The spatial and temporal effects of prairie strip restoration on soil health

by

Cole R. Dutter

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Major: Soil Science & Sustainable Agriculture

Program of Study Committee:
Marshall McDaniel, Major Professor
Bradley Miller
Lisa A. Schulte
Matt Liebman
Rick Cruse

Iowa State University

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DEDICATION

This dissertation is dedicated to my daughters, Jubilee and Daisy. I hope that my work, and others like mine, allows you to continue to grow up in a world better than it was when I was a child. You have tolerated so much in your young lives, and, with the completion of this dissertation, I plan to give you two a far better life than you've had thus far! This dissertation is also the result of professors who believed in me, even when I did not believe I would continue in education. As such, it is also dedicated to Michael Fleming and Ida Bowers.

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ABSTRACT

Prairie strips (PS), or plantings of reconstructed prairie surrounded by cropland, can have disproportionate environmental benefits compared to the amount of land they occupy (< 25% of a field). These benefits include improved water quality, reduced soil movement, improved nutrient retention, and more abundant and diverse wildlife. However, the PS impact on the soil underneath and adjacent cropland is unknown. Because PS are narrow (usually >10 m wide), the soil health benefits may not mirror the more common reconstruction of prairies or grassland, which generally occur in large swaths of contiguous land (>10 ha). Furthermore, we know little about how PS affects the soil and crops adjacent to it.

My overarching hypothesis is that PS have little-to-no effect on adjacent cropland, and soil health recovery underneath the PS would be similar to the conversion of agriculture to grasslands. Namely, we would observe positive effects on soil properties related to soil ecosystem services like nutrient supplying power and soil carbon sequestration. More fine-scale exploration of the PS effects on adjacent crops and soils is needed to fine-tune the management of this integrated cropland-prairie system.

I found that PS increased soil health metrics under the PS and moderately influenced the adjacent cropland. PS accrue microbial biomass, influences plant-available nutrients, and PS affects potential enzyme activity, depending on the year. PS did affect the adjacent cropland (≤ 9 m). PS strongly influenced the distribution of plant available nutrients, potential enzyme activity depending on the year, leaf greenness and had a negligible effect on crop yield. Overall, PS improve soil health metrics by increasing C, influencing enzyme activity (≤ 9 m), and retaining plant available nutrients without significantly affecting grain yields.

CHAPTER 1. GENERAL INTRODUCTION

1.1. Agriculture's legacy in the Midwest US

Cultivation in the Midwest US has resulted in great crop productivity for over a century (Figure 1; Egli 2008). The cultivation of native grasslands in the Midwest USA has had many unintended consequences, and, currently, only about 1% of grasslands in the Midwest USA remain uncultivated (Samson and Knopf 1994). A century or more of converting oak-savannah grasslands of the Midwest US to cropland has resulted in environmental maladies, including staggering soil erosion rates (Thaler et al. 2022), unsustainable losses of soil organic matter (SOM) in the soil that remains (Fenton, Kazemi, and Lauterbach-Barrett 2005), leakage of nutrients that contribute to local and regional water quality issues (Dodds and Kemp 2001), increased greenhouse gas emissions (esp. nitrous oxide; Oates et al. 2016), and reduced floral and faunal diversity (Samson and Knopf 1994). Modern, conventional agriculture in the Midwest US has proven to be a "double-edged sword" – increasingly effective at producing food, fuel, and fiber per hectare but at an increasing environmental cost (Thaler et al. 2022).

1.1.1. Soil loss in Midwest US

Lengthy fallow periods during the year and tillage have greatly increased historical erosion rates (Montgomery 2007; Pimentel et al. 1995). Broadly, soil erosion has many societal costs (or losses to soil ecosystem services), including denuded soil reducing crop production (Fenton et al. 2005; Montgomery 2007), slowed water infiltration and increased runoff (Pimentel et al. 1995), increased flooding susceptibility (Pimentel et al. 1987; Pimentel and Kounang 1998), and loss of soil biota (Pimentel et al. 1995; Pimentel and Kounang 1998). The specific effect of erosion on agricultural land has long been documented and include reduction in productivity, reduction in soil organic matter (SOM), loss of nutrient, reduced water holding capacity, and, broadly, inferior soil health (Bauer and Black 1994; Burke, Lauenroth, and Coffin 1995; Cox, Hug, and Bruzelius 2011; Ricci et al. 2020). Direct costs to the farmer include increased quantities of fertilizer in applications to maintain production (Fenton et al. 2005), and ultimately the productive lifespan of the soil is shortened (Montgomery 2007). The lifespan of productivity is shortened directly by thinning the productive A-horizon and thus removing the highest concentration of organic matter. Human mismanagement is the most significant cause of this degradation (Montgomery 2007; Pimentel et al. 1995; Thaler et al. 2022).

Soil organic matter (SOM) is the keystone to soil health; SOM affects soil's physical, chemical, and biological properties (Oldfield, Wood, and Bradford 2020). Soil organic matter acts as a repository for nutrients, a food source, and a habitat for the microbiome, improves soil structure, and improves water holding capacity (King et al. 2020; Oldfield et al. 2020). Converting native grasslands to cropland has been shown to reduce SOM by 20-70% (Crews and Rumsey 2017; Lal 2002). Cultivation has reduced SOM content of soils in various ways: aggregate disruption through decades of tillage, aeration via tile drainage, liming, and reduced plant biomass inputs by replacing prairie with annual crops maize (*Zea mays*) and soybean (*Glycine max*) (Lal 2002; McLauchlan 2006). Beyond the cropland effect, SOM loss has also played a critical role in climate change. Globally, the C stored in SOM is 1220-1550 Pg and is approximately two times greater than atmospheric CO_2-C and 2-3 times the C stored in plants (Lal 2004). Thus, loss of this SOM can contribute to accumulating carbon in the atmosphere and, hence, to climate change.

1.1.2. Water Quality Impairment

Land cover and land use strongly influence water quality in local and regional waterways (Gerla 2007; Gleason and Euliss 1998). Conversion of grasslands to agriculture, and especially maize and soybean agriculture, has increased nitrogen (N) and phosphorus (P) loss and increased sediment loads to local waterways (Dodds and Kemp 2001; Gleason and Euliss 1998; Habibiandehkordi et al. 2019). These two nutrients and sediment in excess cause significant damage to water quality and aquatic ecosystem function (Carpenter et al. 1998; Gleason and Euliss 1998). In the Midwest USA, there is considerable focus on the Gulf of Mexico hypoxia, yet many local-to-regional aquatic features, including lakes, are affected by these pollutants (Gleason and Euliss 1998). Sediment degrades waterways by physically filling local waterways or increasing turbidity, decreasing aquatic ecosystem productivity and fauna abundance (Gleason and Euliss 1998; Johnston 1991). The impacts of N and P pollution are widespread. Both nutrients can be limiting in aquatic systems, and adding these limiting nutrients to waterways causes algal growth and blooms (Alexander et al. 2008; Carpenter et al. 1998). Excessive algal growth can lead to hypoxia and kill aquatic biota (Carpenter et al. 1998). Hypoxia affects local lakes and rivers, but, as mentioned previously, the hypoxic region that garners most mainstream media attention in the Midwest US is the Gulf of Mexico (Alexander et al. 2008; Carpenter et al. 1998). Maize and soybean production contribute 52% of the N and 25% of the P delivered to the Gulf of Mexico (Alexander et al. 2008). In 2020, the hypoxic zone measured over 5,480 square km, the third smallest since records began in 1985 (NOAA 2021). Beyond hypoxia, N can also contribute to human and animal health issues. Excess N can cause methemoglobinemia in infants and even abortions in cattle (Carpenter et al. 1998). The impact of excess nutrients remains an intractable challenge in Midwest US agriculture.

1.1.3. Biodiversity loss

The spread of agriculture, especially in the Midwest US, has led to sharp declines in biodiversity (Díaz et al. 2006; Samson and Knopf 1994; Sieg, Flather, and McCanny 1999;

Turley et al. 2020). Before hominids, more than 5,000 BCE, the Midwest US was a mosaic of oak-savanna grassland ecosystems with great biodiversity. Native Americans inhabited the area and farmed at a much lower intensity using different agricultural practices for at least 3,000 to 4,000 years before Euro-American settlement (Doolittle 1992). After Euro-American settlement and intense cultivation, Midwest US biodiversity began its decline. This biodiversity loss is most apparent above ground, with the loss of predators, large herbivores but especially the perennial vegetation cover, as agriculture now occupies 85% of the land use (Hanberry and Abrams 2018). These diverse ecosystems have been replaced with simplified agroecosystems (Díaz et al. 2006). These agroecosystems can be valuable, but the biodiversity they replace may be indispensable. Human beings benefit from biodiversity in numerous ways. Humans have gained medicines, food, fiber, and renewable resources from biota (Díaz et al. 2006). Biodiversity directly influences nutrient and water cycling and indirectly affects access to clean water (Cardinale et al. 2012; Díaz et al. 2006). Biodiversity is important for these because it influences the efficiency of the ecosystem to capture and store resources and recycle nutrients, and stabilizes the ecosystem's functioning over time (Cardinale et al. 2012). Loss of biodiversity can have exponential adverse effects as redundancy of function is lost (Cardinale et al. 2012; Reich et al. 2012; Vibha and Neelam 2012). This adverse effect might especially be true when considering the soil microbiome (Brussaard, de Ruiter, and Brown 2007; Vibha and Neelam 2012). Soil microbes are key to nutrient cycling, decomposition of organic materials and can even influence plant community structure and crop productivity (Hendgen et al. 2018; Turley et al. 2020; Vibha and Neelam 2012). Simplifying the ecosystem for agriculture has led to leaky ecosystems that may reverberate for many years to come, even after restoration (Turley et al. 2020).

1.1.4 Climate Change and Soil Carbon Cycling

Soil contains the third largest pool of C, and the conversion of grasslands to agriculture has contributed to the loss of soil organic carbon (SOC) (Crews and Rumsey 2017; Knops and Tilman 2000; Lal 2004; Tang et al. 2019). Soil organic matter is approximately 58% C; thus, the SOM losses mentioned previously are proportional to the C loss from soil. It is estimated that agriculture alone has contributed 50-90 Pg of C to the atmosphere (Lal 2004) and contributes an additional 3.7 Pg of C globally each year (Billings, Brewer, and Foster 2006). Due to this historic and ongoing loss, many of these degraded soils might have the potential to sequester atmospheric C (Al-Kaisi, Yin, and Licht 2005; Follett 2001; Lal 2004; McLauchlan, Hobbie, and Post 2006). This potential to sequester C has been seen in agricultural abandonment (Knops and Tilman 2000), reestablishment of grasslands (McLauchlan et al. 2006), and to a lesser extent, under no-till agriculture (Al-Kaisi and Kwaw-Mensah 2020).

This begs the ultimate question: how can we maintain crop productivity while reducing greenhouse gas emissions, accruing soil C, and reducing nutrient loss? We do have research on which to build.

1.2. Repairing our Agricultural Infrastructure in the Midwest US

Agriculture’s problems seem intractable, but there are solutions for repairing our agricultural infrastructure and the ecosystem services they provide. These solutions fall under an umbrella of agricultural terms with overlapping meanings like the soil health movement, regenerative agriculture, or sustainable intensification. The solutions can be placed in three categories: infield management strategies, edge-of-field practices, and land use changes (Table 1).

Iowa has established a nutrient reduction strategy to help reduce the hypoxic zone in the Gulf of Mexico (Iowa Nutrient Strategy Science Team 2013). This strategy is voluntary and has the stated goal of reducing N loss by 40% and P by 30% (Kling 2013). In this strategy, there are dozens of management practices that include fertilizer management, cropping management, and even land-use changes. For this General Introduction and to provide context for my Dissertation, I will focus on three practices that are relevant to my area of focus: cover crops as an infield practice (mimicking perennialization by adding non-cash-crop that overwinters); vegetation buffers, which are an edge-of-field practice (perennials implemented on farm field edge to 'filter' nutrients and sediment); and planting perennial plants as an infield land use change (Kling 2013). Prairie strips are an amalgamation of these practices with unique benefits and challenges.

1.2.1. Winter Cover Crop

Cover crops, or non-cash crops usually grown during the winter fallow period, are a versatile management practice that addresses many of the Midwest USA agricultural issues discussed above. Cover crop placement decisions can be made annually according to the land manager's choices, reducing the hurdles for producers to implement cover crops. Cover crops have been shown to reduce total runoff by ~80% (Du et al. 2022), reduce soil erosion by 87-96% (Du et al. 2022; Zhu et al. 1989), reduce nitrate-N leaching by 37-70% (Brandi-Dohrn et al. 1997; Tonitto, David, and Drinkwater 2006), reduce P loss by 70-85% (Wortmann et al. 2013), and increase SOC stocks by 3-10% (Mazzoncini et al. 2011; McClelland, Paustian, and Schipanski 2021; McDaniel, Tiemann, and Grandy 2014; Poeplau and Don 2015). With all these benefits, it is estimated that if cover crops were implemented on all maize and soybean cropland in Iowa, it would reduce nitrate loss by 28% (Kling 2013). Kling (2013) stated that low-cost infield options, such as cover crops, would not meet the Iowa Nutrient Reduction Strategy's

(INRS) goal for N or P. Cover crops also increase biodiversity by adding one or two species to the cropland, but this does nothing compared to the scale of lost biodiversity.

Despite the flexibility and benefits of cover crops, adoption has been low. According to the USDA, Iowa has over 404,000 of the 9 million cropland hectares in cover crops (USDA 2021). From 2012 to 2017, Iowa increased cover crop land cover by 156%; however, that was only an additional 1,534 farms that implemented cover crops in that 5-year time frame (USDA 2021). A recent study also found that ~12% of farmers in the Western Erie Basin planned to implement cover crops, but ~14% planned to discontinue the practice (Beetstra, Wilson, and Doidge 2022). In raw numbers, cover crops have gained much ground; however, there are many hurdles to widespread adoption.

1.2.2. Vegetation Buffers

Vegetation filter strip buffers, hereafter just referred to as 'buffers,' have been used to protect water quality and researched extensively in the last 40 years (Dillaha et al. 1989; Gharabaghi, Rudra, and Goel 2006; Lee et al. 1999; Young, Huntrods, and Anderson 1980; Zhou et al. 2010). Buffers are primarily used to intercept cropland runoff to remove nitrate-N, P, and sediment from the runoff (Gharabaghi et al. 2006; Habibiandehkordi et al. 2019; Lee et al. 1999; Patty, Real, and Gril 1997). The focus of buffers is to protect water quality. However, SOM does build under the buffer (Marquez et al. 1998), and depending on the plant species composition of the buffer, it can increase biodiversity.

A new type of riparian buffer, saturated riparian buffer, is becoming more common in the Midwest US (Chandrasoma, Christianson, and Christianson 2019). This buffer type can treat tile drainage water, whereas traditional buffers have only treated overland flow. In a saturated buffer, the tile water is diverted into shallow groundwater, allowing microbes and plants to denitrify the

N moving with subsurface water (Chandrasoma et al. 2019). Buffers are very effective, yet they only focus on water quality and marginally affect biodiversity.

1.2.3. Land Use Change

The conversion of cropland to another land cover, such as grassland, addresses many of the environmental concerns that were previously expressed. I will focus on grassland restoration as a significant land use change for this dissertation. Grassland has ~89% lower erosion rates (Turnage et al. 1997), reduced nitrate-N loss (Dodds and Kemp 2001; Thapa et al. 2018), and increased SOC concentration (De et al., 2020; Thapa et al. 2018). Grassland restoration, however, has a single flaw, it can remove large portions of land from production. As the world population grows, more and more land could be removed from grasslands and put into crop production to fulfill market demand. In other words, grasslands have many benefits but may not withstand an increasing market demand for crops. Grassland cover in large swaths of land does not facilitate environmental and economic sustainability for farmers.

1.2.4. Prairie Strips

Prairie strips (PS) are a new management practice rapidly gaining popularity in the Midwest US. PS are narrow, plantings of a diverse mixture of perennial vegetation usually >10 m in width, which can occupy < 25% of the field area (Figure 1.2). Testament to its rapid rise in popularity, PS are now implemented on 14,000 ha (www.nrem.iastate.edu/research/STRIPS), and PS has been officially entered under CRP CP-43 in the last Farm Bill from 2018 (USDA-FSA 2019).

Prairie strips function similarly to buffers and have many environmental benefits similar to converting a field to grasslands but combine unique features that differ from the two single management practices. First, PS use much more diverse plant communities with up to 50 plant species (Hirsh et al. 2013), generally composed of plants native to the Midwest US. In contrast, buffer strips and farmer-managed grassland areas are usually low-diversity plantings of quick-growing grasses like smooth brome (*Bromus inermis* L). Second, PS can be implemented at various locations within a catchment and not primarily beside a waterbody, unlike saturated riparian buffers, which are proximal to streams. Many of the benefits of PS are similar to buffer strips, though; reduced nitrate export (Schulte et al. 2017; Zhou et al. 2014), reduced P export (Schulte et al. 2017; Zhou et al. 2014), and reduced sediment export (Helmers et al. 2012; Schulte et al. 2017). Prairie strips also have additional benefits, including reduced total water runoff (Gutierrez-Lopez et al. 2014; Hernandez-Santana et al. 2013), reduced nitrate concentration in the vadose zone (Zhou et al. 2010), improving soil quality by increasing total nitrogen (TN) and SOC (Pérez-Suárez et al. 2014), and increased biodiversity (Hirsh et al. 2013; Schulte et al. 2017). However, much of the research surrounding strips is on the macro or catchment scale, and less has been conducted on the sub-catchment scale. Additionally, no studies have examined the effects of prairie strips on the adjacent cropland.

1.3. Restoring Soil Ecosystem Services and the Critical Role of Soil Biota

The USDA defines soil health as the continued capacity of soil to function as a vital living ecosystem that sustains plants, animals, and humans (USDA-NRCS 2021). This definition necessitates a broad assessment of the soil's physical, chemical, and biological aspects. Much work has already been done on prairie's effect on soil's physical attributes (Jastrow 1996; Kucharik 2007; Udawatta et al. 2008), so the following chapters primarily focus on chemical and biological aspects of soil health and restoring soil ecosystem services. In the scope of agriculture and sustaining plants, animals, and humans, these chapters focus on the retention of nutrients and nutrient cycling. Retention of nutrients not only covers the plant available nutrients that are commonly analyzed in soil fertility tests but would also include SOM, which is a reservoir and catalyst of plant-available nutrients (King et al. 2020). Retention of nutrients in agroecosystems is important for two reasons: they are needed for crop growth and the reduction of pollution. Crop growth ties into soil health by sustaining plants and animals and the farmer's livelihood, so it is focused on the farm. Reduction of pollutants is important on a larger scope that includes effects on municipalities and the hypoxic zone in the Gulf of Mexico. Reduction of pollutants would primarily focus on N, and P. Nutrient cycling focuses on the biological aspects of the soil, specifically microbial biomass and enzymes. Microbial biomass is a soil health indicator sensitive to management decisions (Maharjan et al. 2017; Rice, Moorman, and Beare 2015).

1.3.1. Importance of soil microbial biomass, nutrients, and labile SOM to soil ecosystem function

Microorganisms, or microbes, are directly involved with the decomposition of plant matter, nutrient (re)cycling, and stabilization of SOM (Falkowski, Fenchel, and Delong 2008). Through these processes, microbes are involved in nutrient cycling in two ways. First, as the microbes break down SOM, they release nutrients that are plant available (Horwáth 2017). Second, the microbe population turns over and as their cells lyse, the nutrients they contain become plant available (Rice et al. 2015; Yamashita et al. 2022). Microbial biomass is reported in these chapters as microbial biomass carbon (MBC) and microbial biomass nitrogen (MBN). Measuring C and N provides a measure of each element within microbe bodies, but also the relative supply-demand for C (or N) (Buchkowski et al., 2015; Cleveland & Liptzin, 2007; Li et al., 2020) and potential insight into the community composition too (Strickland and Rousk 2010). Both indicators are important because MBC elucidates the population size and activity and is a form of labile carbon with fast turnover in the soil (Rice et al. 2015). Similarly, MBN is a labile form of N that is plant available (Rice et al. 2015; Singh and Gupta 2018).

Microbial biomass is now commonly accepted as a predominant pathway to producing persistent SOM in many soils (Angst et al. 2021; Ding et al. 2020; Geyer et al. 2020). Microbial communities and larger soil biota process biologically available organic matter into more persistent forms (Prescott and Vesterdal 2021); this includes plant matter and microbial necromass (Angst et al. 2021). Microbial residue C is an important contributor to soil C stocks (Ding et al. 2020). One study found that microbial necromass contributed ~50% of mineral-associated organic matter in agroecosystems (Angst et al. 2021). Another study found that 40% of glucose-C added to the soil stayed in the soil for 180 days as non-biomass residue (Geyer et al. 2020).

A couple of recent global meta-analyses have linked soil microbial biomass to N retention and nitrification (Li et al., 2021; Li et al., 2020). N immobilization is the mechanism for N retention in the soil. Microbial biomass N is an important fate of immobilized N (Li et al. 2021). This is due largely to N being an essential nutrient for microbes, and microbes' ability to obtain N, including ammonium and nitrate, from the environment is relatively high (Li et al. 2021). It is unsurprising then that microbial biomass C has been identified as a pivotal driver of immobilization on a global scale (Li et al. 2021). The immobilization of N contributes to the total soil N. Subsequently, total soil N and microbial biomass N are both controlling factors for N nitrification (Li et al., 2020). The immobilized N acts as a substrate for N nitrification, and microbial biomass N stimulates the nitrification (Li et al., 2020).

1.3.2. Soil potential (extracellular) enzyme activities (PEAs) and role in soil ecosystem services

In soils, extracellular enzymes produced by plants and microbes are key to biochemical functions, including the decomposition of fresh plant materials and persistent soil organic matter (Das and Varma 2011). Enzymes are important for the decomposition of organic wastes, stabilization of organic matter, stabilization of soil structure, and nutrient cycling (Bakshi and Varma 2011; Das and Varma 2011). They are also useful biological indicators of soil health as they can indicate general microbial activity (Utobo and Tewari 2015). The enzymes reported here are arylsulphatase (ARSase), β-glucosidase (BGase), cellobiohydrolase (CBHase), Leucine aminopeptidase (LAPase), N-acetyl-β-glucosaminidase (NAGase), phosphatase (PHOSase), polyphenol oxidase (PPOase), and peroxidase (PERase) (Table 1.2).

