N was less in redcedar site compared with prairie, which was in contrast with the finding by McKinely and Blair (2008) who reported that redcedar encroachment in native prairie increased soil N, though it did not change labile soil N pools.

4.4 Redcedar encroachment resulted in the highest C/N ratio in the topsoil.

C/N ratios are expected to decrease with depth. While both C and N concentrations generally decrease with increasing soil depth, the rate of decrease is greater for C concentration due to reduced inputs of SOC from roots and aboveground inputs (Jobbágy and Jackson, 2000). This was largely shown in our data though some points blurred this trend (Figure 2).

The C/N ratio of the top 2 cm soil under redcedar (ERC) was statistically greater than all other land uses, while the C/N ratio of the subsoil under continuous grazing (GP) was statistically lower than all other land uses. However, differences across all treatments were relatively minor. Norris et al. (2001b) found that fresh litter fall in redcedar encroached remnant prairie in the Flint Hills of Kansas made up around 55% of annual aboveground NPP, with litter holding an average C/N ratio of 54.5. This would suggest a notably higher C/N ratio under redcedar encroachment. However, McKinely and Blair (2008) found that both C and N totals increased under redcedar encroached grasslands were not significantly different.

Frank et al. (1995) found that grazing decreased soil N content, potentially increasing the C/N ratio. Schuman et al. (1999) found that grazing increased carbon and nitrogen contents in the top 30 centimeters of the soil under light and heavy grazing. However, grazing intensity influenced the relationship of these variables, with a higher C/N ratio under high grazing intensity and a lower C/N ratio under light grazing intensity. Fuhlendorf et al. (2002) found differences in the C/N ratio between non-grazed and grazed restored grasslands, though the differences were not statistically significant. Potter et al. (2001) found little difference in the C/N ratio in their study examining different stocking rates. Our results were consistent with those of Schuman et al. (1999) and Fuhlendorf et al. (2002).

4.5 C- density incorporates the cofounding effect of land use on ρb

The use of C– density is more relevant than C– content in assessing range management impact on soil carbon pool because the change in C–content is affected by managementinduced ρb change (McSherry and Ritchie, 2013). Also, C– density can be directly integrated on a volume basis to estimate or map terrestrial carbon stock (Minasny et al., 2013). The C– density of grazed prairie (GP) was significantly greater than non-grazed prairie (NGP), although C– content was not significantly different, presumably indicating the impact of grazers on ρb (Table 3). C– density of ERC \rightarrow SWG did not significantly differ from ERC although the carbon content was greater for ERC. This suggests the potential impact associated with land use change and associated compaction need to be incorporated for accurate calculation of C-density.

Both ERC \rightarrow SWG and ERC \rightarrow P experienced compaction associated with the mechanical removal of redcedar in 2015. However, ERC \rightarrow SWG was repeatedly impacted by mechanical harvesting switchgrass contributing to its greatest ρb of any site (1.50 g cm⁻³), while ERC \rightarrow P was enclosed to revegetate without grazers or mechanical harvesting (1.40 g cm⁻³). As a result, the C– density of ERC \rightarrow SWG was significantly greater than ERC \rightarrow P even though their total carbon contents were not significantly different.

C- content and C- density are important parameters used in soil carbon study. Our results suggest that it is important to look into both to understand land use impact on soil carbon if ρb is likely affected.

4.6 C- stock and responses to land use and vegetation in the "go-back" lands

The average C– stock in the upper 30 cm across all land use in our study was $4,671 \pm 523$ g C m⁻² which is substantially lower than the average value reported for the remnant prairie (7,699 ±1004 g C m⁻²) for the top 20 cm (Smith and Johnson, 2003). In northeastern Colorado, Burke et al. (1995) found that in the top 10 cm, sites that had been 50 years out of cultivation held C– stocks 30-40% of sites that had never been cultivated. Remnant prairie sites often remain due to high rock in shallow soil or relatively low depth to base rock and thus poor suitability for cultivation (Smith and Johnson, 2003; McKinley and Blair, 2008). By contrast, these "go-back" lands usually have a mineral soil depth greater than 30 cm, suggesting that they could be a large sink for further carbon sequestration.

As grazing is the principal usage of rangelands (Derner et al., 2006), there is increasing interest in managing the grazing system to maximize its soil carbon sequestration. The interaction between the climate, stocking rate, climate, and grazer-induced changes in the plant community make it challenging to generalize the impact of stocking rate on soil carbon sequestration (McSherry and Ritchie, 2013; Lal et al., 2018). Also, C– content, C– density, and C– stock have been used in different studies, often without detailed information of ρb , making a direct comparison of range management impact on the carbon sequestration potential difficult. Based on the recommendation from FAO (Poeplau, 2019), this study compared C– stock in the 0-30 cm soil and the grazed prairie (GP) had a similar carbon held in the soil compared with the non-grazed prairie (NGP). Schuman et al. (1999) reported that C– stock increased under moderate grazing in tallgrass prairie.

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The impact of woody plants on terrestrial carbon sequestration is another topic of debate. Redcedar woodland has a relatively high aboveground net primary productivity (ANPP) and a large standing aboveground biomass and litter inputs (Norris et al., 2001a: Norris et al., 2001b). For this study location, the ANPP between 2016 and 2019 averaged 5.4 Mg ha⁻¹ yr⁻¹ for redcedar woodlands, compared favorably with 5.1 Mg ha⁻¹ yr⁻¹ for the prairie sites (Schmidt et al., 2021). However, the ANPP of encroaching species may be decoupled from soil organic carbon (Barger et al., 2011). Some studies reported increased C– stock for the 10 cm soil under redcedar woodland in the remnant prairie (McKiney and Blair 2008). In contrast, our study showed that the C– stock under "go-back" grassland was 10 - 15% greater than the encroached redcedar woodland. Redcedar encroachment into the "go-back" land does not appear to show a carbon benefit in the stable mineral soil at our site.

It is also important to point out that the difference in C– stock developed over multiple centuries can be quickly altered by disturbance (Davidson and Ackerman, 1993). The disturbance will have a short or mid-term impact on the existing soil carbon pool. Some studies have shown that the carbon benefits of planting switchgrass for biofuel production may take around a decade or more to be realized (Ma et al., 2000; Arundale et al., 2014). In our study, the loss of soil organic carbon following the conversion of prairie to switchgrass was still detectable after 5 years (P \rightarrow SWG vs. NGP). However, the increased productivity associated with switchgrass may lead to a greater rate of soil organic carbon accrual over time (Ma et al., 2000). For example, C– stock in the switchgrass site converted from redcedar was not significantly different from the redcedar site only after four years of very high ANPP (Schmidt et al., 2021).

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Further research is needed to understand how land use change, especially conversion from grassland and redcedar to both grassland or switchgrass has resulted in a change in soil hydrological properties, belowground productivity such as root growth and turnover to understand the middle or long-term impact of such land use impact on soil carbon pool.

4.7 Soil texture and pre-agricultural land cover impact on soil carbon

Soil type texture and pre-cultivation land cover could be confounding factors in ascribing land-use change to soil organic carbon (Baldock and Nelson, 2000). Before European settlement, the study site was a mosaic of grassland and forest covers (Hoagland et al., 1999), primarily delineated by soil texture (NRCS OSDs). Points determined to fall under "prairie" and "forest" soils based on soil texture map data were found in all sites. Analysis of soil texture and potential historic cover types showed no confounding effect from soil texture and historic cover type on ρb , C–content, N–content, and C–density. These results suggest that the historical plowing and cultivation likely greatly deprived the soil in the cultivated layer of organic matter and the legacy effect of historical land cover prior to cultivation on soil organic carbon (Bürgi et al., 2017). The detected change in ρb , C–content, C–density, and C–stock in this study primarily reflected the impact of land use and cover change after cultivation cessation and recent land disturbances.