PEAs rapidly respond to management practices and land use change (Graham, Ramos-Pezzotti, and Lehman 2021; Katsalirou et al. 2010; King and Hofmockel 2017; Luo, Meng, and Gu 2017), making them a good indicator for changes in soil health after implementing a new management practice (Ajwa, Dell, and Rice 1999; Dong et al. 2019). Management practices, such as no-till, that encourage the accumulation of SOC or SOM, total N, and microbial biomass also elevate PEA (Jian et al. 2016; Katsalirou et al. 2010; Raiesi and Salek-Gilani 2018; Sinsabaugh et al. 2008). Organic matter content affects activities of NAGase and PHOSase at a global scale but not activities for LAPase (Sinsabaugh et al. 2008). Arylsulfatase is correlated to the organic C content of soil (Deng and Tabatabai 1997; Nsabimana, Haynes, and Wallis 2004). N fertilization increases BGase and CBHase (Ajwa et al. 1999; Jian et al. 2016). NAGase and LAPase do not have a consistent response to N fiertilization (Jian et al. 2016). PHOSase activity is increased by N fertilization, which is usually ascribed to a shift from N limitation to P limitation (Ajwa et al. 1999; Dong et al. 2019; Jian et al. 2016). N fertilization reduces both PPOase and PERase (Jian et al. 2016). Land use change increases ARSase and PHOSase (Raiesi and Salek-Gilani 2018). Oxidative enzymes (PPOase and PERase) are less sensitive to management practices and tend to be primarily regulated by soil pH on a global scale (Sinsabaugh et al. 2008).

1.3.3. Crop health as the ultimate 'soil health' indicator

The final metric by which soil health is gauged is, of course, crop health and production. Some have argued that crop productivity, especially without inputs, might be the ultimate integrative measure of soil health (Chaparro et al. 2012; Janvier et al. 2007). The following chapters analyze crop health and production using a Soil Plant Analysis Development (SPAD) meter and the harvested grain. The SPAD meter estimates the chlorophyll content of the leaf and can gauge crop health in real-time (Rostami et al. 2015; Scharf, Brouder, and Hoeft 2006). The grain harvest was measured using a yield monitor on the harvester. The crop health and the yield data are pivotal measurements because they ground-truth soil health for the farmer. The crop health through the season, along with the yield at the end of the season, is the ultimate indicator of soil health for crop production. Crop health and yield are the apex indicator of the biological, chemical, and physical attributes of the soil and give the best indication of the productive health of a soil.

1.4. Ability of Prairie Strips to Restore Functionality to Agroecosystems

The implementation of prairie strips has many documented benefits (Schulte et al. 2017). However, there are still many questions left to answer. Much of the prior research was analyzing buffer strips at the edge of fields (Dillaha et al. 1989; Udawatta et al. 2002; Young et al. 1980) or prairie restoration at the field scale (Burke et al. 1995; Cullum, Locke, and Knigh 2010; Karlen et al. 1999). The research that has been performed on the implementation of PS has mainly focused on water quality and biodiversity (Schulte et al. 2017; Zhou et al. 2014). Little research has concentrated on the PS effect on soil health nor the health/productivity of cropland adjacent to the prairie strips. The following chapters' primary purpose is to determine how PS affects soil health underneath the PS and in the adjacent soil and crops. My primary research questions [and the chapters they are answered] are:

(a) Do PS affect plant-available nutrients, crop health, and crop yield of adjacent cropland (3-9 m) [CHAPTER 2]

(b) Do PS affect soil biology, chemistry, nutrient cycling, and general soil biota functioning in the adjacent soils (0.1 to 9 m)? [CHAPTER 3]

(c) If PS affects soil biology and nutrients, how long does it take for these soil health effects to accrue under and around the prairie strip? [CHAPTER 4]

Prairie strips are a new management practice and were recently added to CRP practices (USDA-FSA 2019). As the prairie strip's popularity grows, farmers and conservationists need to know what benefits to expect (Questions a-b) and how fast to expect benefits to accrue (Question c).

1.5. Approach

In pursuit of answering what benefits PS supply to farmers and conservationists, the bulk of the study will incorporate the oldest known and well-studied PS in the state of Iowa. These strips are located in the Neal Smith National Wildlife Refuge (NSNWR) and were established in 2007. These strips were 12 and 13 years old at the time of sampling. The remaining study sites used to answer question (c) [CHAPTER 4] are found in Table 3.

1.5.1 Question (a) – Do prairie strips affect plant-available nutrients, crop health, and crop yield of adjacent cropland (0.1 to 9 m)

Six catchments were selected, three with PS and three without PS. Distances from the PS are selected along transects at a logarithmic scale, extending three meters upslope from the PS to nine meters downslope from the PS. Specifically, the chosen distances are: upslope 3 m, 1 m, 30 cm, 10 cm; downslope 10 cm, 30 cm, 1 m, 3 m, 9 m. The PS distances are then paired to locations within the non-PS catchment using flow accumulation and plan curvature. The distances within the non-PS catchment are also arranged in similar transects. Composite soil cores are collected at each distance and analyzed for plant available nutrients and organic matter. Chlorophyll content was estimated using a SPAD meter along each transect, and the grain yield was monitored at the 3 and 9 m distances.

1.5.2 Question (b) – Does a prairie strip affect soil biology, chemistry, nutrient cycling, and general soil biota functioning in the adjacent soils (0.1 to 9m)?

Six catchments were selected, three with PS and three without PS. Distances from the PS are selected along transects at a logarithmic scale, extending three meters upslope from the PS to nine meters downslope from the PS. Specifically, the chosen distances are: upslope 3 m, 1 m, 30 cm, 10 cm; downslope 10 cm, 30 cm, 1 m, 3 m, 9 m. A distance (0) is also selected within the PS itself. The PS distances are then paired to locations within the non-PS catchment using flow accumulation and plan curvature. The distances within the non-PS catchment were also arranged in similar transects. Composite soil cores were collected at each distance and analyzed for microbial biomass, soil organic C, total N, and multiple enzymes targeting C, N, P, and S.

1.5.3 Question (c) – If there are indeed effects of prairie strip on soil biology and nutrients, how long does it takes for these soil health effects to accrue under and around the prairie strip?

A chronosequence was used to answer how fast benefits accrue under and around PS. Multiple private farms with PS at different ages were used. PS ages range from two years to 13 years old. On each farm, sampling distances were selected by similar topography and hillslope position. Sample distances include 3 m upslope from the PS, within the PS, 3 m downslope from the PS, and three control points. Multiple decomposition samples were placed at each sampling distance. Decomposition samples consisted of red tea, green tea, and birch sticks. Two samples were placed at each point and collected at two different time points for each material. Differentiation in the decomposition of recalcitrant substrates can indicate a nutrient limitation, such as P (Sinsabaugh et al. 1993), or indicate altered fungal community composition (Hu, Yesilonis, and Szlavecz 2021). Composite soil cores are taken at each sample location in Fall and analyzed for plant available nutrients, organic matter, microbial biomass, soil organic C, and total N.

1.6. Broader Impacts

The broader impacts of this study are comprehensive and far-reaching. Previous data show that the average yield of crops in PS catchments at the catchment scale is lower but not statistically significant (Schulte et al. 2017). The first question (Question a, CHAPTER 2) looks at the sub-catchment scale to determine if PS affects nutrient dynamics, crop health, and yield adjacent to the PS (0.1 to 9 m). This question will reveal whether PS affects crop production adjacent to the PS and allow farmers to improve nutrient management decisions near the PS accordingly. The second question (Question b) looks at the biological effects of PS on the soil under the PS and in the adjacent cropland. These findings will elucidate the PS influence on biochemical processes and help ecologists better understand cropland-grassland ecotones. The third question (Question c) will clarify for farmers and conservationists the expected timeline before PS benefits take effect and further reveal if there is an ideal length of time a PS should remain in place. This is important as soil health monitoring is increasingly gaining traction in public and private spheres, as well as with the emergence of C markets (Keenor et al. 2021).

Agricultural studies examining cropland soil ecotonal influences are scarce, especially those including grasslands. Agricultural ecotones influence soil's physical and chemical properties (Marfo et al. 2019) and microbial community composition (Guo et al. 2018). The soil pH influences microbial community composition (Högberg, Högberg, and Myrold 2007) and PEAs (Waldrop, Balser, and Firestone 2000). Implementing PS introduces two ecotones into a crop field. Thus, understanding the effects of implementing PS on soil chemistry, biology, and plant health is crucial for scientific understanding, conservational practice, and farmer management.

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Tables and Figures

Table 1.1 Three categories of conservation practices. Table adapted from Nowatzke and Benning 2020

Category of Practice	Definition of Practice	Example of Practice
In-field practices	Annual or short-term management practices	Cover crops, extended rotations, reduced and no-tillage, and fertilizer management
Edge-of-field practices	Structural practices or vegetation implemented at the edge of a farm field that prevent nitrate and/or sediment from leaving the field and entering nearby surface water or subsurface drainage	Bioreactors, saturated buffers, terraces, and nutrient removal wetlands
Land-use change	Practices that convert row crops to perennial vegetation	Conversion to pasture or prairie or perennial bioenergy crops

Table 1.2 Potential enzyme activities (PEAs) assayed in this project, their functions, and influencers.

Enzyme	EC	Abbreviation	Function	Fertilizer	Grassland Restoration
Arylsulfatase	EC 3.1.6.1	ARSase	Hydrolysis of sulfate esters	• Reduced by N fertilizer (Wang et al. 2019)	• +43% (Raiesi and Salek-Gilani 2018)
β-1,4-glucosidase	EC 3.2.1.21	BGase	Hydrolysis of cellulose	• Increased by N fertilizer (Geisseler and Scow 2014; Jian et al. 2016)	**No Consensus**
Cellobiohydrolase	EC 3.2.1.91	CBHase	Hydrolysis of cellulose	• Reduced by N fertilizer (Fan et al. 2012)	**No Consensus**
Leucyl aminopeptidase	EC 3.4.11.1	LAPase	Cleaving of peptide bonds in proteins	**No Consensus**	**No Consensus**
β-N-acetylglucosaminidase	EC 3.2.1.14	NAGase	Hydrolysis of chitooligosaccharides	• Increased by N fertilizer (Chen et al. 2018)	• Increased (Sun et al. 2022)
Acid/Alkaline Phosphatase	EC 3.1.3.1	PHOSase	Cleaving of Phosphate from P-containing organic matter	• + 24% by N fertilizer (Deng et al. 2017) • Decreased by P fertilizer (Zhang et al. 2015)	• Increased (Yang et al. 2020)
Polyphenol oxidase	EC 1.10.3.2	PPOase	Oxidize recalcitrant aromatic compounds into readily available substrates	• Reduced by N fertilizer (Jian et al. 2016)	**No Consensus**
Peroxidase	EC 1.11.1.7	PERase	Oxidize recalcitrant aromatic compounds into readily available substrates	• Reduced by N fertilizer (Jian et al. 2016)	**No Consensus**

Table 1.3 Sample site description.

Farm Abbreviation	Age of Strip	MAP	MAT	Soil Series
CLY	2	938.9561	9.839061	Nicollet
MCB	2	938.9561	9.839061	Tama
NYK	3	936.881	10.181392	Clearfield
RDM	3	1065.2932	9.067114	Lawler
STN	3	1160.2661	9.573883	Tama
SMI	4	946.2246	8.220472	Clarion
GUT	5	970.6678	9.103066	Webster
RHD	5	938.9561	9.839061	Downs
ARM	6	936.881	9.610326	Marshall
MCN	6	971.4981	9.396409	Arispe
SLO	7	959.5658	9.161046	Readlyn
RDB	8	977.3561	7.934269	Festina
NSNWR	12-13	922.5342	9.576038	Ladoga

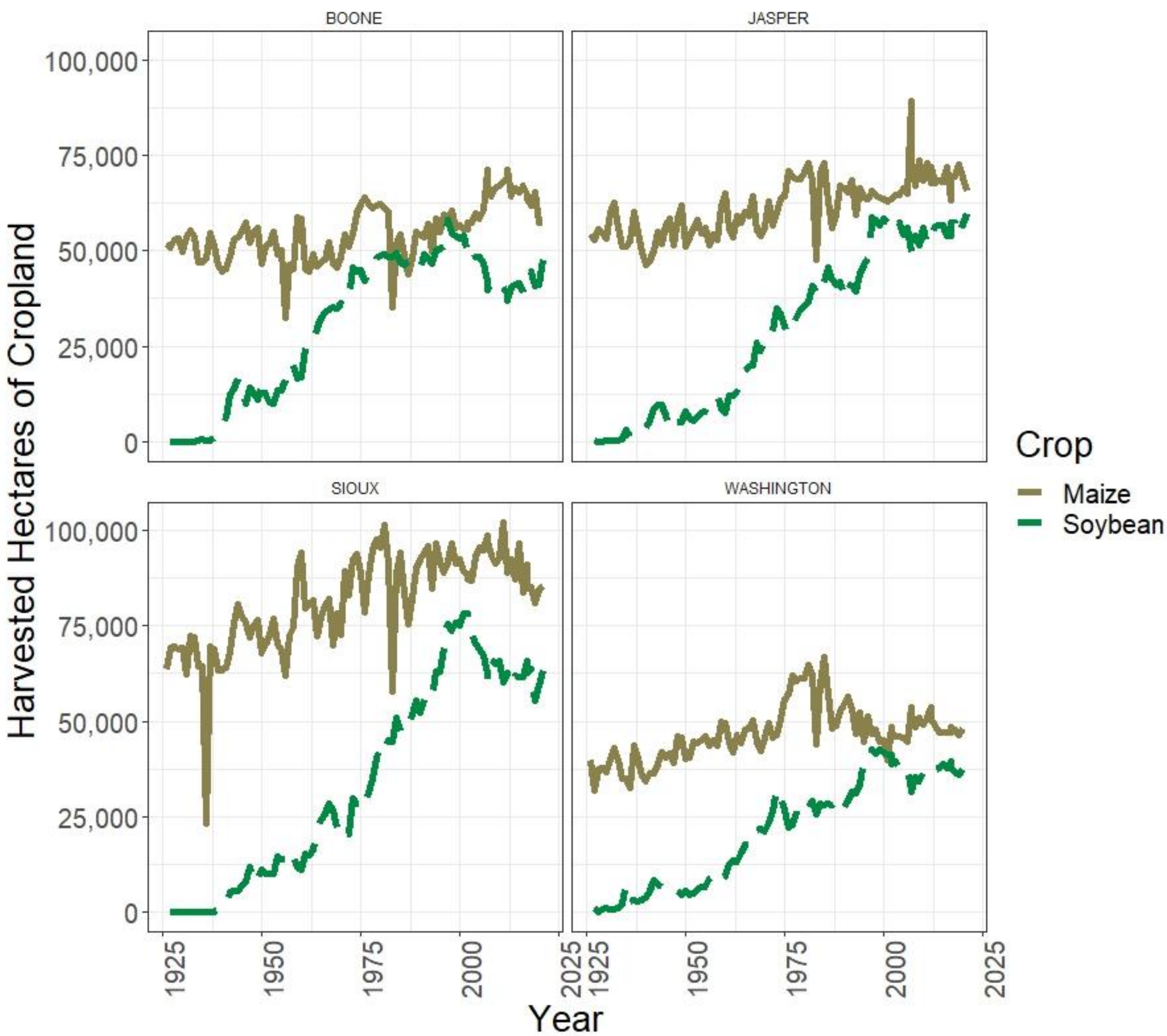

Figure 1.1 Hectares harvested of maize and soybeans in four counties of Iowa, USA. These four counties are positioned along the precipitation gradient within Iowa. Boone and Jasper are in Central Iowa, Sioux county is in northwest Iowa, and Washington is in southeast Iowa. Data from National Agriculture Statistics Service.

Figure 1.2 Overhead photograph of prairie strip planted in a soybean field near Traer, Iowa, USA. Photo was taken by Omar de Kok-Mercado.

CHAPTER 2. CONTOUR PRAIRIE STRIPS AFFECT ADJACENT SOIL BUT HAVE ONLY SLIGHT EFFECTS ON CROPS

Cole Dutter[1*], Jarad Niemi[2], Bradley Miller[1], Lisa A. Schulte[3], Matt Liebman[1], Matt Helmers[4], Rick Cruse[1], Marshall McDaniel[1]

1 Iowa State University, Department of Agronomy
2 Iowa State University, Department of Statistics
3 Iowa State University, Department of Natural Resource Ecology and Management and Bioeconomy Institute
4 Iowa State University, Department of Agriculture and Biosystems Engineering
* Corresponding author
Email: cdutter@iastate.edu
Address:
2531 Agronomy Hall
716 Farm House Lane
Ames, IA 50011
Phone: (515) 350-8286

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Abstract

Prairie strips (PS), or plantings of diverse perennial vegetation surrounded by cropland, can have disproportionate ecological benefits compared to the amount of land they occupy. These benefits include improved water quality, reduced soil movement, improved nutrient retention, and more abundant and diverse wildlife. However, the impacts of PS on the adjacent cropland soil and crop health are unknown. We assessed the effect of a 12-year-old PS on nearby soybean (*Glycine max* (L.) Merr.) and maize (*Zea mays* L.) yield, leaf greenness (via soil plant analysis development or SPAD), gravimetric soil moisture, and plant-available nutrients in adjacent soils (from 0.1 to 9 m distance from the PS). We found that PS had minimal adverse effects on grain yields. PS had a marginal benefit to soybean SPAD and decreased maize SPAD

by 7% within 1 m of the PS. PS reduced soil moisture by 6% in adjacent cropland soils (<1 m) during a wet year and had even stronger effects on plant-available nutrients. PS increased Mehlich-III phosphorus and potassium by 63 and 24%, respectively, upslope compared to downslope of the PS. PS also decreased salt-extractable nitrate by 23% within 1 m of the strip compared to further distances. Phosphorus also appeared to be related to impacts on maize SPAD. Our results show little effect on maize and soybean grain yields but stronger effects on early crop health and retention of plant-available nutrients. The crop year was a strong determinant of the PS effect on adjacent soils and crops. We need to further understand this interaction to enhance the implementation of this conservation practice.

1. Introduction

While global crop production has increased rapidly due to technological advances, yield increases have come at an environmental cost. Therefore, we must balance high productivity levels with environmental stewardship, often called 'sustainable intensification.' Taking land out of production that is either low yielding or highly vulnerable to degradation is one path toward reconciling these economical, agronomic, and environmental goals. However, taking potentially productive land out of production may be an overcorrection. Can we achieve environmental goals while also maintaining or even increasing crop productivity?

Within the United States of America (USA), growers can choose to remove land from production and put it into Conservation Reserve Program (CRP) to address soil erosion, water quality, or other environmental issues (McGranahan et al. 2013; Skold, 1989). In the U.S.A., 8.4 million ha were enrolled in a CRP program in 2020 (USDA-FSA, 2020). In Iowa, USA. In 2017, the average conservation easement was 35 ha per farm (USDA, 2021). Additionally, when cropland is converted to CRP, however, it is intended to be out of production for ten or more years, and thus lowers the local crop production potential.

An alternate to this dichotomous choice of producing crops or land retirement is implementing prairie strips (PS) within croplands. PS are narrow, plantings of a diverse mixture of perennial vegetation usually >10 m in width, which can occupy < 25% of the field area (Figure 1). Contour PS are positioned perpendicular to the dominant slope of a catchment to slow overland water flow and minimize sediment and nutrient losses from fields. They can add alternate sources of income through leasing land to beekeepers (Dolezal et al., 2019), the potential for renewable natural gas production (Schulte et al., 2021), and emerging C markets (Keenor et al., 2021). While they are a new practice, PS are rapidly gaining popularity in the Midwestern USA, with up to 5,000 ha of PS protecting over 56,000 ha of cropped catchments (Iowa State University, 2021). Prairie strips offer the ability to maintain crop production while regenerating soil health and mitigating the environmental consequences of annual cropping systems and are now offered as a practice within CRP (USDA-FSA, 2019).

Prairie strips provide 'disproportionate benefits' in terms of environmental quality. At the catchment scale, converting 10% of the cropland area to PS can reduce nitrate export by 38-84% (Schulte et al., 2017; Zhou et al., 2014), reduce phosphorus export by 77-90% (Schulte et al., 2017; Zhou et al., 2014), and reduce sediment export by 95% (Helmers et al., 2012; Schulte et al., 2017). Prairie strips have additional benefits, including reduced total water runoff (Gutierrez-Lopez et al., 2014; Hernandez-Santana et al., 2013), reduced nitrate concentration in the vadose zone (Zhou et al., 2010), and improved soil quality under the PS (Pérez-Suárez et al., 2014).

The in-field soil and crop health effects of PS remain unknown, specifically those related to crop health and productivity. At the catchment level, previous research showed PS slightly but insignificantly lowered maize yield (8.9 vs. 7.9 Mg ha^{-1}) and soybean yields (3.6 vs. 3.3 Mg ha^{-1}) after accounting for the 10% of land taken out of production for the PS compared to control catchments (Schulte et al., 2017). Averaging crop yields across catchments, however, as done in this previous study, may obscure the proximal effects of PS on crop production. This topic warrants further exploration.

There are several pathways whereby PS might negatively (or even positively) affect nearby crops. First, there could be microclimate effects of the perennial vegetation on airflow, temperature, shading seedlings, and relative humidity (M. Schmidt et al., 2019). Second, PS may be a source of ‘weeds’ that migrate outward from the prairie strip and compete with crops for resources, although some research shows this is not a significant factor with PS (Hirsh et al., 2013). Third, PS could be a refuge and habitat for insect pests of crops, but research has not borne this out (Fiedler & Landis, 2007). Instead, a recent study showed that spider abundance, butterfly abundance, and pollination services increased with the presence of PS (Kemmerling et al., 2022). Fourth, PS could affect the local water balance and perhaps even soil moisture under the adjacent crop (Anderson et al., 2009), but this has not been confirmed in PS. Fifth, the PS could compete with adjacent crops for nutrients, but this is likely weather-dependent (Banik et al., 2020), and this too has not yet been tested in PS. Lastly, PS may positively or negatively alter adjacent crops and soils through mechanism(s) of which we are unaware.

Our two primary objectives were to quantify the PS effect on 1) crop health assessed via measurements of leaf greenness and grain yield and 2) soil water and nutrient availability in adjacent cropland (< 9 m). Our null hypothesis is that PS will have no effect on crops or adjacent soils since there is no evidence otherwise (Schulte et al., 2017). If we rejected the null hypothesis for crops and soils, a secondary objective was determining what soil properties drive PS effects on crops.

2. Materials and Methods

2.1. Site description & experimental design

The study occurred on the Neal Smith National Wildlife Refuge (NSNWR 41° 33' N;93°16' W), a 3000-ha area managed by the U.S. National Fish and Wildlife Service. The NSNWR is located within the Walnut Creek catchment of Jasper County, Iowa. Some areas of this complex await prairie restoration and are leased to area farmers for crop production. The site is located on the Southern Iowa Drift Plain (Major Land Resource Area 108C; USDA Natural Resources Conservation Service, 2006). This area consists of steep rolling hills of Wisconsinan loess on pre-Illinoian till (Prior, 1991). Most of the research sites are mapped as Ladoga (Fine, smectitic, mesic Mollic Hapludalf) or Otley (Fine, smectitic, mesic Oxyaquic Argiudolls) soil series with 5 to 14% slopes and are highly erodible (Nestrud & Worster, 1979; Soil Survey Staff, 2003). The 50-year mean annual precipitation (MAP) plus/minus standard error is 876 ± 205 mm, and the mean annual temperature (MAT) is 9.6 ± 0.9 ℃.

In 2007, a catchment scale PS experiment was established within NSNWR. Before 2007 these fields were in perennial grassland cover dominated by smooth brome (*Bromus inermis* L.) cover for at least ten years. Prairie strips were established in a randomized, balanced, incomplete block design on 12 catchments in four blocks ranging in size from 0.47 to 3.2 ha. PS occupied 0, 10, and 20% of the catchments and were situated within the cropland (shoulder/backslope) and at the foot slope (Zhou et al., 2010). During the establishment phase, the prairies were mowed periodically for two years. Since establishment, the cropland adjacent to each PS was planted in alternate years with soybean at 38 cm row spacings and maize at 91 cm row spacings. Before soybean in 2019, no fertilizer was added to the catchments. Before maize in 2020, catchments were fertilized with 211 kg N ha^{-1}, 311 kg P_2O_5 ha^{-1}, and 224 kg K_2O ha^{-1}.

For this study, we selected two treatments out of all the catchments for comparison. We selected the 10% PS catchments as our treatment of interest because previous research showed that 10% of a field with PS was enough to observe disproportional environmental benefits (Schulte et al. 2017). We also chose the catchments with 0% PS, hereafter referred to as '*control'* (Figure S2.1). Three transects, 34 - 80 m apart, perpendicularly bisecting PS (including control '*strip'* locations) in all catchments, were chosen based on a digital map of a 3x3 m^2 digital elevation model (DEM), plan curvature (r.param.scale with analysis window of 69 m; GRASS GIS 7.8, GRASS Development Team 2021; Miller 2014; Chapter 2) and flow accumulation (D_∞, ArcGIS Pro v 2.2 ESRI Redlands, CA). The DEM was derived from LiDAR (Light Detection and Ranging) elevation data collected by the Iowa Department of Natural Resources (IDNR; available at http://www.geotree.uni.edu/lidar). At each transect location, we sampled at distances 0.1, 0.3, 1, 3 m upslope and 0.1, 0.3, 1, 3, 9 m downslope perpendicularly of the PS and paired control 'strip of cropland' (Figure S2.1). Transects and sampling distances were marked using the Arrow 100 ®GNSS receiver.

2.2. Crop yield measurements from 2007 to 2020

Grain yields were measured using a continuous yield monitor on a 7120 Case IH combine, which records the geo-position and numerous grain attributes at a fixed time step. Due to the width of the combine, grain yields were integrated over polygons centered on points 3 m upslope, 3 m downslope, and 9 m downslope of the PS (Figure S2.2). For each location and year, the three nearest neighbors were selected based on the recorded GPS coordinate, and their grain yield was averaged to estimate the point mean yield (Figure S2.2).

2.3. SPAD and soil sampling/analyses in 2019 and 2020

Soil sampling and soil plant analysis and development (SPAD) readings co-occurred at all sampling distances mentioned above (9 distances from strips × 3 transects × 3 catchments × 2 treatments) in soybean and maize. SPAD readings were performed with a Minolta SPAD-502 plus meter. SPAD provides a general measurement of crop health as approximated by greenness which is correlated with chlorophyll concentration (Markwell et al., 1995). In maize, it is frequently used to determine the degree of N-limitation (Rostami et al., 2015; J. Schmidt et al., 2011). SPAD readings were averaged from 10 plants at each sampling distance for each transect in a catchment. SPAD measurements were performed on both crops. Soybean measurements occurred as the plant was in bloom and pods started to form (R2/R3 stage; July 22, 2019; Licht 2014). Maize measurements occurred as ear shoots became visible before tassel emergence (V10 stage; July 12, 2020; Nleya and Kleinjan 2019).

We collected composited soil samples, 10 × 0-15 cm cores, from each sample distance taken perpendicular to the PS with a 2-cm diameter probe. Soil samples were collected on July 1st in both years of sampling. Composite samples were sieved to <2 mm and subdivided for analysis. About 15 g was weighed and dried at 105°C for 24 h to determine gravimetric water content (GWC). A 5 g amount of soil was extracted with 25 ml of 0.5 M K_2SO_4, and extracts were measured for ammonium-N and nitrate-N using a Synergy HTX Multi-Mode Microplate Reader (BioTek Instruments, Winooski, VT, USA) with Gen5 software. The remaining soil was dried and sent to a commercial lab for additional analyses.

Dried soils were analyzed for plant-available nutrients. Soil test phosphorus, hereafter referred to as phosphorus (P), was extracted with 2 g per 20 ml of Mehlich III extract and analyzed on an ICP-OES 7300 Machine (Perkin Elmer, Waltham, MA, USA). Potassium (K), calcium (Ca), and magnesium (Mg) were also extracted using a Mehlich III extraction, 2 g soil to 20 ml extractant, and were read on an ICP-OES 7300 Machine (Perkin Elmer, Waltham, MA, USA). Sulfur was extracted with a monocalcium phosphate extraction, 10 g soil to 25 ml of extractant, and read on an ICP-OES 7300 Machine (Perkin Elmer, Waltham, MA, USA). Zinc was measured using a diethylenetriaminepentaacetic acid extraction, 10 g soil to 20 ml extractant, and read using an ICP-OES 7300 (Perkin Elmer, Waltham, MA, USA). Soil organic matter (SOM) was measured using loss on ignition for 2 hours at 360°C using a Blue M oven and TSI weighing system.

2.4. Data handling and statistical analysis:

The collected data were analyzed via a linear mixed effect model. That model used the following response variables on a log scale: SPAD meter readings, gravimetric water content, nitrate-N, phosphorus, potassium, calcium, magnesium, sulfur, zinc, soil organic matter, water holding capacity, soil pH, cation exchange capacity. The fixed effects were treatment (control vs. PS), distance (a 9-level categorical variable) from PS, and treatment × distance interaction. The random effects were catchment (six levels) and transect within the catchment (3 per catchment). The contrast coefficients and estimated effects are reported in Table S2.1. The global contrast (Prairie Strip vs. Control) estimates the ratio for PS over control mean response averaged over distance and catchment-transect, i.e., $r_1 = y_{PS}/y_{CT}$ where the numerator and the denominator are the median response for an observation in a PS catchment and a paired control catchment, respectively. Values near one indicate that PS had little effect on the median of the response variable.

Noting that all catchments were defined along a slope, consider $d_{A-B} = y_A - y_B$ the difference in response variables between observations located upslope (upslope distances of -3, -1, -0.3, -0.1, m) and downslope (downslope distances of 0.1, 0.3, 1, 3 m) the PS. This 'Upslope vs. Downslope contrast estimates the ratio for such differences in a treatment catchment over a control, i.e., $r_2 = d_{A-B,PS}/d_{A-B,CT}$ where the numerator and the denominator were the mean upslope-minus-downslope difference for an observation in a PS catchment and a control catchment. Values near one imply that PS had little effect on the response variable across the slope.

Consider d_{N-F} the difference in the response variable between observations located near (distances ≤ 0.3 m) and far (distance ≥ 1 m) from the PS. This 'Near vs. Far' contrast estimates the ratio for differences in PS catchment over control, i.e., $r_3 = d_{N-F,PS}/d_{N-F,CT}$, where the numerator and the denominator are the mean near-minus-far difference for an observation in the PS and control catchment. Values near one imply that prairie strips had little effect on the response variable over proximity. Note that the 'Upslope vs. Downslope' and 'Near vs. Far' contrasts exclude the coefficients at 9 m, to keep the contrasted groups balanced.

All dynamic variables (plant-available nutrients, soil water content, yield, SPAD) were analyzed separately within years, i.e., the model was fit independently for a given response and year. The year variable was confounded with crop type (soybean vs. maize), land management decisions (no N fertilizer vs. N fertilizer applied), and weather conditions in 2019 and 2020. The exceptions were three static soil variables (pH, organic matter, and CEC), which were analyzed across years because these factors were not expected to change in one year. Thus, an additional fixed effect term (year) was added. The unknowns are estimated via residual maximum likelihood (REML) using the software defaults in lme4 (Bates et al., 2015) and emmeans (Lenth, 2021) packages in the statistical software R (R Core Team, 2020).

Random forest analysis was performed with R Statistical Software (R Core Team, 2020) and the randomForest package (Liaw & Wiener, 2002). The goal was to explain which soil or management variables affected crop SPAD and yield, so these both were set as the target response variables. The explanatory variables included all continuous soil properties (e.g., median particle size, pH, SOM, plant-available nutrients) and categorical management and site variables (e.g., catchment, treatment, distance, and transect). Random forest analyses were performed on each year's data separately to explain maize and soybean SPAD meter readings separately. The data were analyzed for collinearity, and secondary variables with high collinearity were removed from the data set. Each forest was grown to 500 trees, and eight variables were randomly used at each split.

3. Results

3.1. Environmental conditions for intensive sampling during 2019 and 2020

The weather in 2019, when the cropland was under soybean, was anomalous compared to the historical climate (Figure S2.6). The spring was unusually cold, and there was nearly 206 mm of precipitation in May, the wettest month of 2019 and the fifth greatest amount during the 50-year record. In 2020, during maize, the late spring was somewhat cooler, but precipitation was not as extreme leading up to SPAD and soil sampling in July.

The PS affected soil moisture, measured as GWC, but soil moisture strongly depended on the cropping year (Figure 2.3). In 2019, PS decreased GWC by 8.5% across the catchments (Figure 2.3). The PS also reduced GWC downslope and nearby the PS by 6% (Table 2.2). Under maize in 2020, however, the PS did not affect GWC (Tables 2.2 & 2.3, Figure 2.3).

3.2. Prairie strip effect on crop yields from 2007 to 2020

Prairie strips had little-to-no effect on adjacent soybean yields between 2007 and 2019 (Table 2.1; Figure 2.2, S2.3). Across this timespan and over all six catchments, soybean yields had a mean of 3.22 and 3.54 Mg ha^{-1} for PS and control catchments, respectively, but the yield was highly variable within and across catchments (Table S2.2; Figure S2.3). This compares to the Jasper County, Iowa, mean soybean yield of 3.64 Mg ha^{-1} during this same time period. There was a marginally significant Treatment×Distance×Year interaction ($p=0.063$; Figure S2.3), and in a pairwise comparison, the soybean yield was, on average, 2.2 Mg ha^{-1} less under PS than compared to the control in 2009 and 2011 ($p<0.073$).

Prairie strips also had little effect on maize yields between 2008 and 2020 (Table 2.1, Figure 2.2; S2.3). Within that time, across all six catchments, maize yields had a mean of 8.55 Mg ha^{-1} and 9.29 Mg ha^{-1} for PS and control catchments, respectively. The Jasper County maize yield mean for the same time period was 11.3 Mg ha^{-1}. Like soybean, there was a marginal Treatment×Distance×Year interaction ($p=0.088$; Figure S2.3), and pairwise comparisons showed significant differences between treatments at 3 m downslope in 2010 and 3 m upslope in 2012 ($p<0.087$).

Further exploration into the year by catchment-specific crop yields did not illuminate the complex interactions we found between PS treatments, distance, and year. However, one control catchment seemed to strongly out-perform its PS counterpart in soybean and maize yield in 2011 and 2012 (Figure S2.3, S2.4). The 2011 and 2012 growing seasons were dry, especially in 2012, with only 594 mm precipitation compared to the 30-year MAP of 850 mm. A response ratio of yield to the PS treatment shows a decline in crop yields during these years, but yields recovered after that (Figure S2.5). A post hoc power analysis revealed that 34 to 52 samples were needed to achieve a $\beta \geq 0.8$, and our study analyzed 27 grain yield samples per year (Table S2.3).

3.3. Prairie strip effect on greenness via SPAD meter in 2019 and 2020

Prairie strips affected both soybean and maize SPAD readings in July when soybeans were at R2/R3 and maize was at V10 growth stages (Table 2.2 & 2.3, Figure 2.3; See Table S2.4 for all Confidence Intervals). In both years, we observed interactive effects of PS and distance on SPAD (Table S2.5), and the PS effects were strongest in maize (Tables 2.2 & S2.4, Figure 2.3).

Across both PS and control catchments, soybean SPAD readings ranged from 36.1 to 45.9, with a mean of 41.2. There was a significant PS interaction with distance (Table S2.5). More specifically, the PS effect was isolated to the downslope of the perennial vegetation, and PS increased SPAD by 3% on average across all distances (Table 2.2, Figure 2.3).

Across both treatments, maize SPAD readings ranged from 37.4 to 65.7, with an average of 58.4. There was a significant PS interaction with distance (Table S2.5). The PS effect on maize SPAD was isolated to < 1 m from the PS and primarily downslope from the PS (Figure 2.3). Prairie strips reduced maize SPAD by 5% compared to the control, reduced readings by 6% downslope from the PS compared to upslope from the PS, and reduced the readings by 7% near the strip compared to farther from the strip (Table 2.2).

3.4. Prairie strip effect on soils in 2019 and 2020

Twelve to thirteen years of prairie strips had little to no effect on adjacent static soil properties or those soil properties that change over two or more years (Figure 2.5). For example, we observed no statistically significant effect of PS on soil pH (ranging from 5.08 to 6.8). In addition, we found no statistically significant effect of PS on CEC in the adjacent cropland soils, which ranged from 13.9 to 27.9 meq 100 g^{-1} across all catchments (Table S2.7).

PS had marginal effects on soil nitrate in 2019 but not 2020 (Table S2.5, Figure 2.6). Nitrate was greater in both treatments under maize, likely due to the spring application of anhydrous ammonia. There was no significant difference among treatments (8.6 ± 10.6 vs. 11.8 ± 13 mg kg^{-1} in the PS vs. control catchments). PS decreased soil nitrate in soybeans by 25% compared to control, or 5.5 ± 1.8 versus 7.1 ± 2.1 mg kg^{-1} (Table 2.2). PS reduced soil nitrate for the soybean crop near the strip by 23% compared to farther away from the strip within the same treatment catchments in 2019 (Table 2.2; Figure 2.6).

PS had complex effects on plant-available, Mehlich-III extractable phosphorus (P, Figure 2.6). Both crops had significant PS interactions with distance (Table S2.5). PS increased P availability upslope from the PS versus downslope from the PS by 63% in soybean and 64% in maize (Table 2.2, Figure 2.6).

PS also had complex effects on plant-available, Mehlich-III extractable potassium (K, Figure 6). There was an overall increase from 2019 to 2020, presumably due to K fertilization. PS significantly affected K upslope from the PS in 2019 and 2020 (Table S2.5). PS increased soil K by 8% and 24% upslope versus downslope from the PS in soybean and maize, respectively (Table 2.2, Figure 2.6).

The PS had marginal effects on other primary soil macronutrients and micronutrients within the catchment – mostly increasing the plant-availability upslope versus downslope the PS. For example, PS increased plant-available calcium in soybeans by 4% upslope from the PS compared to downslope from the PS (Tables 2.2 & S2.4; Figure 2.6). PS also increased magnesium availability in the soybean year by 10% upslope compared to downslope from the PS (Tables 2.2 & 2.3; Figure 2.6). Prairie strips decreased sulfur availability in the soybean year by 8% near the PS compared to further away from the PS (Table 2.2; Figure 2.6). Prairie strips increased zinc availability in both crop years upslope from the PS by 28% compared to downslope (Table 2.2; Figure 2.6).

3.5. Relationship between prairie strip effects on soil and crops

Random forest regressions between soil and crop variables do not provide cause and effect but rather offer insights into any observed mechanisms underlying PS effects. Since we did not find any PS effects on crop yields during 2019 and 2020, we only focused on random forest analysis with SPAD readings. The random forest analyses explained 28% of the variation for soybean SPAD and 11% for maize SPAD. Soybean SPAD was best explained by catchment, indicating that, despite sampling multiple soil parameters, there was still an inherent property or properties of the catchments that were not captured. Catchments had a 1.2% mean squared error (MSE) increase and a node purity of 54. Node purity indicates how accurately each variable node splits the data. The other important parameters were treatment with a 0.48% increase of the MSE and a node purity of 16 and fine clay content, with a 0.26% increase of the MSE and a node purity of 44. Maize SPAD was best explained by P with a 2.4 % increase of the MSE and node purity of 225, treatment with a 1.8% increase in the MSE and a node purity of 65, and soil nitrate with a 1.3% increase in the MSE and a node purity of 313. Overall, soybean SPAD was better related to unmeasured soil properties of the catchments, and maize SPAD was related to primary, plant-available macronutrients (Table S2.8).

4. Discussion:

4.1. Prairie strips had minor effects on crop yield

We showed that PS had minor effects on crop yields –four out of 36 distances over 12 years with lower yields in PS than controls. These isolated incidents were 29 to 58 % lower at each location (Figures 2.2). The generalized lack of effect corresponds to, and confirms, catchment-level crop yields reported earlier in this longer-term experiment by Schulte et al. (2017). However, the power of our analysis was low (~0.58), and more samples are needed (Table S2.3).

Row crop yields can be very sensitive to nearby vegetation, but there seem to be negligible effects for PS. Previous studies had shown that maize yields increased when strip-cropped with soybeans, and soybean yields decreased when planted next to maize (Francis et al. 1986; Ghaffarzadeh et al. 1994). Ghaffarzadeh et al. (1994) found that the yield benefit to maize was moisture dependent. Many other studies have shown that perennial vegetation can affect nearby soybean and maize physiology or yields (Banik et al., 2020; Rivest & Vézina, 2015;

Senaviratne et al., 2012; Udawatta et al., 2016). Speculation concerning this sensitivity includes competition for water (Rivest & Vézina, 2015; Senaviratne et al., 2012) and nitrate (Banik et al., 2020; Zhou et al., 2010). In our study, the PS affected both water and nitrate, yet there was no concomitant effect on yield.

4.2. The prairie strips effect on early crop health, i.e. greenness, is complex

Prairie strips had divergent and complex effects on maize and soybean SPAD (Tables 2.2 & S2.4, Figure 2.3). These effects differed by crop year (Figure 2.3). First, PS increased soybean SPAD by 3% downslope from the PS compared to upslope (Figure 2.3). Second, PS decreased maize SPAD by 5-7% compared to the control catchment (Table 2.2, Figure 2.3). The simplest explanation for this is decreased nitrate-N due to competing prairie plants since maize SPAD is so strongly related to nitrate-N in previous studies (Ma et al., 2005; Tremblay et al., 2010). Indeed, many studies find a so-called "edge effect" on maize SPAD that, like our study, did not manifest in a yield penalty (Banik et al., 2020; Senaviratne et al., 2012). Researchers in Iowa found intercropped perennial red fescue insignificantly decreased SPAD, delayed maize development in some sites and years, reduced plant-available N, and lowered yield (Banik et al., 2020; Bartel et al., 2017). Similarly, contour grass strips and agroforestry strips have shown the ability to reduce grain yield by 15-49% (Senaviratne et al., 2012).

Despite PS significant effect on crop health early in the season, both maize and soybean plants were able to compensate such that there was no difference in end-of-season grain yield. SPAD readings are often used as a general indicator of crop health or stress (Tremblay et al., 2010; Vollmann et al., 2011). With regard to maize, several studies have reported strong relationships between SPAD and crop yield (Ma et al., 2005; Scharf et al., 2006). We did not find a strong relationship between maize SPAD and yield (r = 0.35, unpublished data), and this may be due to a disconnect between our fine-scale SPAD measurements (<1 m) and yield monitor data resolution (3-7 m). In contrast, most published studies take SPAD readings from a randomized, replicated block with large plots and can more easily compare SPAD and yield. Regardless, the impact of PS on SPAD was incongruent with the lack of effect on crop yield. This highlights the coarse resolution of crop yield from combines and the importance of looking at more plant-scale measurements of productivity and health.

In an attempt to explore mechanisms driving the PS effect on SPAD, and hypothesis generation, we used machine learning via *Random Forest* package in R (Breiman, 2001; Liaw & Wiener, 2002). Random forest did not explain a substantial portion of SPAD variation – only explaining 28% for soybean and 11% for maize. In maize, the random forest showed that P, treatment, and nitrate were the largest drivers of the SPAD readings (Table S2.8). In 2020, despite fertilization, P was insignificantly reduced downslope near the PS (<1 m; Figure 2.6). This reduction in P coincides with the reduction in the SPAD meter. If the overland flow is filtered by the PS and re-enters the cropland with a minimal nutrient load, this could cause desorption of nutrients, such as P, from the soil until equilibrium has been reached. Research has related limited nitrate uptake under P limitation (De Magalhães et al., 1998; Jeschke et al., 1997; Pilbeam et al., 1993). This interaction could cause a reduction in SPAD reading in maize even after P fertilization. The lack of significance in grain yields could be explained by the maize plants compensating for the P limitation (Jeschke et al., 1997; Pilbeam et al., 1993).

4.3. Prairie strips affect the adjacent soils

Twelve to thirteen years of PS did not significantly affect adjacent, static soil properties (Figure 2.5). We define static soil properties as those that change on three or more-year time scales – like soil pH, CEC, WHC, and SOM. Proper management, including soil testing, of any field, regardless of whether a PS exists, can optimize soil pH for crop productivity and other ecosystem services. Lime is added to all fields on a 3-4 year basis based on soil test results. It is not surprising that PS had little-to-no effect on these static soil properties, especially CEC and SOM, since these variables are slow to change in this region even when under more direct and drastic changes in management, e.g., converting cropland to grassland (De et al., 2020; McLauchlan et al., 2006; Ye & Hall, 2020). It is interesting, however, that SOM was somewhat consistently lower (3.2 vs. 3.0 %) in the soils adjacent to a PS compared to control. This is currently unexplainable but may be a natural variation in catchments. Alternatively, this could be due to the PS effect on soil water or nutrient dynamics since soil water and nutrients regulate both inputs (e.g., crop growth and residues) and outputs (e.g., mineralization rates) to SOM (Mahal et al., 2019; Stanford & Epstein, 1974). Or some other mechanisms we are unaware of here, like soil carbon priming from the C-rich PS soils (Kuzyakov, 2010; Kuzyakov et al., 2000). The PS themselves had 0.31% greater SOM than adjacent soils (data not shown), but whether this is a real effect of PS on adjacent SOM needs further exploration.