5. Conclusion

With the increasing societal awareness of climate change and the importance of rangeland management in slowing atmospheric carbon concentration increase, more emphasis is shifting to climate-smart rangeland management. While eastern redcedar encroachment into remanent prairie was widely reported to increase soil carbon, our study found that converting "go-back" grassland to redcedar woodland at the ecosystem transition zone was associated with reduced soil carbon storage in the 0 - 30 cm soil profile at the watershed scale. Conversion of redcedar woodland to restored prairie or planting switchgrass will result in a loss of SOC detectable half a decade later. A life cycle analysis might be needed for large-scale land conversion to maximize the climate benefit, especially associated with planting biofuel in the previously cultivated grassland.

Our systematic study indicates that the sites that have undergone previous cultivation currently have sequestered a substantial amount of carbon and built up a large carbon pool in the upper 30 cm after cultivation abandonment over half a century later. This is nearly 60% compared with that sites never cultivated. Still, there is great potential for these lands to continue sequestering carbon. Further study on the mechanism regarding the soil microbe, rooting growth, and the organic carbon dynamic is needed to assist the climate-smart management of the vast rangeland in the southern and northern Great Plains region.

TABLES

Table 1. Percentage contribution of each soil type to the total area of each watershed. StDD: Stephenville–Darnell complex (fine-loamy, siliceous, active, thermic Ultic Haplustalfs – loamy, siliceous, active, thermic, shallow Udic Haplustepts); Coy B: Coyle loam in upper 10 inches (fine-loamy, siliceous, active, thermic Udic Argiustolls); Coy: Coyle loam; HaPE: Harrah–Pulaski complex (fine-loamy, siliceous, active, thermic Ultic Paleustalfs–coarse-loamy, mixed, superactive, nonacid, thermic Udic Ustifluvents]; ZaHC: Zaneis–Huska complex (fine-loamy, siliceous, active, thermic Udic Argiustolls – fine, mixed, superactive, thermic Mollic Natrustalfs]; ReGr: Renfrow and Grainola soils (fine, mixed, superactive, thermic Udertic Paleustolls – fine, mixed, active, thermic Udertic Haplustalfs]; CoyZ: Coyle and Zaneis soils; GrLE: Grainola–Lucien complex (loamy, mixed, superactive, thermic, shallow Udic Haplustolls]; StSL: Stephenville fine sandy loam; CoLC: Coyle-Lucien complex.

Site*	Area	StDD	CoyB	Coy	ReGr	CoyZ	GrLE	StSL	CoLC	HaPE	ZaHC
	(m ²)										
<i>G1</i>	22641	63.67	20.32	0.00	0.00	0.00	0.00	0.00	0.00	15.04	0.97
<i>G2</i>	33347	67.37	14.49	18.15	0.00	0.00	0.00	0.00	0.00	0.00	0.00
G3	40293	54.75	22.90	22.35	0.00	0.00	0.00	0.00	0.00	0.00	0.00
F2	13478	22.42	0.00	0.00	0.00	55.75	21.83	0.00	0.00	0.00	0.00
F3	31816	30.39	0.00	0.00	33.87	0.00	8.45	8.49	18.79	0.00	0.00
F3	23295	75.42	0.00	0.00	11.86	0.00	3.14	9.58	0.00	0.00	0.00

* G1: non-grazed prairie (NGP); G2: prairie to switchgrass ($P \rightarrow SWG$), and G3: grazed prairie (GP); F2: eastern redcedar (ERC); F3: eastern redcedar to switchgrass (ERC \rightarrow SWG); F4: eastern redcedar to restored prairie (ERC \rightarrow P).

Table 2. Statistical summary of the site, depth, and their interactions on soil bulk density $(\rho b, \text{ g cm}^{-3})$, carbon content (C-content, %), nitrogen content (N-content, %), C/N ratio (%), carbon density (C–density, mg cm⁻³,), and carbon stock (C–stock, g C cm⁻²) for the top 30 cm mineral soil with recent land-use change in mesic grasslands.