Prairie strips strongly affected more dynamic soil properties like soil moisture (Figure 2.3) and plant-available nutrients (Figure 2.6). Prior studies have shown that PS decrease surface runoff by 37% over three years (Hernandez-Santana et al., 2013; Schulte et al., 2017), which is in line with other strip vegetation. For example, agroforestry strips and grass contour strips reduced runoff by 1% and 10% (Udawatta et al., 2002); narrow grass strips also reduced total runoff by 22-52% (Gilley et al., 2000). PS can reduce soil moisture content at shallow soil depths, likely due to increased evapotranspiration, especially in the early growing season (Gutierrez-Lopez et al., 2014; Zhang & Schilling, 2006). Here we documented the PS can reduce soil moisture by 6% in 2019 when cropland was under soybean and when the early growing season was especially wet, but this effect was absent the following year under maize (Figure 2.3).

The influence of strips of perennial vegetation – whether PS, grassed waterways, or vegetation on terraces – on sub-catchment plant-available nutrients has been seldom studied. At the catchment scale, buffers with restored prairie have been shown to reduce nitrate loss by 26%-100% (Patty et al., 1997; Udawatta et al., 2002). A previous study at our site found that PS decreased nitrate concentration in the vadose zone and shallow groundwater by 73% and 88%, respectively (Zhou et al., 2010). This aligns with our findings of decreased, salt-extractable (plant-available) nitrate in 0-15 cm depth across a wide swath around the prairie strip in both years, with the effect being most prominent < 1 m adjacent to the PS and under soybean (Table 2.2, Figure 2.6). The PS effect on plant-available sulfur (i.e., sulfate) further supports the notion that PS can reduce mobile, plant-available nutrients in soybean (Table 2.2, Figure 2.6). This effect of PS on mobile, plant-available nutrients may have been exacerbated by the PS-induced decrease in soil water content (Figure 2.3).

Strips of perennial vegetation have been studied at a catchment scale regarding less mobile nutrients, especially P losses. For example, agroforestry and grass buffer contour strips have been shown to reduce P export from catchments by 8-89% (Patty et al., 1997; Udawatta et al., 2002). This effect is likely due to the perennial vegetation reducing P-laden sediment export (Syversen et al., 2001; Syversen & Borch, 2005). Our study did not measure sedimentation behind the PS but did find a buildup of P behind the strip that could be attributed to sedimentation (Figure 2.6; Zhou et al., 2014). At the sub-catchment scale, we found strong evidence across both years that PS accumulated plant-available P < 1 m upslope by 63-64% compared to a control (Table 2.2, Figure 2.6). This is additional evidence that PS performs its agroecological function of slowing sediment and P export. We expected K to behave similarly to P since it is a cation and less mobile in soils than anionic nutrients like nitrate-N and sulfate-S.

Indeed, PS also increased in plant-available K < 3 m upslope compared to control, but to a lesser degree, only 8% to 24% for 2019 and 2020, respectively (Table 2.2, Figure 2.6).

Prairie strips had a weak effect on secondary macronutrients, e.g., Ca or Mg, but did have a stronger effect on the plant-available micronutrient, Zn. The PS effect on Zn, especially under maize (Figure 2.6), appeared similar to P and K, supporting the idea that PS slowed sediment flow with surface runoff.

5. Conclusion:

We found that PS had little effect on maize and soybean grain yields but did have stronger effects (both positive and negative) on early crop health as represented by leaf greenness and assessed by a SPAD meter. This was accompanied by strong PS effects on soil moisture and plant-available nutrients in the adjacent cropland soils (especially nitrate, phosphorus, potassium, and zinc). Overall, PS effects on crops were minor, limited to early growth stages, and decreased yield only at particular distances for four of twelve years (Figures 2.2). Since the PS effects on adjacent cropland soils (>9 m away) were more apparent further research is warranted, especially on soil carbon and nitrogen pools and microbial activity. This seems all the more important considering our surprising findings that, over the long-term, PS might decrease the adjacent soil organic matter (Figure 2.5).

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Tables and Figures

Table 2.1 Analysis of variance for 2019-2020 crop yields.

		Soybean 2019		Maize 2020	
Effect	**Df**	**F-statistic**	**p-value**	**F-statistic**	**p-value**
Treatment	1	0.87	0.404	0.41	0.559
Distance	2	2.50	0.084	11.62	**<0.001**
Year	5	11.65	**<0.001**	7.59	**<0.001**
Treatment:Distance	2	3.62	**0.028**	0.42	0.655
Treatment:Year	5	1.11	0.353	1.17	0.326
Distance:Year	10	0.91	0.522	1.26	0.254
Treatment:Distance:Year	10	1.78	0.063	1.67	0.088

Table 2.2 Prairie strip effect on crop SPAD and soil metrics expressed as relative effect size†

Year	Crop or Soil Variable	Prairie Strip vs. Control	Upslope vs. Downslope	Near vs. far
2019	Soybean SPAD		**(-) 3%**	
	Gravimetric Water Content		**(+) 6%**	**(-) 6%**
	Nitrate	(-) 25%		**(-) 23%**
	Phosphorus		**(+) 63%**	
	Potassium		**(+) 8%**	
	Calcium		(+) 4%	
	Magnesium		(+) 10%	
	Sulfur			(-) 8%
	Zinc		(+) 28%	
2020	Maize SPAD	**(-) 5%**	**(-) 6%**	**(-) 7%**
	Gravimetric Water Content			
	Nitrate			
	Phosphorus		**(+) 64%**	
	Potassium		**(+) 24%**	
	Calcium			
	Magnesium			
	Sulfur			
	Zinc		(+) 28%	

† All values are significant (<0.1), and bolded values (<0.05) respectively indicate significance in 90% confidence intervals (CI), and bold indicates significance at 95% CI. CIs are shown in Table S3.

Figure 2.1 Prairie strips in practice. A) Overhead photograph of a prairie strip near Traer, Iowa, USA, at the catchment scale. B) Close-up photograph showing strip with diverse prairie species planted in between rows of soybeans. Photos were taken by Omar de Kok Mercado.

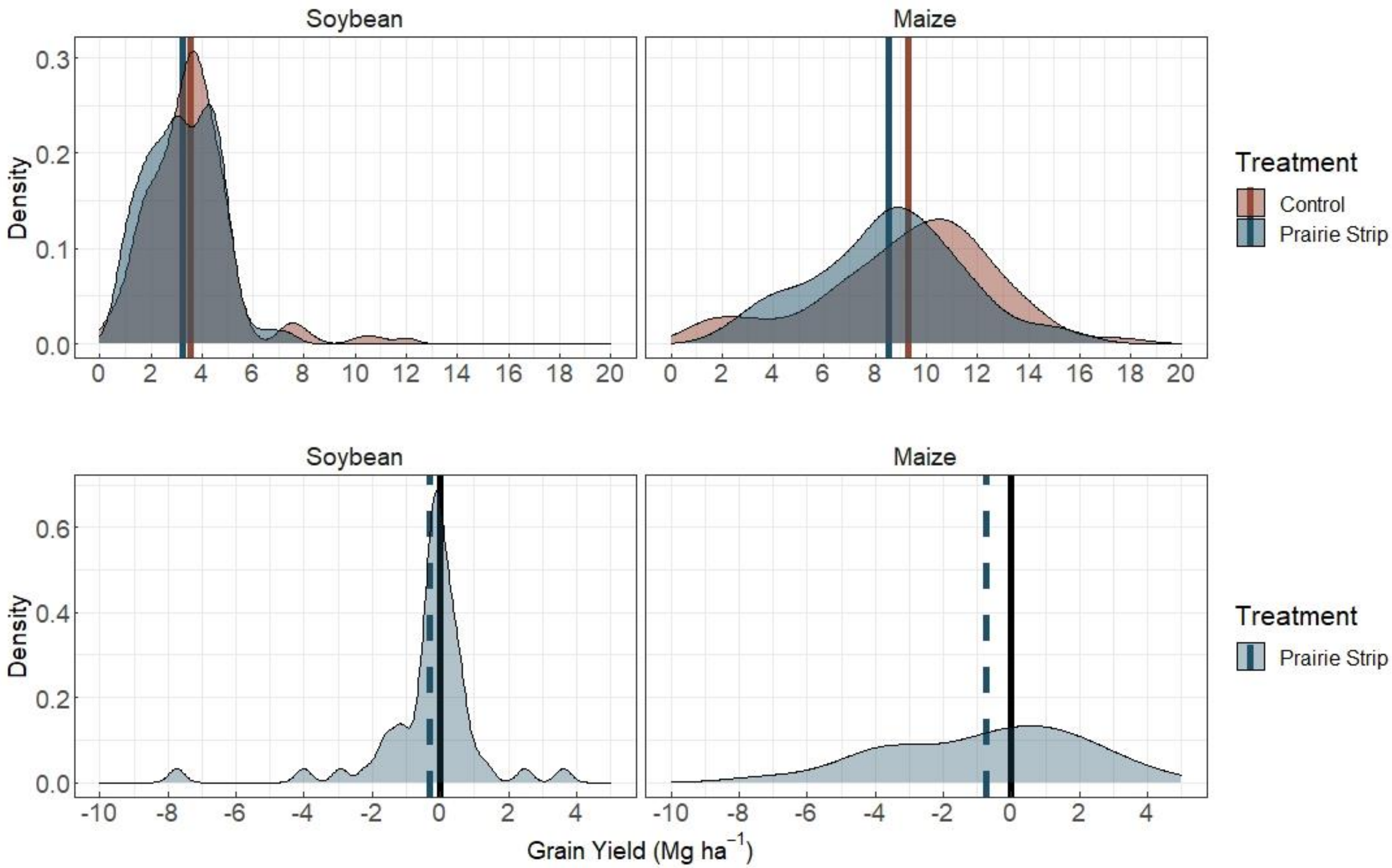

Figure 2.2 Soybean and maize yield distribution from 2007 to 2020 for all catchments; data from 2016 and 2017 was unavailable. Harvest was measured at three distances from the prairie strip 3 m upslope, 3 m downslope, and 9 meters downslope from the prairie strip. Vertical lines indicate the treatment means. The second row illustrates the yield difference between treatments; the prairie strip yield was corrected by the control yield. The vertical dashed line indicates the PS treatment mean.

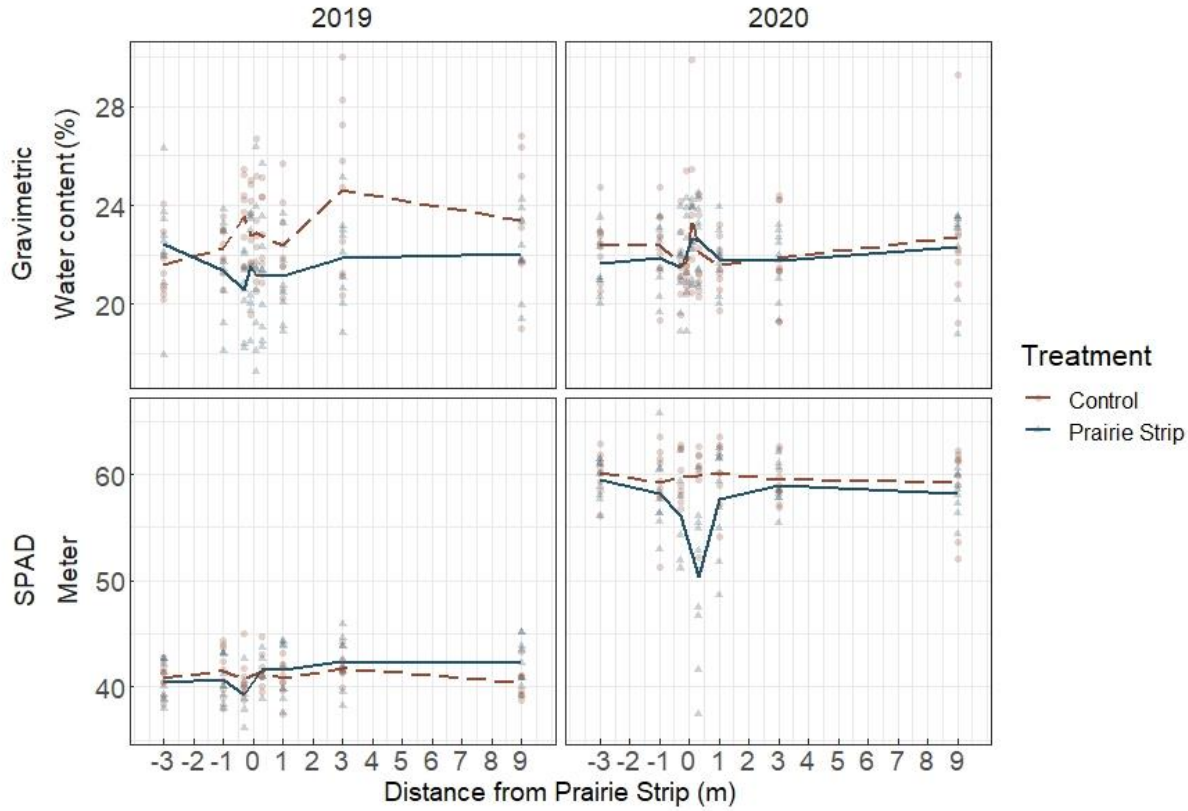

Figure 2.3 Gravimetric water content and SPAD meter by crop from three meters upslope (-3 m) to nine meters downslope (9 m) the prairie strip (0 m). The lines represent the treatment average at each distance (n = 9).

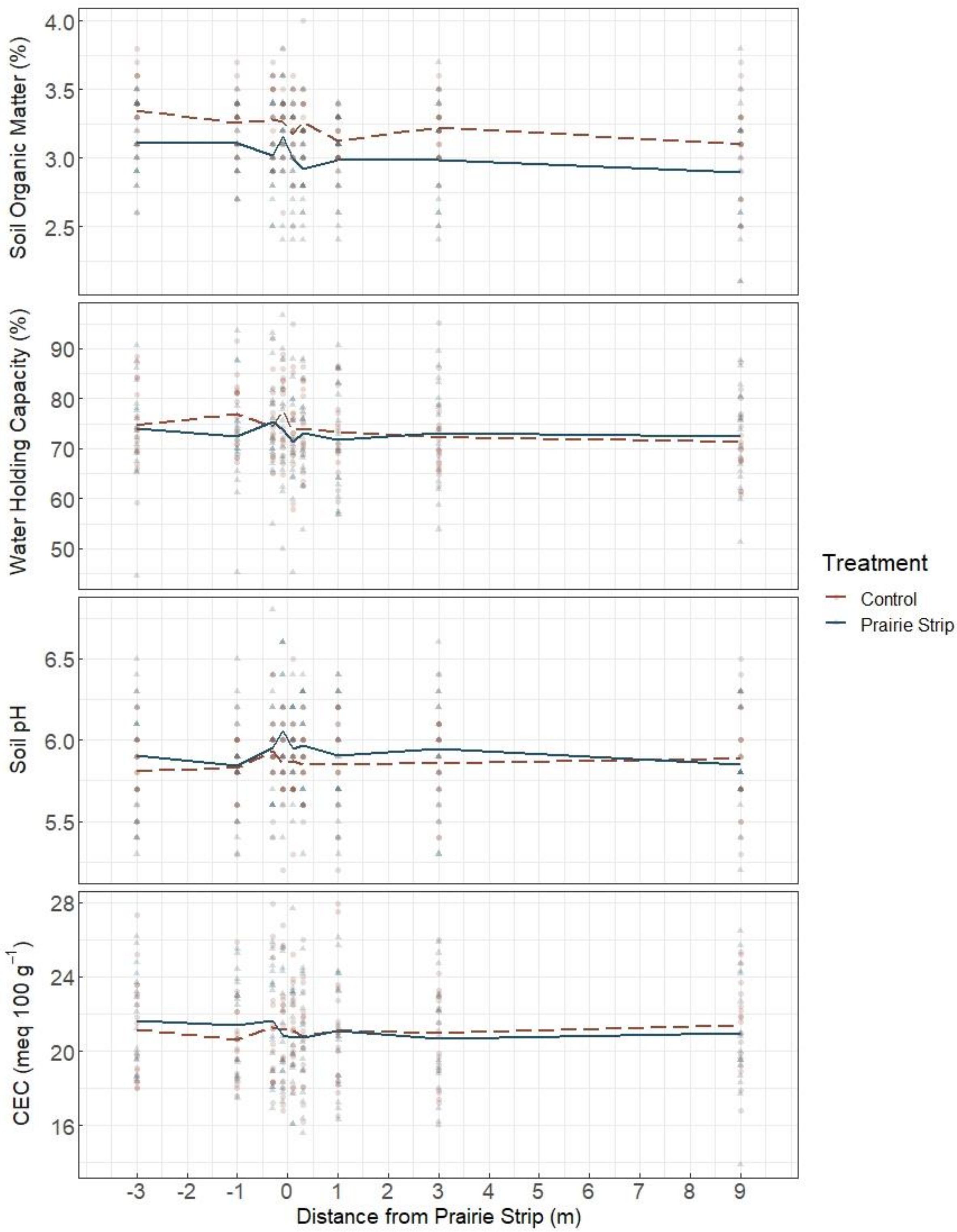

Figure 2.4 Static soil properties from three meters upslope (-3 m) to nine meters downslope (9 m) the prairie strip (0 m). SWHC = soil water holding capacity, CEC = cation exchange capacity). The lines represent the treatment average at each distance (n = 9).

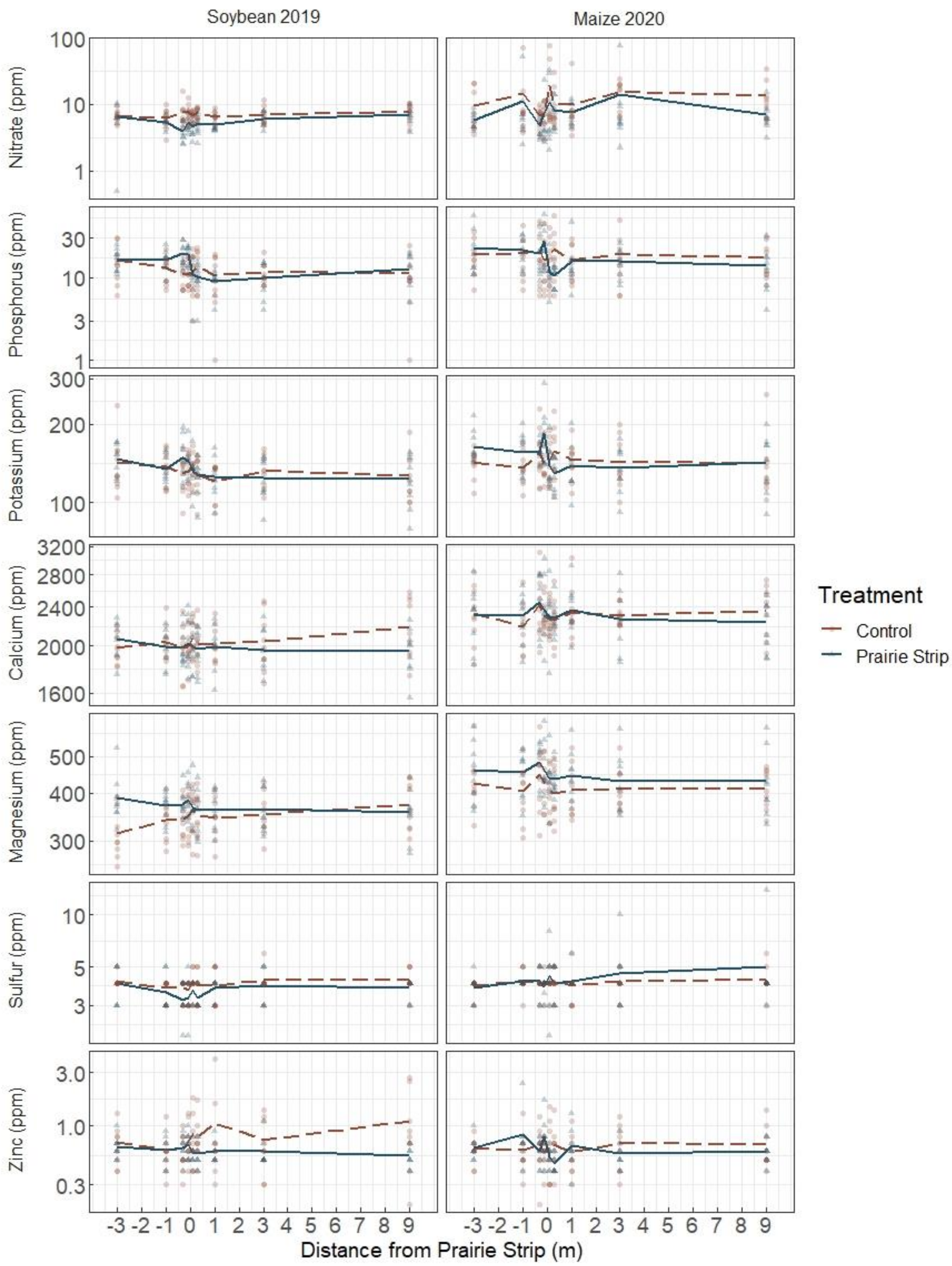

Figure 2.5 Soil plant-available nutrients from three meters upslope (-3 m) to nine meters downslope (9 m) the prairie strip (0 m). The lines represent the treatment average at each distance (n = 9). Y-axes are log scales.

Appendix: Supplemental Tables and Figures

Table S2.1 Three specific contrasts were used in this study (a) Prairie Strip vs. Control, (b) Upslope vs. Downslope from the Prairie Strip, and (c) Nearby vs. Farther from the PS.

(a)		(b)		(c)	
Marginal mean†	**Prairie Strip - Control‡**	**Marginal mean†**	**(Upslope-Downslope PS) / (Upslope - Downslope CL) ‡**	**Marginal mean†**	**(Near-Far PS) / (Near-Far CL) ‡**
Control	-1	Control -300	-0.25	Control -300	0.25
Prairie Strip	1	Prairie Strip-300	0.25	Control -100	0.25
		Control -100	-0.25	Control -30	-0.25
		Prairie Strip-100	0.25	Control -10	-0.25
		Control -30	-0.25	Control 10	-0.25
		Prairie Strip -30	0.25	Control 30	-0.25
		Control -10	-0.25	Control 100	0.25
		Prairie Strip -10	0.25	Control 300	0.25
		Control 10	0.25	Control 900	0
		Prairie Strip 10	-0.25	Prairie Strip -300	-0.25
		Control 30	0.25	Prairie Strip -100	-0.25
		Prairie Strip 30	-0.25	Prairie Strip -30	0.25
		Control 100	0.25	Prairie Strip -10	0.25
		Prairie Strip 100	-0.25	Prairie Strip 10	0.25
		Control 300	0.25	Prairie Strip 30	0.25
		Prairie Strip 300	-0.25	Prairie Strip 100	-0.25
		Control 900	0	Prairie Strip 300	-0.25
		Prairie Strip 900	0	Prairie Strip 900	0

Table S2.2 Historic grain yield (Mg ha-1) by crop, prairie strip treatment, and distance from the prairie strip.

		Soybean					Maize			
		Prairie Strip		Cropland			Prairie Strip		Cropland	
Year	Distance from Strip	Mean	SD	Mean	SD	Year	Mean	SD	Mean	SD
2007	-300	4	1	4	0	2008	12	3	9	3
2007	300	4	1	4	0	2008	9	3	9	3
2007	900	4	1	4	0	2008	9	2	9	3
2009	-300	4	2	4	2	2010	9	5	9	5
2009	300	3	1	4	2	2010	6	3	9	5
2009	900	3	2	4	2	2010	6	3	9	5
2011	-300	3	2	4	3	2012	7	3	8	5
2011	300	4	2	4	3	2012	8	4	8	5
2011	900	2	1	4	3	2012	6	2	8	5
2013	-300	3	2	3	1	2014	9	2	10	2
2013	300	3	1	3	1	2014	9	2	10	2
2013	900	2	1	3	1	2014	9	2	10	2
2015	-300	4	1	4	1	2018	10	2	10	3
2015	300	4	1	4	1	2018	9	1	10	3
2015	900	3	1	4	1	2018	10	3	10	3
2019	-300	3	1	2	1	2020	10	2	10	2
2019	300	2	1	2	1	2020	8	2	10	2
2019	900	3	1	2	1	2020	9	2	10	2

Table S2.3 Sample size power analysis for historical grain yield measurements

Crop	Effect Size	Power	α = 0.05 Sample Size	α = 0.10 Sample Size	Current Study Sample Size
Soybean	0.205	0.8	52	43	27
Maize	0.229	0.8	42	34	27

Table S2.4 Table S3. Prairie strip effect on crop and soil metrics. Values indicate significance in a 90% CI and bold indicates significance at 95% CI (complimentary to Table 2.2 in the main manuscript).

Response	Year	Prairie Strip / Control	(Upslope-Downslope PS) / (Upslope - Downslope CL)	(Near-Far PS) / (Near-Far CL)
Ca	2019	(0.8528,1.1236)	(0.9958,1.0798)	(0.9563,1.0368)
Ca	2020	(0.8965,1.1224)	(0.9517,1.0832)	(0.9430,1.0733)
GWC	2019	(0.8073,1.0430)	**(1.0094,1.1320)**	**(0.8911,0.9993)**
GWC	2020	(0.9130,1.0803)	(0.9482,1.0282)	(0.9725,1.0545)
Harvest	2019	(0.6194,2.3936)	(0.6982,1.9244)	(0.8982,1.3711)
Harvest	2020	(0.7096,1.1391)	(0.7731,1.1026)	(0.9771,1.1600)
K	2019	(0.8141,1.2667)	**(1.0042,1.1656)**	(0.9687,1.1243)
K	2020	(0.8408,1.2620)	**(1.1199,1.3823)**	(0.8748,1.0798)
Mg	2019	(0.9519,1.2007)	**(1.0320,1.1727)**	(0.9092,1.0331)
Mg	2020	(0.9074,1.2825)	(0.9411,1.0918)	(0.9254,1.0735)
NO3	2019	(0.5524,1.0094)	(0.7944,1.2106)	**(0.6268,0.9552)**
NO3	2020	(0.3319,1.6654)	(0.7236,1.6157)	(0.6938,1.5492)
P	2019	(0.7482,1.8104)	**(1.2460,2.1218)**	(0.8982,1.5295)
P	2020	(0.4554,2.0594)	**(1.2185,2.2027)**	(0.6689,1.2091)
S	2019	(0.6924,1.1876)	(0.9018,1.0800)	(0.8431,1.0098)
S	2020	(0.8800,1.1626)	(0.8440,1.1040)	(0.8515,1.1137)
SPAD	2019	(0.9089,1.0974)	**(0.9405,0.9937)**	(0.9672,1.0219)
SPAD	2020	**(0.9052,0.9979)**	**(0.8939,0.9812)**	**(0.8850,0.9702)**
Zn	2019	(0.4382,1.6928)	**(1.0431,1.5611)**	(0.7811,1.1691)
Zn	2020	(0.5809,1.7287)	**(1.0576,1.5450)**	(0.7358,1.0749)

† Significant values are bolded (<0.05)

Table S2.5 Leaf greenness, water content, and soil plant-available nutrient analysis of variance results for soybean 2019 and maize 2020†.

			Soybean 2019		**Maize 2020**	
Crop or Soil Variable	**Effect**	**Df**	**F-statistic**	**p-value**	**F-statistic**	**p-value**
SPAD Meter	Treatment	1	0.00	0.989	7.82	**0.042**
	Distance	6	3.47	***0.004***	3.15	**0.005**
	Treatment:Distance	6	2.31	***0.040***	4.84	**<0.001**
Gravimetric water content	Treatment	1	7.24	0.136	0.05	0.831
	Distance	8	1.46	0.331	2.03	**0.048**
	Treatment:Distance	8	1.38	0.074	0.45	0.888
Nitrate	Treatment	1	7.24	0.055	1.04	0.365
	Distance	8	1.46	0.177	1.78	0.085
	Treatment:Distance	8	1.38	0.213	0.55	0.813
Phosphorus	Treatment	1	0.47	0.532	0.01	0.912
	Distance	8	6.42	**<0.001**	1.98	0.053
	Treatment:Distance	8	5.07	**<0.001**	2.48	**0.015**
Potassium	Treatment	1	0.04	0.852	0.16	0.706
	Distance	8	3.95	**<0.001**	2.05	**0.045**
	Treatment:Distance	8	1.42	0.194	2.90	**0.005**
Calcium	Treatment	1	0.18	0.691	0.01	0.915
	Distance	8	0.78	0.622	1.24	0.281
	Treatment:Distance	8	2.45	**0.017**	0.34	0.947
Magnesium	Treatment	1	2.48	0.135	1.36	0.309
	Distance	8	0.42	0.907	1.90	0.066
	Treatment:Distance	8	2.49	**0.015**	0.15	0.997
Sulfur	Treatment	1	0.90	0.396	0.05	0.823
	Distance	8	3.61	**<0.001**	0.59	0.789
	Treatment:Distance	8	0.51	0.846	0.26	0.977
Zinc	Treatment	1	0.38	0.573	0.00	0.992
	Distance	8	0.56	0.809	0.82	0.582
	Treatment:Distance	8	1.51	0.161	2.06	**0.045**

† Significant values are italicized (<0.1) and bolded (<0.05)

Table S2.6 Soil characteristics at 0-15 cm depth for the site (n=360).

	Mean	**Standard Deviation**	**Coefficient of Variation**	**Minimum**	**25th Percentile**	**Median**	**75th Percentile**	**Maximum**
% Clay	26.0	1.9	7.1	20.6	24.7	26.0	27.2	30.8
% Silt	53.2	1.6	3.0	49.0	52.2	53.1	54.3	56.6
% Sand	20.7	2.6	12.6	15.1	18.9	20.8	22.3	29.7
Water Holding Capacity (%)	73.7	9.0	12.2	44.6	68.2	72.8	80.0	96.6
Gravimetric Water Content (g g^{-1})	0.22	0.02	10.61	0.17	0.21	0.22	0.23	0.36
Nitrate (ppm)	8.2	8.8	106.8	0.5	4.8	6.3	8.0	77.8
Phosphorus (ppm)	16	9	60	1	9	13	19	58
Potassium (ppm)	140	29	20	79	121	137	155	289
Magnesium (ppm)	396	69	18	256	349	386	435	622
Calcium (ppm)	2166	282	13	1563	1947	2157	2330	3117
Sulfur (ppm)	4	1	24	2	3	4	4	14
Zinc (ppm)	1	0.36	54	0.2	1	1	1	4
Cation Exchange Capacity (meq 100 g^{-1})	21.1	2.8	13.0	13.9	18.9	20.8	23.1	27.9
Soil pH	5.89	0.30	5.08	5.20	5.70	5.90	6.10	6.80
Soil Organic Matter (%)	3.12	0.32	10.35	2.10	2.90	3.15	3.40	4.00

Table S2.7 Random forest analyses for soybean 2019 and maize 2020.

Soybeans			Maize		
Soil Parameter Explaining Soybean SPAD	**% Increase MSE**	**Node Purity**	**Soil Parameter Explaining Maize SPAD**	**% Increase MSE**	**Node Purity**
Catchment	1.23	54	Phosphorus	4.01	246
Treatment	0.45	16	Treatment	2.04	67
% Fine Clay	0.34	44	Nitrate	1.65	326
Block	0.30	14	% Fine Clay	1.11	121
CEC	0.22	36	Potassium	0.91	155
Distance from Prairie Strip	0.18	20	Organic Matter	0.81	122
Primary Mode of Soil Particles	0.18	24	Distance	0.57	72
% Clay	0.17	39	CEC	0.51	247
Phosphorus	0.16	27	Zinc	0.43	95
pH	0.11	18	Transect	0.39	21
Potassium	0.06	29	Catchment	0.30	36
Nitrate	0.05	34	Water Holding Capacity	0.26	95
Sulfur	0.04	10	Primary Mode of Soil Particles	0.15	72
Gravimetric Water Content	0.03	26	% Clay	0.08	147
Zinc	0.03	13	pH	0.06	41
Water Holding Capacity	-0.02	32	Sulfur	0.00	24
Soil Organic Matter	-0.04	19	Gravimetric Water Content	-0.01	110

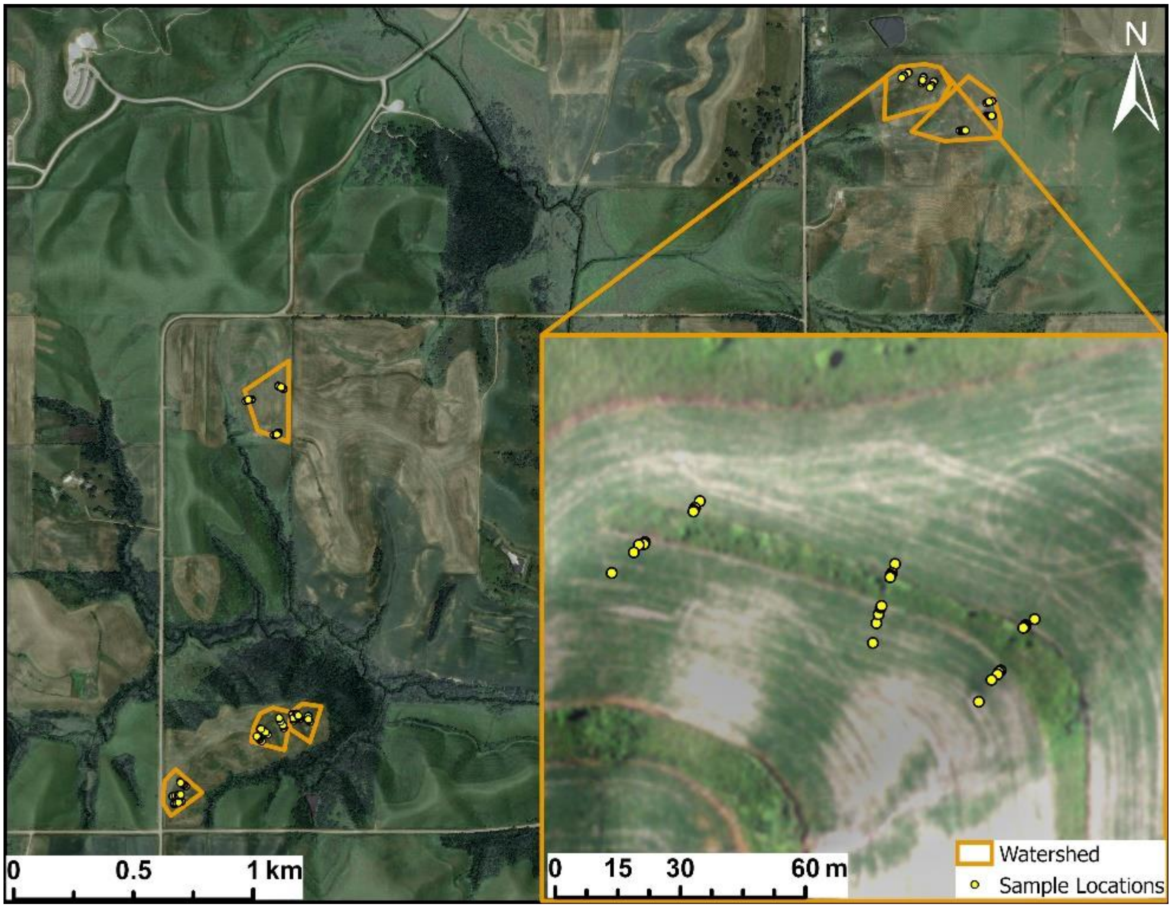

Figure S2.1 Map shows treatment and control catchments and transects (yellow dots). Inset: close-up of transects used in one prairie strip catchment for soil and crop sampling. Meyer Bohn created the map.

Figure S2.2Locations of harvest monitor polygons used for grain yield estimation. Red dots are the GPS locations of the soil samples, and yellow polygons are the yield monitor locations used

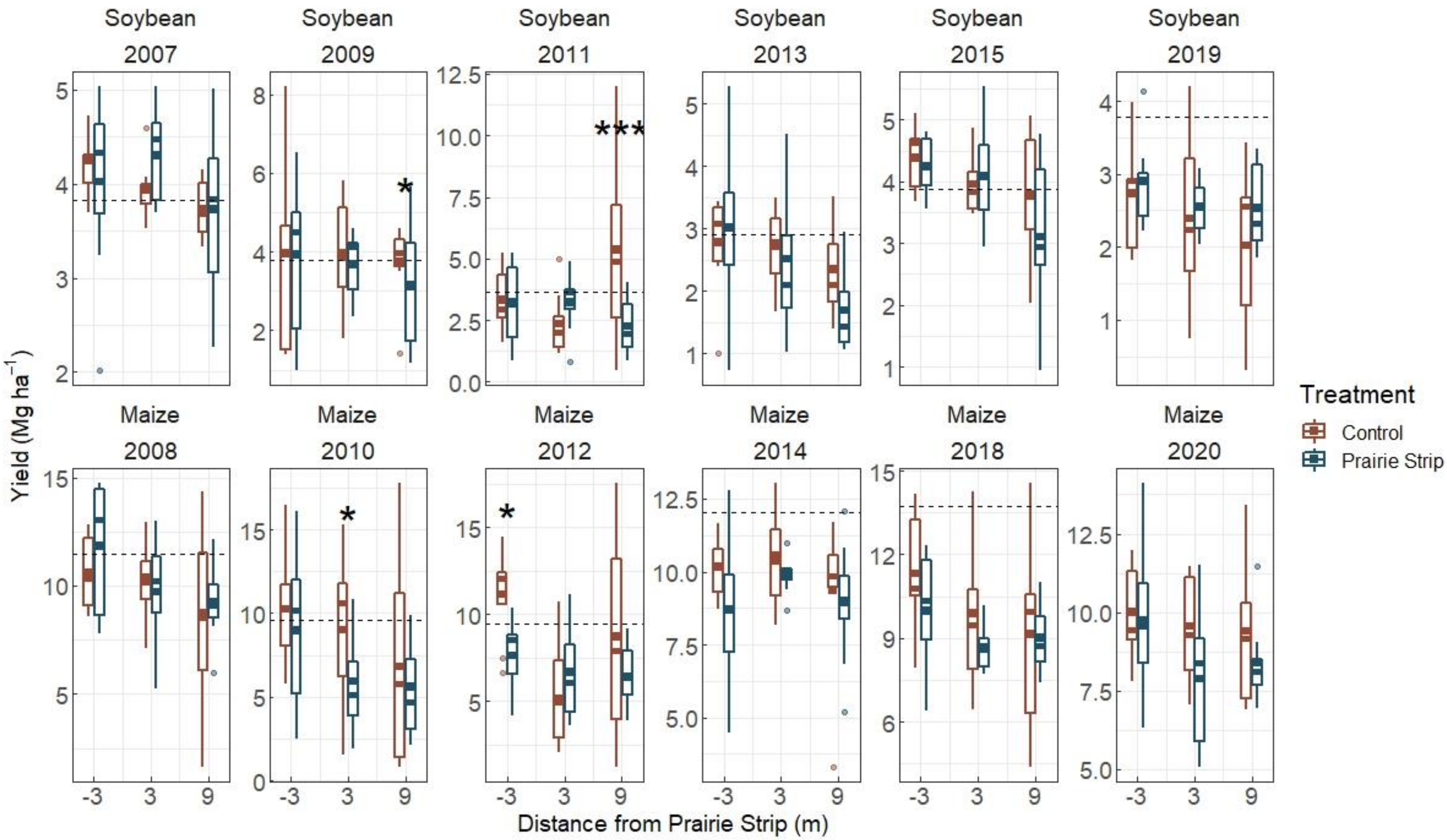

Figure S2.3 Soybean and maize yield from 2007 to 2020 for all catchments; data from 2016 and 2017 was unavailable. Harvest was measured at three distances from the prairie strip – 3 m upslope (-3), 3 m downslope (3), and 9 meters downslope (9) the prairie strip. The dashed line in each plot is the Jasper County average for that year, 2020 average was not reported. * indicates p-value<0.1 for treatment comparisons; *** indicates p-value < 0.001

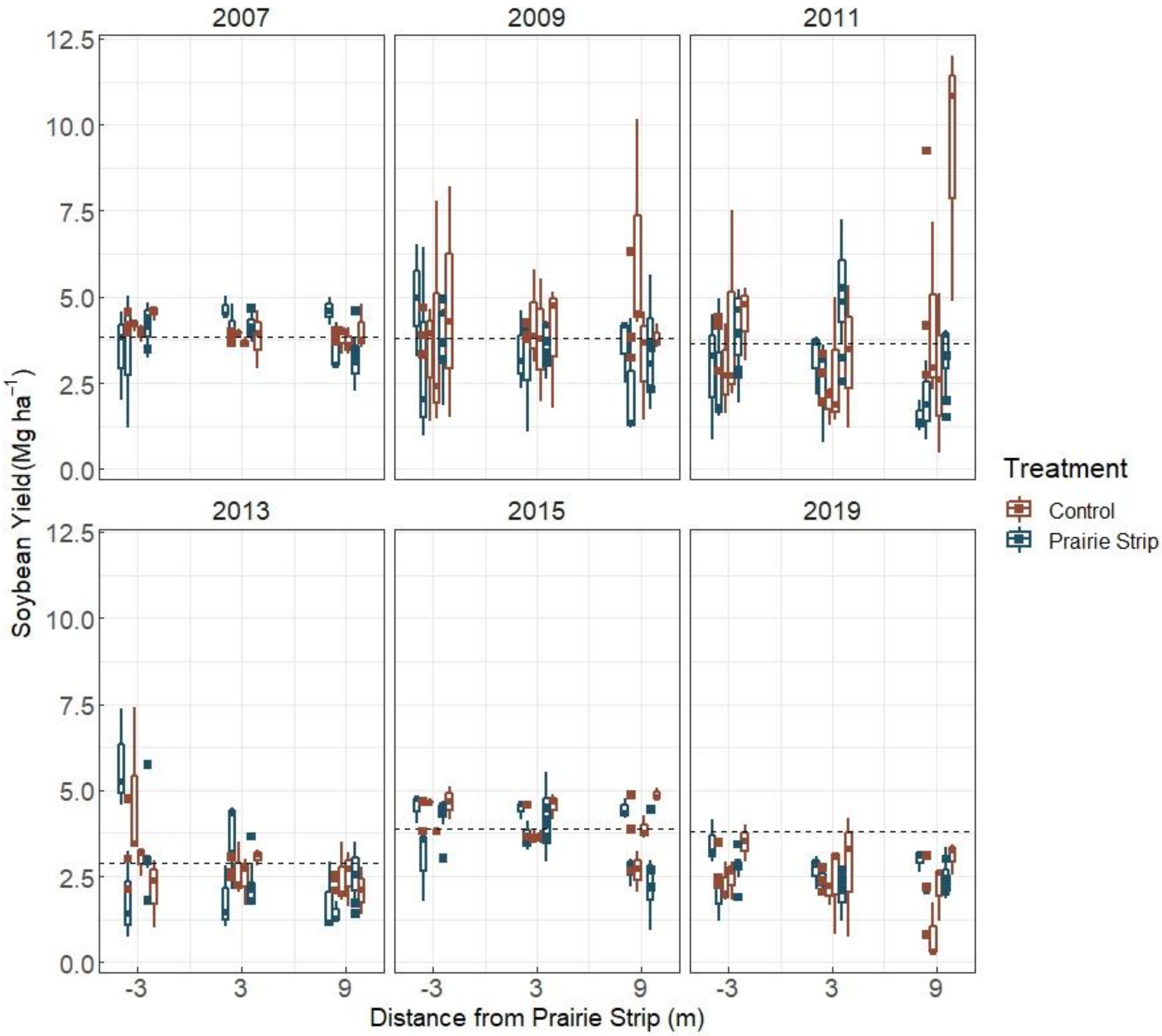

Figure S2.4 Historic soybean yield by catchment and treatment at NSNWR from 2008 to 2020; data from 2017 is unavailable. The yield was measured at three distances from the PS and paired locations in the control catchments. Data was collected using a continuous yield monitor. The dashed line in each plot is the Jasper County average for that year.