Variable	Site	Depth	Site \times Depth
$\rho b (\mathrm{g \ cm^{-3}})$	P < 0.0001	P < 0.0001	P=0.001
C-content (%)	P <0.0001	P < 0.0001	P = 0.037
N-content (%)	P <0.0001	P < 0.0001	P = 0.106
C/N ratio (%)	P <0.0001	P < 0.0001	P=0.019
C-density (mg cm ⁻³)	P < 0.0001	P < 0.0001	P=0.021
C-stock (g C cm ⁻²)	P < 0.0001	P < 0.0001	P=0.186

Table 3. Soil bulk density (ρb , g cm⁻³), carbon content (C-content, %), nitrogen content (N-content, %), C/N ratio (%), carbon density (C–density, mg cm⁻³), and carbon stock (C–stock, g C cm⁻²) for the top 30 cm mineral soil with recent land-use change in mesic grasslands. Data are mean \pm SE (n =20). The different superscript capital letters for each variable denote significant differences among the land uses. C–stock was the accumulated carbon at the top 30 cm. Analyses were conducted on log transformed data, but non-transformed means are presented.

Site*	$\rho b (\mathrm{g \ cm^{-3}})$	C–Content (%)	N–Content (%)	C/N ratio (%)	C–Density (mg cm ⁻³)	C–Stock (g C m ⁻²)
G1	1.35±0.02 ^C	1.74±0.13 ^A	0.14 ± 0.01^{B}	12.17 ^A	21.92±0.78 ^B	5,152.56±208.96 ^A
G2	$1.44{\pm}0.01^{B}$	$1.46 \pm 0.09^{\circ}$	0.12±0.01°	12.24 ^A	$18.99 \pm 0.91^{\text{DE}}$	4,317.69±204.63 ^B
G3	1.44 ± 0.01^{BC}	$1.92{\pm}0.07^{\rm A}$	0.17 ± 0.01^{A}	10.98 ^B	$21.64{\pm}0.78^{\rm A}$	$5,769.19 \pm 185.59^{\text{A}}$
F2	$1.38 \pm 0.03^{\circ}$	$1.64{\pm}0.15^{B}$	$0.13 \pm 0.01^{\circ}$	12.90 ^A	$20.94{\pm}1.45^{\circ}$	4,560.61±274.35 ^B
F3	1.50 ± 0.02^{A}	$1.40 \pm 0.13^{\circ}$	$0.12 \pm 0.01^{\circ}$	12.12 ^A	19.27 ± 1.17^{CD}	$4,505.97{\pm}226.50^{B}$
F4	1.40 ± 0.02^{BC}	$1.46 \pm 0.09^{\circ}$	$0.12 \pm 0.01^{\circ}$	12.30 ^A	$18.07 \pm 0.67^{\rm E}$	$3,986.68 \pm 150.75$ ^B

*F2: eastern redcedar (ERC); F3: eastern redcedar to switchgrass (ERC \rightarrow SWG); F4: eastern redcedar to restored prairie (ERC \rightarrow P); G1: non-grazed prairie (NGP); G2: prairie to switchgrass (P \rightarrow SWG), and G3: grazed prairie (GP)

FIGURES

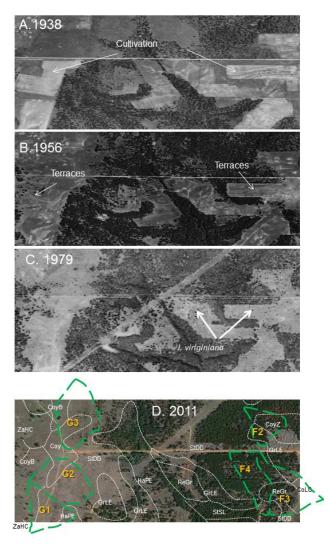


Figure 1. Change of land use and cover in the past 70 years of the study site. Soil types were delineated based on USDA Soil Survey (USDA Web Soil Survey) (Fig. 1D, white lines). Six experimental watersheds (three grassland watersheds to the west – G1(NGP), G2 (P \rightarrow SWG), and G3 (GP) and three watersheds encroached by *Juniperus viriginiana* – F2 (ERC), F3 (ERC \rightarrow SWG) and F4 (ERC \rightarrow P) ranging from 1.30 to 4.02 hectares were established in 2008 for a water budget study. The green lines are watershed boundaries.