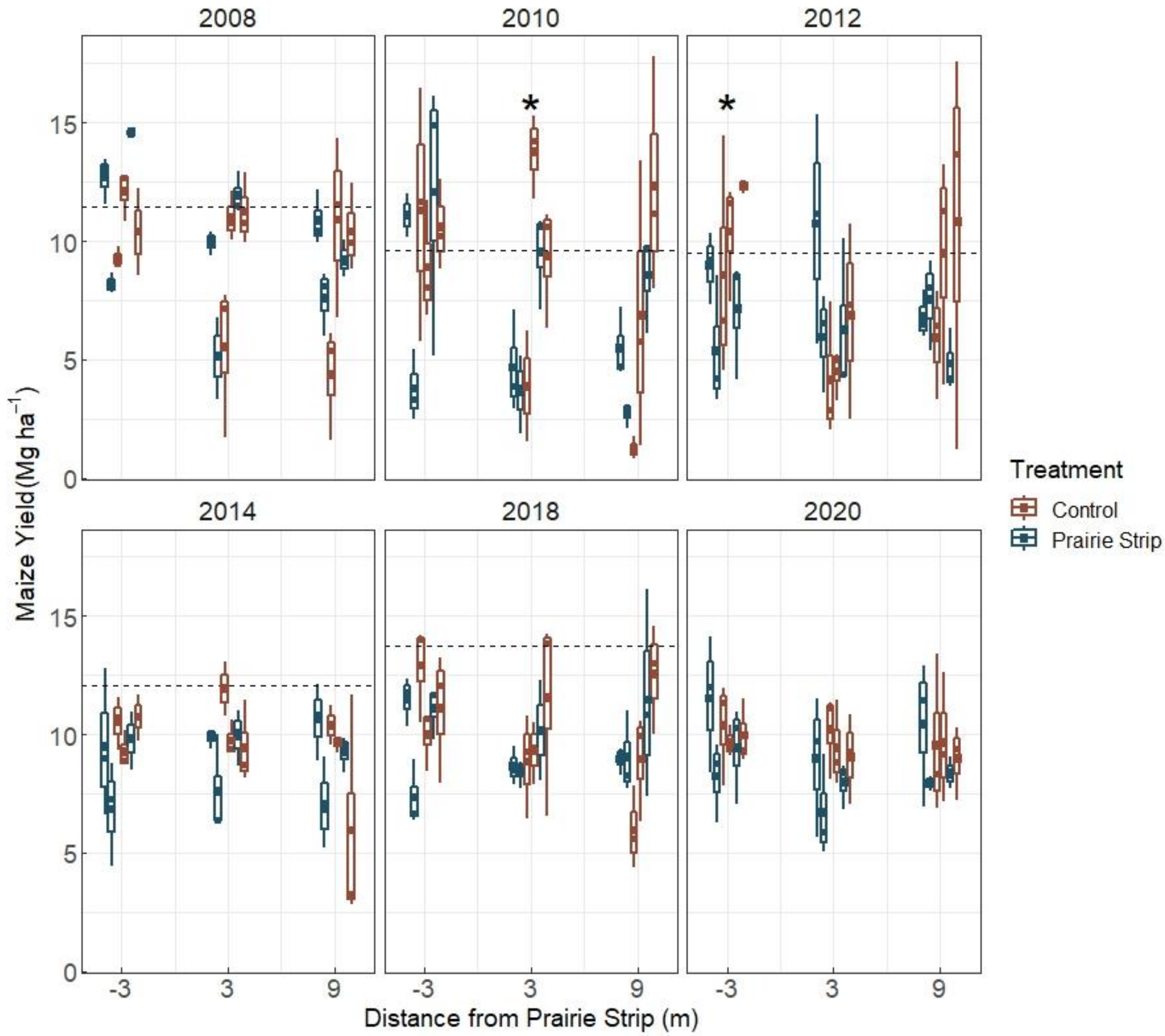

Figure S2.5 Historic Maize Yield by catchment and treatment at NSNWR from 2008 to 2020; data from 2016 is unavailable. Harvest was measured at three distances from the PS and paired locations in the control catchments. Data was collected using a continuous yield monitor. The dashed line in each plot is the Jasper County average for that year. The county average for 2020 is unavailable.

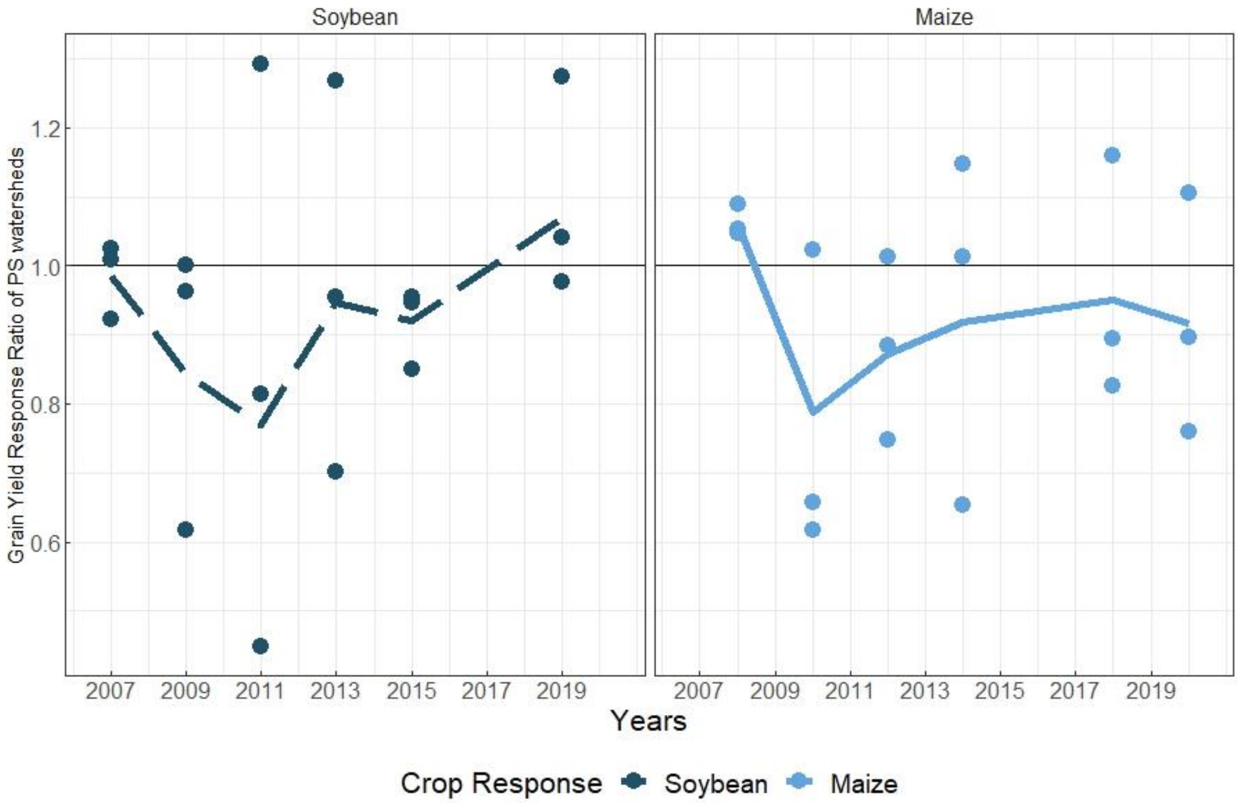

Figure S2.6 Historical soybean and maize yield from 2007 to 2020 for all catchments; data from 2016 and 2017 are unavailable. Harvest was measured at three distances from the prairie strip – 3 m upslope (-3), 3 m downslope (3), and 9 meters downslope (9) the prairie strip, then averaged for each catchment. The yield ratio indicates the PS catchments average compared to control catchments. Data were collected using a continuous yield monitor. The dashed line represents the mean of the soybean yield, and the solid line represents the maize yield's mean.

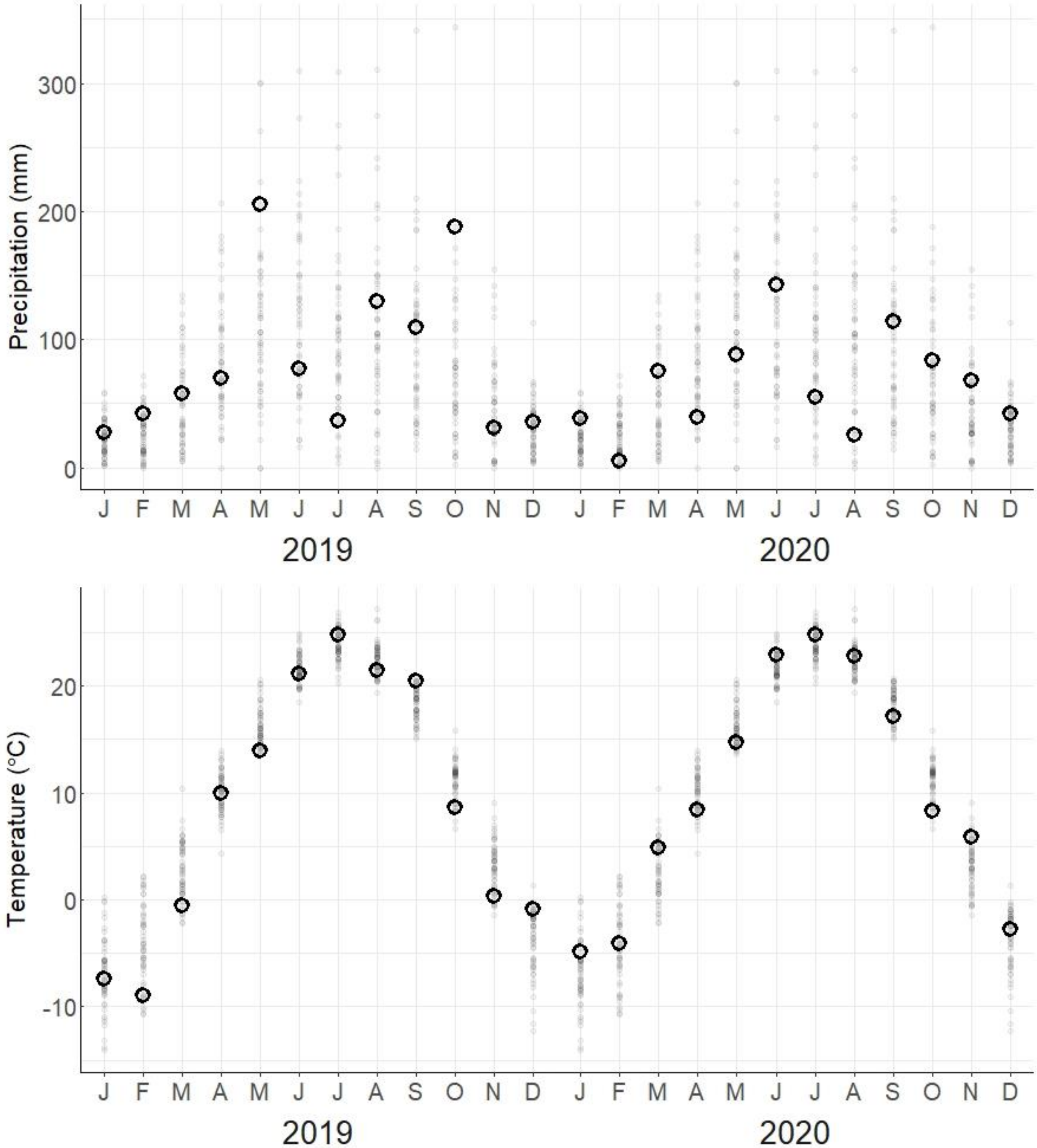

Figure S2.7 Mean monthly temperature and precipitation for the two years of the intensive study (open circles). The filled, shaded dots are historical data from the prior 50-year record for each month. Data are from Iowa Mesonet station in Jasper County, IA weather station that is 30 km from the site (IA Mesonet 2021).

CHAPTER 3. EFFECT OF CONTOUR PRAIRIE STRIPS ON MICROBIAL BIOMASS AND MICROBIAL ACTIVITY UNDER THE PRAIRIE STRIP AND ADJACENT CROPLAND

Cole Dutter[1*], Sarah Evans[2], Marshall McDaniel[1]

1 Iowa State University, Department of Agronomy
2 Michigan State University, Department of Integrated Biology
* Corresponding author
Email: cdutter@iastate.edu
Address:
2531 Agronomy Hall
716 Farm House Lane
Ames, IA 50011
Phone: (515) 350-8286

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Abstract:

Prairie strips (PS) are narrow rows of prairie (>10 m) that have disproportionate benefits, including reducing runoff, nutrient loss, and sediment export. A previous study showed that PS could affect soil gravimetric water content plant-available nutrients in adjacent soil from 0.1 to 9 m away (CHAPTER 2). However, the impact of this new conservation practice on soil biochemistry and microbial function underneath and around the PS is not known. Still, it may be important to restore soil ecosystem services and increase soil organic carbon (C). We assessed the PS effect on soil carbon (C) and nitrogen (N) pools as well as potential enzyme activities (PEA) in soils under 12-year-old PS and adjacent cropland under soybean (*Glycine max* (L.) Merr.) and maize (*Zea mays* L.) from 0.1 to 9 m from the PS. We found that PS affected soil pools across both years: microbial biomass C (+56%), microbial biomass N (+149%), and decreased salt-extractable inorganic N (-63%) under the PS. PS affected PEAs only under soybean year: cellobiohydrolase (+77%), N-acetyl-β-glucosaminidase (+108%), phosphatase (+46%), and Peroxidase (-28%) under the PS. PS affected PEAs in the adjacent cropland across the treatment during the soybean year: β-glucosidase by 27%, N-acetyl-β-glucosaminidase by 31%, and phosphatase by 38%. PS Understanding these ecotonal effects of PS on adjacent cropland and cropland on PS can inform strategic integration of diverse perennial vegetations within annual crop fields to maximize all field-level agroecosystem services.

1. Introduction

Intensive agricultural production is a double-edged sword. While steadily increasing per ha productivity of most grain crops (Cassman and Grassini 2020), there have been a plethora of deleterious impacts of modern agriculture, including degrading soil ecosystem services (SES) (Baldwin-Kordick et al. 2022; Gerla 2007). This is especially the case for SESs regulated by soil biota. Soil microorganisms and fauna regulate many SESs important to agricultural productivity and environmental quality. Soil biology regulates nutrient cycling (Horwáth 2017), helps to aggregate soils, protecting them from erosion (Jastrow, Miller, and Lussenhop 1998), and was more recently shown to be an important regulator of long-term accumulation of soil organic matter (Kallenbach, Frey, and Grandy 2016; Ma et al. 2018). Restoring SESs in agroecosystems requires regenerating the biomass and activity of soil biota.

In regions where grasslands or savannahs once predominated the landscape, landowners use grassland restoration to alter soil biochemistry and restore SESs. There are a plethora of studies on restoring perennial grasslands and the positive influence on soil chemistry and biota: increased microbial biomass (Bach and Hofmockel 2015; Li et al. 2018), increased microbial activity measured as respiration or potential enzyme activities (Bach and Hofmockel 2015; Raiesi and Salek-Gilani 2018); reduction in mobile nitrate nitrogen (N; (Baer et al. 2002; Karlen et al. 1999), increased labile C (De et al. 2020; Hurisso, Norton, and Norton 2014), and increase soil organic C (Li et al. 2017; Munson, Lauenroth, and Burke 2012; Pérez-Suárez et al. 2014). These biochemical measurements nearly always coincide with measures of larger and more stable aggregates (Jastrow 1996), less nutrient leaching (Daigh et al. 2015), and lower greenhouse gas emissions (Oates et al. 2016) – all critical soil or agroecological services critical for improving environmental quality. The downside, however, of fully restored grassland is that it can be economically detrimental to a grower.

Implementing prairie strips (PS) within cropland is a new conservation practice that offers both the environmental benefits of grassland restoration with the economic benefit of crop production. Instead of taking an entire cropland field out of production, PS use narrow strips of diverse perennial plants (>10 m width) planted parallel to the dominant slope of a catchment and are intended to slow overland water flow and minimize sediment and nutrient losses from fields The advantage of PS is that they 'disproportionately benefit' environmental quality on the catchment scale. Even though they might occupy only 10% of a given catchment, PS have reduced sediment export by 95% (Helmers et al. 2012; Schulte et al. 2017) and reduced total water runoff (Gutierrez-Lopez et al. 2014; Hernandez-Santana et al. 2013). These PS also have the added benefit of increasing plant diversity and wildlife abundance and activity (Hirsh et al. 2013; Schulte et al. 2016).

A small \`island\` of prairie integrated within croplands may have unique effects on soil organic matter, carbon and nitrogen pools, and the soil biota regulating these elements cycling. This effect may be bi-direction or 'go both ways.' In other words, the PS may affect the adjacent cropland soils, as a previous study indicates it does affect soil water and plant-available nutrients (CHAPTER 2). Also, the cropland may affect how PS changes the soil biochemistry under the

PS relative to the previously mentioned studies where whole fields are converted to grassland or prairie. We could anticipate that relatively narrow plantings (> 10 m) of prairie might not increase soil biota and activity the same as a large, contiguous field.

In agroecosystems, humans can create clear boundaries by controlling the vegetation in a particular location and managing that vegetation to have distinct boundaries. However, despite management and the appearance of clear boundaries, the PS and the cropland will likely interact, even if in subtle ways. Nutrients and carbon may be imported or exported from one ecosystem to another via water transport, migrating roots or mycorrhizal fungi, or motile fauna. Additionally, the PS and cropland may affect each other through microclimate variations or competition of light, water, and other resources at the boundaries between PS and cropland (Senaviratne et al., 2012).

These complex agroecosystem dynamics of water, nutrients, and energy transfer that occur at a very large or small scale are known in ecology as an *ecotone*. Ecotone studies in ecology have long recognized that constraints and scale of an ecotone influence sampling density and placement (Gosz 1993), and in the microbiome, scaling can be 10s of millimeters (Baldrian 2014). Though some examples exist, grassland-cropland soil ecotone studies are scarce (Guo et al. 2018; Marfo et al. 2019). Soils within ecotones have altered soil physical properties between forest and cropland (Marfo et al. 2019) and altered microbial community composition within ~2 m of the boundary between pasture and cropland (Guo et al. 2018). However, PS's influence on C and N dynamics and PEAs may be limited due to the small scale (10s of millimeters) of soil properties influencing enzyme ecotone and the intrinsic unexplained variation possibly due to biogeochemical hotspots within ecotones (Blackwood et al. 2018). Integrating narrow strips of prairie vegetation may have both positive or negative effects of the PS on cropland and vice versa.

Given the potential of PS to increase soil biological functioning and alter microbial community structure under and in adjacent cropland soil (CHAPTER 2), we established the following objectives. Our primary objectives were to quantify the PS effect on soil carbon and nitrogen, microbial biomass, and PEAs: 1) under the PS and 2) in adjacent cropland (< 9 m). We hypothesize that the PS will 1) increase SOC, TN, microbial biomass, and PEAs under the PS, and 2) will not alter SOC, TN, microbial biomass, and PEAs in the cropland, as the dominant land use is expected to regulate the biochemical processes and microbial activity. Our goal was to determine whether narrow PS have the same beneficial effects on soil biochemistry as larger swaths of croplands converted to grassland and explore potential co-benefits or trade-offs in the adjacent cropland to help maximize agroecosystem environmental and economic sustainability.

2. Materials and Methods

2.1. Site description and experimental design

The study was located on the Neal Smith National Wildlife Refuge (NSNWR; 41° 33' N;93°16' W), a 3000-ha mosaic of forest, pristine prairie, restored prairie, and cropland managed by the U.S. National Fish and Wildlife Service. NSNWR is in the Walnut Creek watershed in Jasper County, Iowa, which lies on the Iowa southern drift plain (Major Land Resource Area 108C; USDA Natural Resources Conservation Service, 2006). This area consists of steep rolling hills of Wisconsinan loess on pre-Illinoian till (Prior 1991). The research watershed soils are classified as Ladoga (Mollic hapludalf) or Otley (Oxyaquic argiudolls) soil series with 5 to 14% slopes and are highly erodible (Nestrud and Worster 1979; Soil Survey Staff 2003). The 50-year mean annual precipitation (MAP) is 876 ± 205 mm, and the mean annual temperature (MAT) is 9.6 ± 0.9 ℃.

In 2007, a catchment scale PS experiment was established within NSNWR. Prairie strips were established in a randomized, balanced, incomplete block design on 12 catchments ranging in size from 0.47 to 3.2 ha. Prairie strips were planted such that they covered 0, 10, and 20% of the catchment area and were situated within the cropland (shoulder/backslope) and at the foot slope (Zhou et al. 2010). Before 2007 these fields were in a brome cover for at least ten years. Since its establishment, the adjacent cropland was planted in a maize-soybean rotation (CHAPTER 2).

For this study, we selected the 10% PS catchments as our treatment of interest because previous research showed PS occupying 10% of the cropland was enough to observe disproportional ecological benefits (Schulte et al. 2017). We also chose the catchments with 0% PS, hereafter referred to as '*control.*' Three transects, 34 - 80 m apart, perpendicularly bisecting PS in all catchments, were chosen based on a digital map of a 3x3 m^2 digital elevation model (DEM), plan curvature (r.param.scale with analysis window of 69 m; GRASS GIS 7.8, GRASS Development Team 2021; Miller 2014; Chapter 2) and flow accumulation (D_∞, ArcGIS Pro v 2.2 ESRI Redlands, CA). The DEM was derived from LiDAR (Light Detection and Ranging) elevation data collected by the Iowa Department of Natural Resources (IDNR; available at http://www.geotree.uni.edu/lidar). Soil samples were collected along PS and control catchments where a PS was absent at ten distances: -3, -1, -0.3, -0.1, 0, 0.1, 0.3, 1, 3, and 9 m from the upslope of the PS to the downslope. The 0 m distance is in the center of the PS or equivalent position in the control transect. Transects and sampling locations were marked using the Arrow 100 ®GNSS receiver.

2.2. Soil Sampling and analysis

Ten soil cores (0-15 cm) were taken with a 2 cm diameter probe from each transect distance and composited. Soil cores were taken on July 1^{st} in both years of sampling. Composite samples were sieved to <2 mm and subdivided for analysis. A 15 g amount of soil was weighed and dried at 105°C for 24 h to get gravimetric water content (GWC). To measure microbial biomass C and N, twin replicates from each soil were weighed to ~ 5 g. One replicated was fumigated with $CHCl_3$. Both replicates were extracted with 25 ml of 0.5 M K_2SO_4, non-purgeable organic carbon, and total nitrogen were measured with a Shimadzu TOC-L analyzer (Shimadzu Corporation, Kyoto, Japan) and compared between each replicate (Brookes et al. 1985; Vance, Brookes, and Jenkinson 1987). The C and N in salt-extracted but unfumigated samples are hereafter referred to as salt-extractable organic C (SEOC) and organic N (SEON). The non-fumigated extracts were also measured for ammonium-N and nitrate-N, hereafter referred to as salt-extractable inorganic N (SEIN), using a SynergyTM HTX Multi-Mode Microplate Reader (BioTek Instruments, Winooski, VT, USA) with Gen5TM software. A 5 g amount of soil was immediately frozen after sieving at -20 ℃ and then lyophilized within 2-3 months before PEAs were measured.

The remainder of the soil was air dried at 24℃ until stable weight (~1 month). Soil organic matter (SOM) was measured using loss on ignition for 2 hours at 360℃ using a Blue M oven and TSI weighing system. Air-dried soils were ground with a ball mill and dried at 105℃ for 24 h before analyzing for total organic C and total N. Soil organic C and total N analyses were performed using a ThermoFinnigan Delta Plus XL mass spectrometer attached to a GasBench II with a CombiPal autosampler. One hundred nine of 180 soil samples had a pH >6 and were acid fumigated to remove carbonates.

2.3. Potential Enzyme Activity Assays

The potential activities of both hydrolytic and oxidative enzymes were measured according to standard protocols (Table 3.1). Hydrolytic enzymes – arylsulfatase (ARSase), β-glucosidase

(BGase), cellobiohydrolase (CBHase), β-N-acetylglucosaminidase (NAGase), leucine aminopeptidase (LAPase), phosphatase (PHOSase) – were assayed following Deng et al.'s (2011) protocol. One gram of freeze-dried soil was weighed and put into suspension with 150 ml of DI water and stirred for 30 min. Afterward, 200 µl of soil solution were incubated for 1 hr at 37°C with 50 µl of the substrate. After the incubation, 50 µl of the substrate was added to the control columns, and 50 µl of THAM was added to all columns. Then pre-incubation and post-incubation samples were compared. Autohydrolysis controls were also used for each enzyme, and standard curves for each catchment were calculated. Enzyme activity was determined from fluorescence and excitement at 360 nm and emission at 460 nm.

Oxidative enzyme activities – polyphenol oxidase (PPOase) and peroxidase (PERase) – were quantified using the colorimetric assay method (Saiya-Cork, Sinsabaugh, and Zak 2002). One gram of freeze-dried soil was weighed, put into suspension with 125 ml of Acetate buffer, and incubated with L-DOPA for 22 hrs at 25°C. Activities were calculated from absorbance of 450 nm, and the standard emission coefficient of 7.9 was used for these equations (DeForest 2009). All enzyme activities, both fluorometric and colorimetric, were read using a SynergyTM HTX Multi-Mode Microplate Reader (BioTek Instruments, Winooski, VT, USA) with Gen5TM software.

2.4. Data handling and statistical analysis

The data were analyzed via a mixed effect linear model. The PS and cropland linear model used the following response variables on the log scale: microbial biomass C and N, salt-extractable inorganic N, salt-extractable organic C and N, soil organic C, total N, ARSase, BGase, CBHase, LAPase, NAGase, PHOSase, PPOase, and PERase. Data were analyzed for normalcy and homoscedasticity. The fixed effects were treatment (control vs. PS), distance (9-

level categorical variable) from PS, and treatment-distance interaction. The random effects were catchment (6 levels) and transect within the catchment (3 per catchment).

All variables are analyzed separately within years, i.e., the model was fit independently for a given response and year. We chose this because the year variable was confounded with crop type (soybean vs. maize), land management decisions (fertilizer vs. none), and weather conditions in 2019 and 2020. The unknowns were estimated via residual maximum likelihood (REML) using the software defaults in lme4 (Bates et al., 2015) and emmeans (Lenth, 2021) packages in the statistical software R (R Core Team, 2020).

Principal Component Analysis (PCA) was performed on potential enzyme activities by including all sample points to discern the effect of PS on enzyme activity. Enzyme activities and environmental variables were analyzed using the vegan (Oksanen et al. 2022) package in the statistical software R (R Core Team, 2020).

3. Results

3.1. Effect on soil under PS

Prairie strips strongly affected dynamic C and N pools but not SOC nor TN pools (Figure 3.1, Table 3.2). There was no effect, or even a slightly negative effect in the case of TN (although not statistically significant), of PS on total SOC and N. The dynamic pools were more responsive to PS, and this response was consistent across the years. Prairie strips increased MBC and MBN by 56% and 149% across 2019 and 2020. Prairie strips did not affect SEOC nor SEON, SEON trended lower with prairie strips, but the difference was not statistically significant. Prairie strips lowered SEIN by 63% across 2019 and 2020 – and, on average, measured as 50% nitrate-N and 50% ammonium-N across all PS soils (Figure 3.1).

Prairie strips had inconsistent effects on the PEA of soils underneath when expressed per g of SOM (Figure 3.2, Table 3.2). For example, PS did not significantly affect BGase or ARSase in either year, and even the direction of effect was inconsistent. PS had the most consistent positive effects on PEA in 2019 when the adjacent cropland was under soybean, and during the growing season, conditions were relatively wet (CHAPTER 2). PS significantly increased hydrolytic PEAs – CBHase by 77%, NAGase by 108%, and PHOSase by 46% – compared to cropland control. Unlike hydrolytic PEAs, however, PS had a negative effect on oxidative PEAs. For instance, PS decreased PERase by 28% in 2019 and PPOase by 33% in 2020 (Figure 3.2; Table 3.2).

3.2. Effect of PS on adjacent cropland soil

Prairie strips had marginal effects on soil C and N pools. For example, there was an overall negative but marginally significant effect of PS on adjacent cropland (Figure 3.3). PS decreased adjacent cropland SOC by 9% compared to the control catchment. There were no significant effects on the more dynamic, labile C and N pools aside from SEIN. Salt-extractable inorganic N, comprised mostly of nitrate-N (85%), was lower in the soil adjacent to the prairie strip but only in 2019 under soybean (also see CHAPTER 2).

Prairie strips more clearly affected PEAs in the adjacent cropland, but these effects were highly inconsistent among enzymes and dependent on the year (Figure 3.4, Table S3.1). Furthermore, the effects of PS on adjacent cropland were largely independent of distance from the PS (up to a distance of 9 m). Similar to the predominant effects of prairie vegetation on soils underneath (Figure 3.1), positive PS effects occurred more often in 2019 when cropland was under soybean (Figure 3.4). PS significantly increased three hydrolytic PEAs – BGase by 27%, NAGase by 31%, and PHOSase by 38% – in 2019 compared to cropland control across all distances. In 2020 under maize, however, there was a PS Treatment × Distance interaction on

LAPase, whereby the PS increased LAPase PEA by 164% but only 0.3 m downslope from the PS compared to control (Figure 3.4). In 2020, There was also a significant positive main effect of PS on PERase, where PS increased adjacent cropland PERase by 29% compared to the control across all distances.

The principal component analysis (PCA) revealed greater heterogeneity overall in 2019 compared to 2020 (Figure 3.5). PCA axes 1 and 2 explained 43% and 18% for 2019 and 45% and 14% for 2020. Treatment affected PC 1, and catchment affected PC 1 and PC 2 in 2019. Catchment affected PC 1 and PC 2 in 2020. Loadings for variables on PC 1 in 2019 were ranked: BGase, PHOSase, CBHase, and NAGase. For PC 2, the most important variables were PPOase, PERase, and LAPase. Loadings for PC 1 in 2020 ranked: BGase, CBHase, PHOSase, NAGase, and LAPase. Important variables for PC 2 in 2020 were PPOase and PERase.

4. Discussion

There were strong effects of PS both on the soil beneath and adjacent cropland soil biochemistry, but they were highly dependent on the cropping year. The cropping effect was further confounded by weather differences between the years. There was a wet spring in the 2019 soybean year, and the 2020 maize year was dry. These clear but inconsistent effects indicate that the factors that make each year different alter the effects of PS on soils under the PS and in the adjacent cropland. These consistent and inconsistent patterns are discussed further below and put in the context of grassland restoration and ecotone literature. This discussion is separated by the effects of PS on soils underneath – which are more analogous to traditional land-use change studies converting cropland to restored grasslands – and on adjacent cropland soil. Some of the effects of PS on adjacent cropland soil are surprising, and additional research is needed here to explain some of these findings.

4.1. PS affected C, N, and enzyme activities underneath the PS

Generally, 12-13 years of PS had positive effects on soil C and N pools and hydrolytic PEAs, supporting our hypothesis, with the exception of inorganic N and SOC (Figures 3.2 & 3.3). The PS effect on both dynamic pools of soil C and N and PEAs highly depends on the year.

It was not surprising that PS did not significantly increase SOC or TN after 13 years. When comparing bulk density, SOC, and SOM concentrations, we found 12% more SOM under the PS than the control, but differences in bulk density minimize this change (Figure 3.6). Recent interest in voluntary C markets has driven public and scientific interest in tracking changes in SOC after a change in management practice (Keenor et al. 2021). However, we know that inherent variability, measurement error, and slow change in SOC contribute to difficulty tracking changes. This appears to be especially true for Mollisol soils of the Midwest, USA. For example, several studies in Iowa have found no significant change in SOC from 11-year conversion to prairie (Dietzel, Liebman, and Archontoulis 2017; Ye and Hall 2020), 40-year chronosequence of grasslands (De et al. 2020), nor a 15-year comparison of conventional versus diversified cropping systems (Poffenbarger et al. 2018). However, other studies have found increases in SOC over time with changes in vegetation and farming practices. Al-Kaisi & Kwah Mensah (2020) measured SOC from 0-60 cm annually in seven 12-year tillage experiments and observed changes in SOC from -0.39 to +0.38 Mg C ha^{-1} y^{-1}. De et al. (2020) summarized several grassland restoration chronosequence studies in the US and found SOC increases by about 1.6% SOC per year or 0.42 Mg C ha^{-1} y^{-1}. However, these measurements have wide variability, and their study did not find a detectable difference in SOC concentration even at 40 years.

Prairie strips had the most consistent effect on soil microbial biomass C and N (Figure 3.1). It is well documented in several other studies that prairie restoration increases microbial biomass by 100 to 500% (Bach and Hofmockel 2015; Purakayastha, Smith, and Huggins 2009;

Rosenzweig et al. 2016). Despite a consistent positive effect of prairie or grassland restoration on microbial biomass, the magnitude of the effect may depend on variability in annual weather or surrounding management, as we showed some variation between years (Figure 3.1). Annual weather may be the most important driver of variability in the magnitude of PS effect on microbial biomass, as was found in the third year of restored prairie in IA (Bach & Hofmockel (2015)

There were clear positive effects of PS on hydrolytic PEAs (esp. CBHase, NAGase, and PHOSase), but mostly in 2019. This divergence between the consistent increase in microbial biomass and the inconsistent effect of PS on PEAs implies that PEAs are not increasing or decreasing because of increases in the microbial population but because of year-to-year shifts in available resources to plants and microbes. CBHase degrades cellulose and may increase in the presence of increased cellulose (i.e., plant residue) (German, Chacon, and Allison 2011). NAGase degrades chitin and is considered a C and N-acquiring enzyme. Our finding is consistent with other studies that found grasslands increase NAGase activities compared to cropland (Shahariar et al. 2021; Xu et al. 2019). This elevated activity may be due to the decrease in N under the PS (Figure 3.1; CHAPTER 2). In addition, Xu et al. (2019) suggested that elevated NAGase activity could indicate microbial demand for organic forms of N, such as dead fungi cell walls made of chitin (Guggenberger et al. 1999). Phosphatase activity was only elevated under PS in 2019 (Figure 3.2). Phosphatase cleaves PO_4 from organic sources and can be secreted by plants and microbes (Utobo and Tewari 2015). Elevated PHOSase activity might be an artifact of the increased plant roots and competition for the organic P in the PS as P fertilizer is not added to the PS (Curtright and Tiemann 2021; Margalef et al. 2017). In 2019 the adjacent cropland was planted in soybeans, and no N fertilizer would have been added. This coincided with the PS causing a depletion of plant-(bio)available N (ammonium and nitrate) both under the PS (Figure 3.1) in the adjacent cropland soils (Figure 3.3; CHAPTER 2). This may be some evidence for the effect of the adjacent cropland management on soil functioning under the PS.

There were clear negative effects of the PS on oxidative PEAs (PPOase and PERase) that were somewhat consistent (Figure 3.2). PPOase can degrade lignin or humus, detoxify phenolic compounds and metal ions, and as an antimicrobial defense (Sinsabaugh 2010). PERase activity can also indicate lignin degradation, detoxification, and oxidative stress (Sinsabaugh 2010). The reduction in PPOase and PERase activity, but significant in different years, under PS can most parsimoniously be attributed to the aforementioned increase in labile C and N pools (microbial biomass) and decrease in plant-available N. This is consistent with other grassland restoration studies that find a 39% decrease after converting cropland to grassland (Wang et al. 2011). Polyphenol oxidase activity was diminished under the PS in 2020 (Figure 3.2). This reduction in 2020 has very similar implications to the PERase reduction in 2019.

4.2. PS had minimal effects on adjacent cropland C and N pools, but strong effects on potential enzyme activities

Prairie strips had minimal effects on the adjacent cropland C and N pools after 12-13 years (Figure 3.3). Inorganic N, ammonium and nitrate, and SOC concentration are notable exceptions. Inorganic N was decreased near the prairie strip in the soybean year, and SOC concentrations were reduced across the PS treatment (Figure 3.3). However, samples taken from 2005 showed that PS catchments began with insignificantly lower SOC concentrations (Figure 3.6). This highlights the importance of taking a baseline sample before comparing two treatments

(Sanderman and Baldock 2010). If we had not sampled SOC before implementing prairie strips, we might have concluded that PS decreased SOC in adjacent cropland.

Prairie strips had decreased plant-available N in the adjacent soils, but only in 2019 when cropland was under soybeans. A prior study also showed PS altered other plant-available nutrients in adjacent cropland (CHAPTER 2). This study showed nitrate was reduced by 23% in soil within 1 m of the PS (CHAPTER 2). The change in plant-available nutrients, especially mobile nutrients, might be due to greater uptake under PS or PS changing belowground water balance either by increasing evapotranspiration or limiting subsurface flow and transport of nutrients.

Contrary to our hypothesis, PS increased some PEAs in adjacent croplands depending on the year and distance from the PS in one case (Figure 3.4). Surprisingly three enzymes – BGase, NAGase, and PHOSase – were all greater in cropland adjacent to the PS than in control catchments regardless of distance from the PS. The latter two hydrolytic enzymes were also found to have greater activities under the PS, but BGase was not. BGase is a C-acquiring enzyme that tends to be elevated in soils with easily decomposable organic matter (Ferraz De Almeida et al. 2015). Prairie strips have been shown to reduce runoff from catchments, presumably by increasing infiltration (Hernandez-Santana et al. 2013). This increased infiltration in the PS coupled with increased evapotranspiration of the PS could dry out the cropland catchments adjacent to the PS. This drying effect of the PS may increase BGase activity due to a reduction in soil moisture (Figure S3.1; Steinweg et al., 2012). NAGase activities have been correlated to DOC (Wang et al. 2013) and do not seem to be inhibited by increased moisture (Hewins et al. 2016), which was observed in this catchment (CHAPTER 2). Thus, increased NAGase activity may be due to increased microbial activity or change in a resource that was not measured in this study. PHOSase was elevated at all distances from the PS and has been shown to correlate and respond to P availability (Allison and Vitousek 2005; Hernández and Hobbie 2010). Mostly PHOSase decreases with P availability. However, previous research on these soils shows PS only increased Mehlich III P, a plant-(bio)available form of P, <1 m upslope from the PS (Chapter 2), and a reduction in PHOSase activity in this area was not found.

Prairie strips only induced a Treatment x Distance interaction in 2020 for LAPase, an exclusively N-acquiring enzyme that hydrolyzes leucine amino acid from proteins and peptides. Leucine aminopeptidase was elevated downslope of the PS, at the same locations that maize plants were N-stressed or chlorotic measured as greenness on SPAD (CHAPTER 2). These distances from the PS were also depleted in nitrate during 2019. These downslope locations also show lower SOC and TN concentration (Figure 3.3). This all may be coincidental, or more likely, it could be indicators of greater plant and microbe demand for bioavailable N downslope of a PS. This effect could indicate an N demand near the PS that is not alleviated by the N supplied by fertilizer. Peroxidase activity in 2020 was elevated across the entire PS treatment (Figure 3.4). Elevated peroxidase activity in the PS cropland could indicate a C limitation coupled with less labile forms of C since the cropland was fertilized with N, P, and K in 2020.

PCA revealed a treatment effect on PEAs in 2019 but not in 2020. Increased hydrolytic PEAs were associated with increased soil pH and increased microbial biomass in both years. Oxidative PEAs in 2019 were associated with increased Zn, gravimetric water content, P, and S. In 2020, oxidative PEAs were not strongly associated with any measured soil variables. The PS influences soil pH, microbial biomass, Zn, and P under the PS (Chapter 2, Chapter 4). As a whole, PS affected adjacent cropland soil functioning in complex ways that interact with crop/climate year.

5. Conclusion

Prairie strips are a new conservation practice aimed at increasing biodiversity on the landscape, reducing pollution, and regenerating soil health. Some of these benefits have already been documented elsewhere (Kemmerling et al. 2022; Pérez-Suárez et al. 2014; Schulte et al. 2017; Zhou et al. 2014). I examined the soil health effects of the oldest PS in Iowa (12-13 years old). We found that PS had many effects on soil biochemistry underneath the PS and in the adjacent cropland. Prairie strips affected the soil underneath the PS by increasing microbial biomass and PEAs while decreasing salt-extractable inorganic N and oxidative PEAs. PS had little effect on adjacent cropland C and N pools. PS did have strong positive effects on several hydrolytic and oxidative PEAs (BGase, NAGase, PHOSase, and PERase), but the effect depended on the cropping year. Overall, there was strong evidence for positive PS effects on the soil underneath the PS and adjacent to them, but they were strongly dependent on the crop and year.

Future research should explore the effects of PS on deeper soil C and N pools, including total SOC and TN, as the PS are expected to increase carbon at deeper depths. Monitoring the change in SOC and TN further in time could also elucidate what might be happening under and around PS. These findings and a deeper understanding of the PS effect on soils are important to holistically manage agroecosystems and maximize ecosystem services provided by integrating contour PS in the Midwestern US landscape and beyond.

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Tables and Figures

Table 3.1 Extracellular enzymes assayed in this paper and the corresponding substrates.

Enzyme	**EC**	**Abbreviation**	**Substrate**
Arylsulfatase	EC 3.1.6.1	ARSase	4-MUB-sulfate
β-1,4-glucosidase	EC 3.2.1.21	BGase	4-MUB-β-D-glucoside
Cellobiohydrolase	EC 3.2.1.91	CBHase	4-MUB-β-D-cellobioside
β-N-acetylglucosaminidase	EC 3.2.1.14	NAGase	4-MUB-N-acetyl-β-D-glucosaminise
Leucyl aminopeptidase	EC 3.4.11.1	LAPase	L-Leucine-7-amido-4-methylcoumarin
Acid (alkaline) Phosphatase	EC 3.1.3.1	PHOSase	4-MUB-phosphate
Polyphenol oxidase	EC 1.10.3.2	PPOase	L-3,4-dihydroxyphenylalanine
Peroxidase	EC 1.11.1.7	PERase	L-3,4-dihydroxyphenylalanine and H_2O_2

Table 3.2 Prairie strip effects on the soil underneath the strip compared with the control strip (n = 9).

Soil Properties	**Soybean 2019** Treatment p-value	**Maize 2020** Treatment p-value
Soil Organic Carbon	N.D.	0.483
Total Nitrogen	N.D.	0.788
Microbial Biomass C	**0.03**	**0.021**
Microbial Biomass N	**0.014**	**0.02**
Salt-extractable Organic C	0.98	0.259
Salt-extractable Inorganic N	**0.029**	**0.018**
Salt-extractable Organic N	0.131	0.135
Enzyme Activity		
Arylsulfatase	0.348	0.257
β-glucosidase	0.135	0.477
Cellobiohydrolase	**0.01**	0.925
Leucine Aminopeptidase	0.345	0.646
N-acetyl-β-glucosaminidase	**0.023**	0.534
Phosphatase	**0.026**	0.291
Polyphenol Oxidase	0.137	**0.029**
Peroxidase	**0.025**	0.667

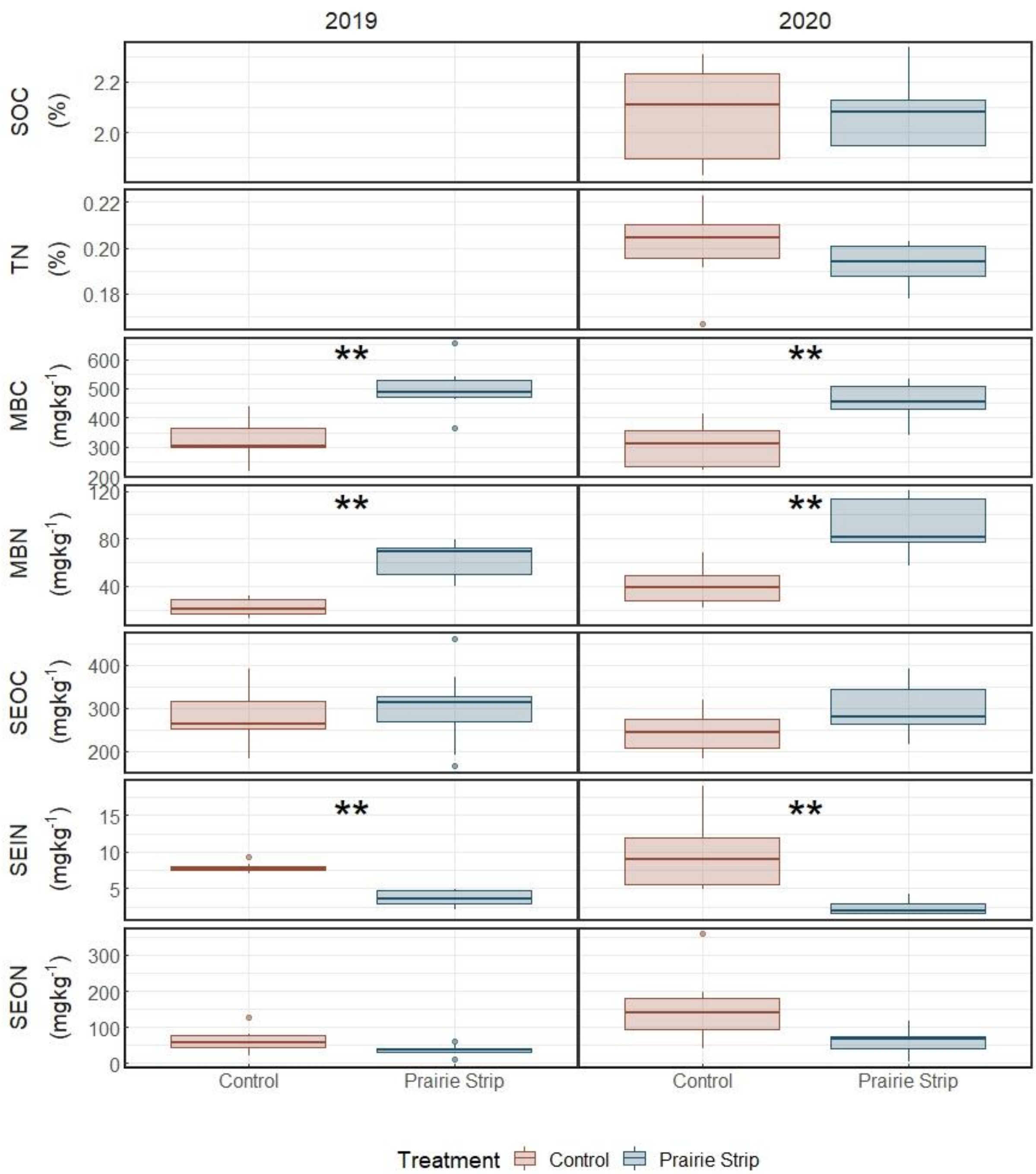

Figure 3.1 Soil carbon and nitrogen pools under prairie strips in 2019 and 2020. Boxplots of n=9 samples across 3 catchments. ** indicates p-value <0.05. Abbreviations: SOC = soil organic C, TN = total N, MBC = microbial biomass C, MBN = microbial biomass N, SEOC = salt-extractable organic C, SEIN = salt-extractable inorganic N, SEON = salt-extractable organic N.