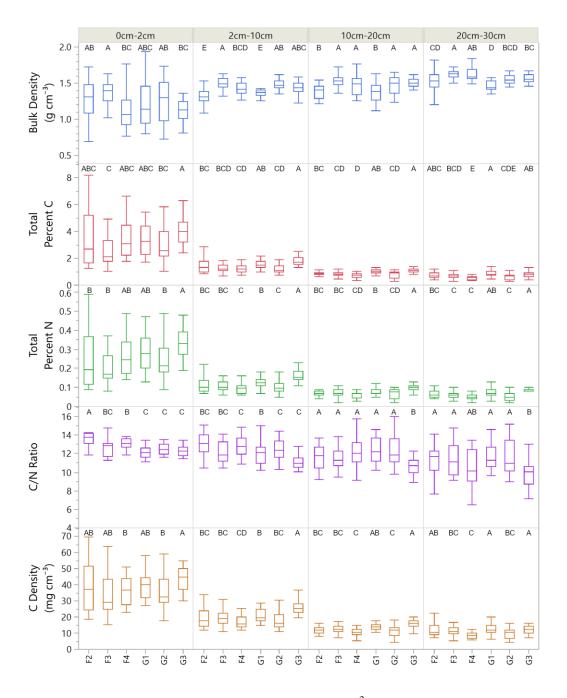


Figure 2. Comparison of soil bulk density (ρb , g cm⁻³), carbon content (C-content, %), nitrogen content (N-content, %), C/N ratio (%), carbon density (C–density, mg cm⁻³) across site by depth. Analyses were conducted on log transformed data, but non-transformed medians are presented in a box plot, in which the box extends from the 25th quantile to the 75th quantile and the horizontal line within each box indicates the sample median.

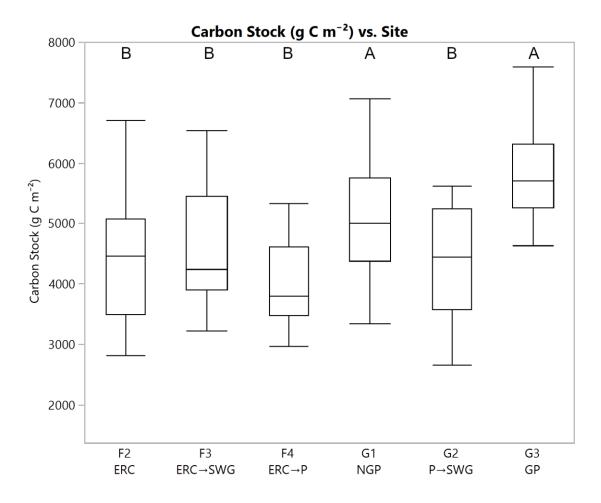


Figure 3. Comparison of carbon stock (C–stock, g C cm⁻²) for the top 30 of mineral soil across sites. Analyses were conducted on log transformed data, but non-transformed medians are presented in a box plot, in which the box extends from the 25th quantile to the 75th quantile and the horizontal line within each box indicates the sample median.

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VITA

J Harrell Johnson

Candidate for the Degree of

Master of Science

Thesis: LAND MANAGEMENT PRACTICES ON BELOWGROUND CARBON IN THE ECOSYSTEM TRANSITIONAL ZONE IN THE SOUTHCENTRAL GREAT PLAINS Major Field: Natural Pasource Feelogy and Management

Major Field: Natural Resource Ecology and Management

Biographical:

Education:

Completed the requirements for the Master of Science in Natural Resource Ecology and Management at Oklahoma State University, Stillwater, Oklahoma in July, 2022.

Completed the requirements for the Bachelor of Science in Natural Resource Ecology and Management Oklahoma State University, Stillwater, Oklahoma in 2014.

Completed the requirements for the Bachelor of Science in Zoology at Oklahoma State University, Stillwater, Oklahoma in 2014.

Experience:

Graduate Research Assistant NREM/Oklahoma State University. Fall 2019-Present

Paddlefish Research Center Intern Oklahoma State Department of Wildlife. March – April 2016, 2018, 2019

American Conservation Experience Natural Resources Intern National Park Service. November 2016- November 2017

AmeriCorps Natural Resources Field Technician Intern Bureau of Land Management. April 2015-September 2015