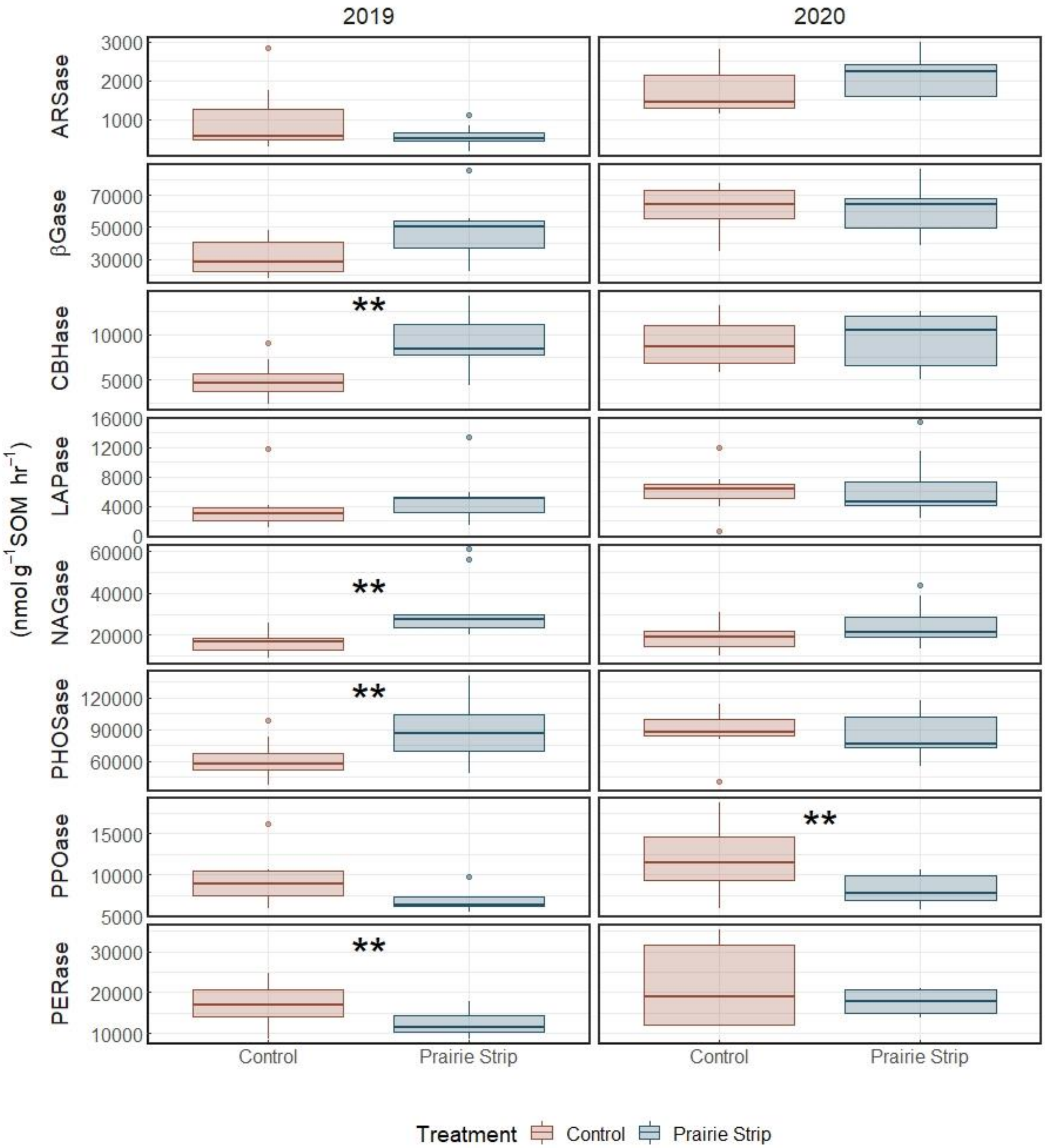

Figure 3.2 Potential enzyme activity per g organic matter under the PS in 2019 and 2020.

Boxplots of n=9 samples across 3 catchments. ** indicates p-value <0.05. Abbreviations: ARSase= arylsulfatase, βGase=β-glucosidase, CBHase=cellobiohydrolase, LAPase=leucine aminopeptidase, NAGase=N-acetyl-glucosaminidase, PHOSase=phosphatase, PPOase=polyphenol oxidase, PERase=peroxidase.

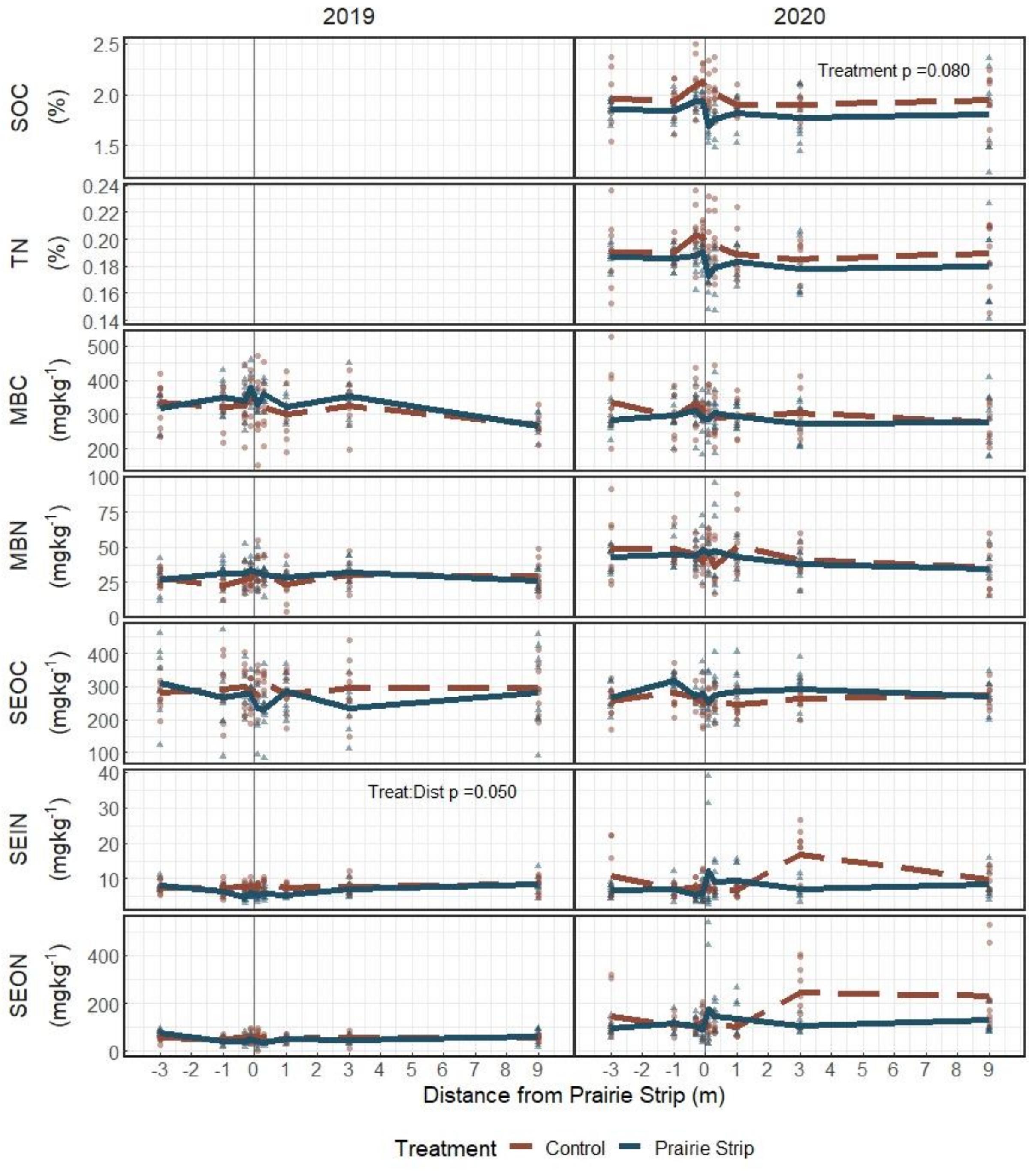

Figure 3.3 Soil carbon and nitrogen pools within cropland adjacent to the prairie strip in 2019 and 2020. Significant treatment or treatment × distance interaction with corresponding p-values shown within graph panels ($p < 0.1$). Insignificant p-values are not shown. Abbreviations: SOC = soil organic C, TN = total N, MBC = microbial biomass C, MBN = microbial biomass N, SEOC = salt-extractable organic C, SEIN = salt-extractable inorganic N, SEON = salt-extractable organic N.

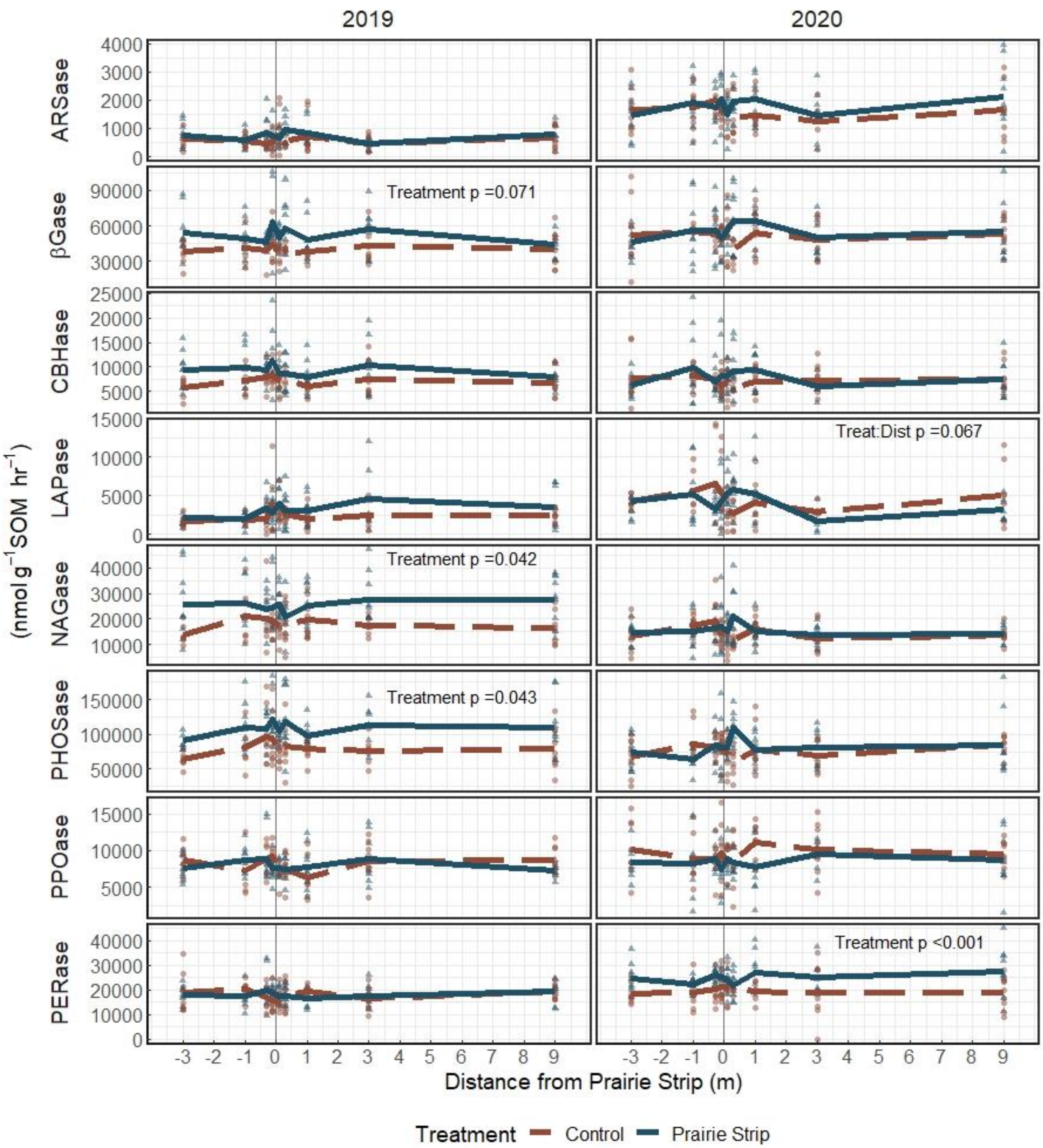

Figure 3.4 Potential enzyme activity per gram of organic matter in cropland adjacent to the PS in 2019 and 2020. Significant treatment or treatment × distance interaction and p-values are shown within graph panels ($p < 0.1$). Insignificant p-values are not shown. Abbreviations: ARSase= arylsulfatase, βGase=β-glucosidase, CBHase=cellobiohydrolase, LAPase=leucine aminopeptidase, NAGase=N-acetyl-glucosaminidase, PHOSase=phosphatase, PPOase=polyphenol oxidase, PERase=peroxidase.

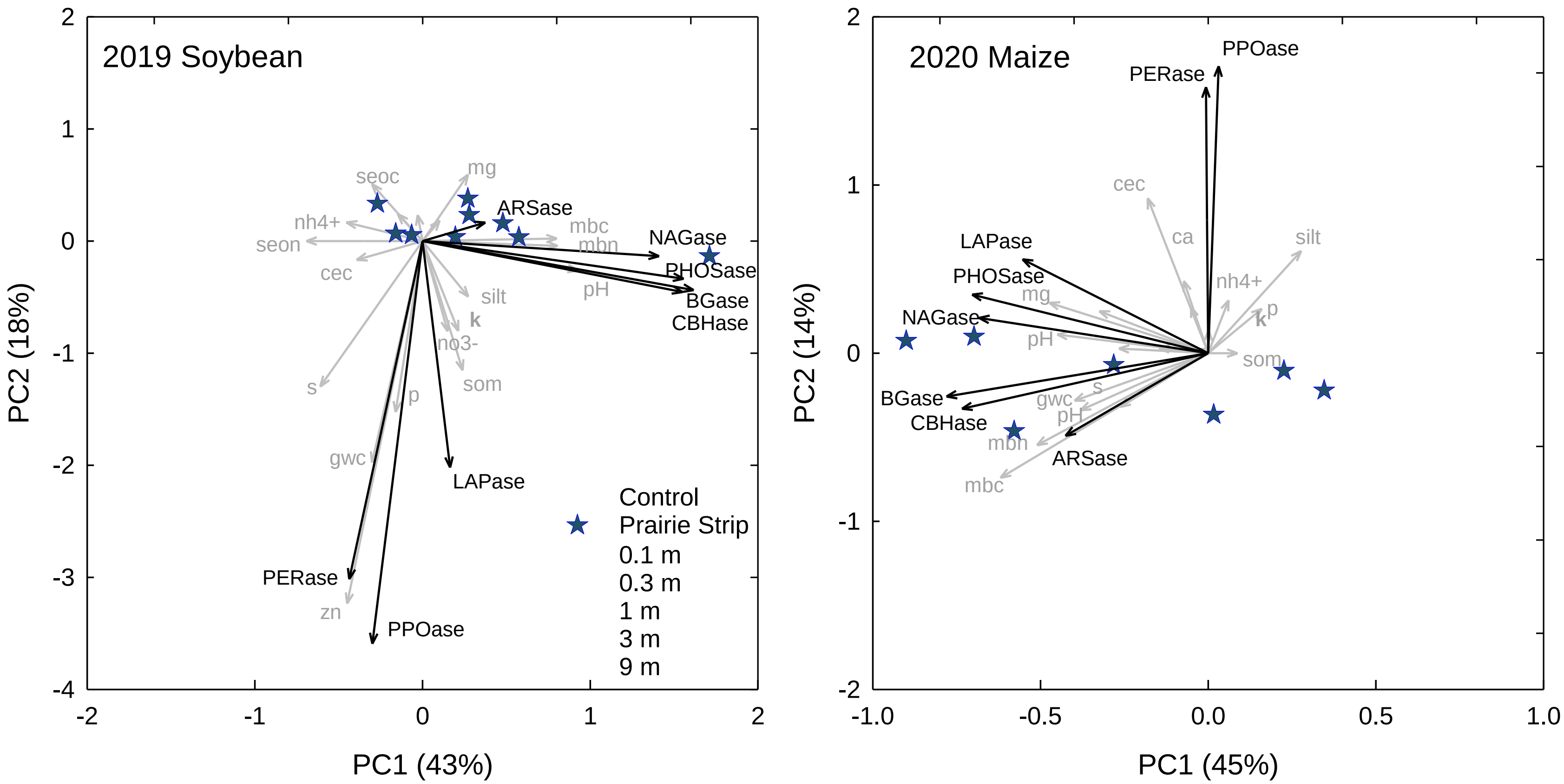

Figure 3.5 Principal component analysis of potential enzyme activity overlaid with explanatory soil data for 2019 and 2020. Prairie strip catchment samples are labeled by distance (Prairie Strip, 0.1 to 9 m), and prairie strip samples are indicated with a star. Black lines indicate enzyme activity vectors; grey lines indicate explanatory soil variables.

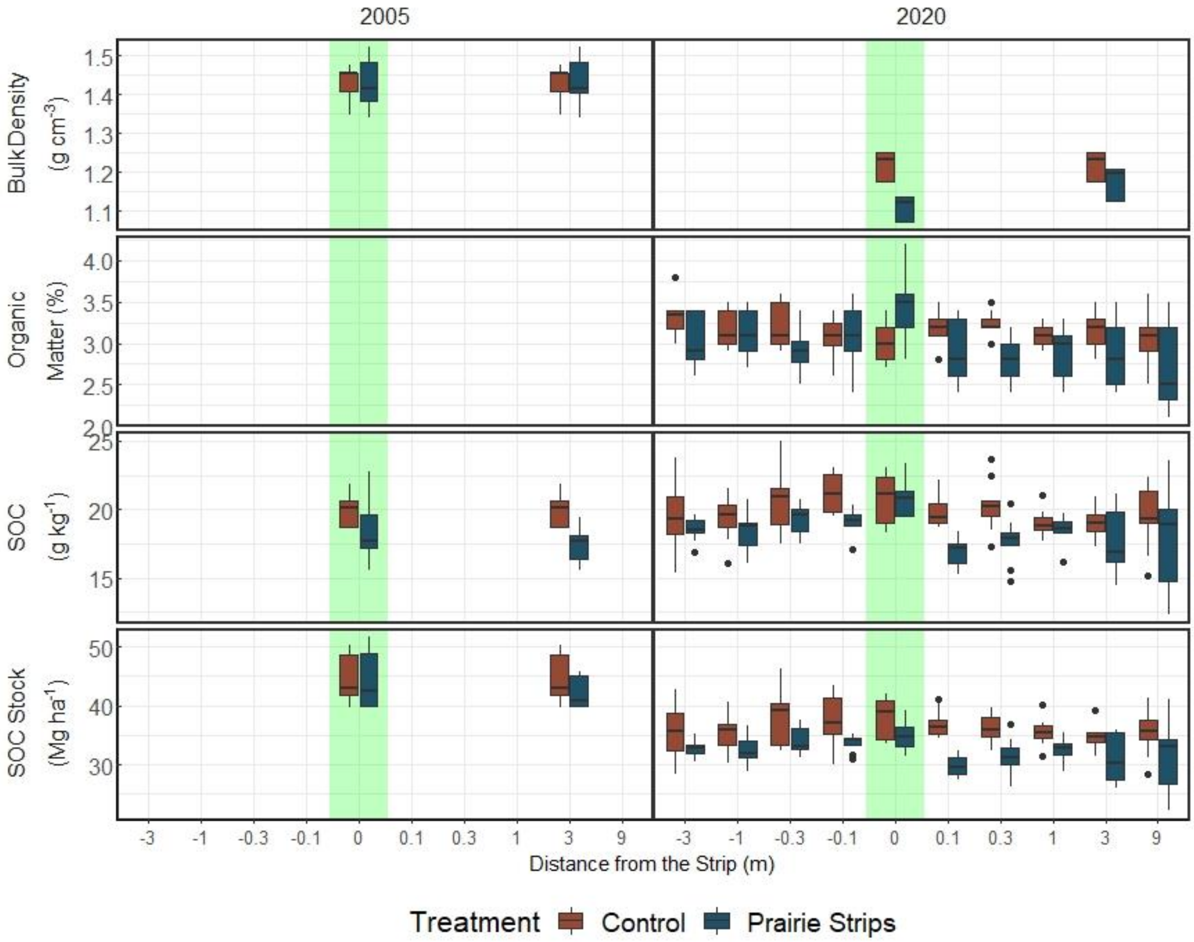

Figure 3.6 Bulk density, organic matter, SOC, and SOC stock as measured in 2005 and 2020.

Samples in 2005 were taken by hillslope position (summit, backslope, toeslope), and GPS locations were used to pair 2020 sampling positions to the 2005 sampling locations. Bulk density samples in 2020 were taken within the prairie strip and 3 m downslope. Cropland bulk density values in 2020 were used at all cropland locations to calculate SOC stock. Green indicated the PS position

Appendix: Supplemental Tables and Figures

Table S 3.1 Prairie strips' effect on adjacent cropland soil compared with the control strip (n=81).

	Soybean			Maize		
	Treatment	**Distance**	**Treat:Dist**	**Treatment**	**Distance**	**Treat:Dist**
Soil Properties						
Soil Organic Matter	0.167	0.331	0.744	0.270	**0.048**	0.868
Soil Organic Carbon	*N.D.*	*N.D.*	*N.D.*	<u>0.080</u>	0.242	0.477
Total Nitrogen	*N.D.*	*N.D.*	*N.D.*	0.277	0.132	0.400
Microbial Biomass C	0.477	**0.002**	0.154	0.605	0.401	0.888
Microbial Biomass N	0.453	0.205	0.446	0.976	<u>0.064</u>	0.979
Salt-extractable Organic C	0.554	0.691	0.167	0.528	0.177	0.637
Salt-extractable Inorganic N	<u>0.065</u>	0.231	**0.05**	0.346	<u>0.078</u>	0.861
Salt-extractable Organic N	0.434	<u>0.095</u>	0.584	0.463	0.117	0.881
Enzyme Activity						
Arylsulfatase	0.186	0.782	0.789	0.316	0.907	0.305
β-glucosidase	<u>0.071</u>	0.985	0.683	0.642	0.969	0.425
Cellobiohydrolase	0.196	0.902	0.915	0.663	0.934	0.736
Leucine Aminopeptidase	0.253	0.349	0.158	0.710	0.847	<u>0.067</u>
N-acetyl-β-glucosaminidase	**0.047**	0.935	0.416	0.573	0.566	0.315
Phosphatase	**0.033**	0.910	0.769	0.509	0.756	0.188
Polyphenol Oxidase	0.942	0.524	0.715	0.379	0.615	0.524
Peroxidase	0.753	0.978	0.433	**<0.001**	0.470	0.334

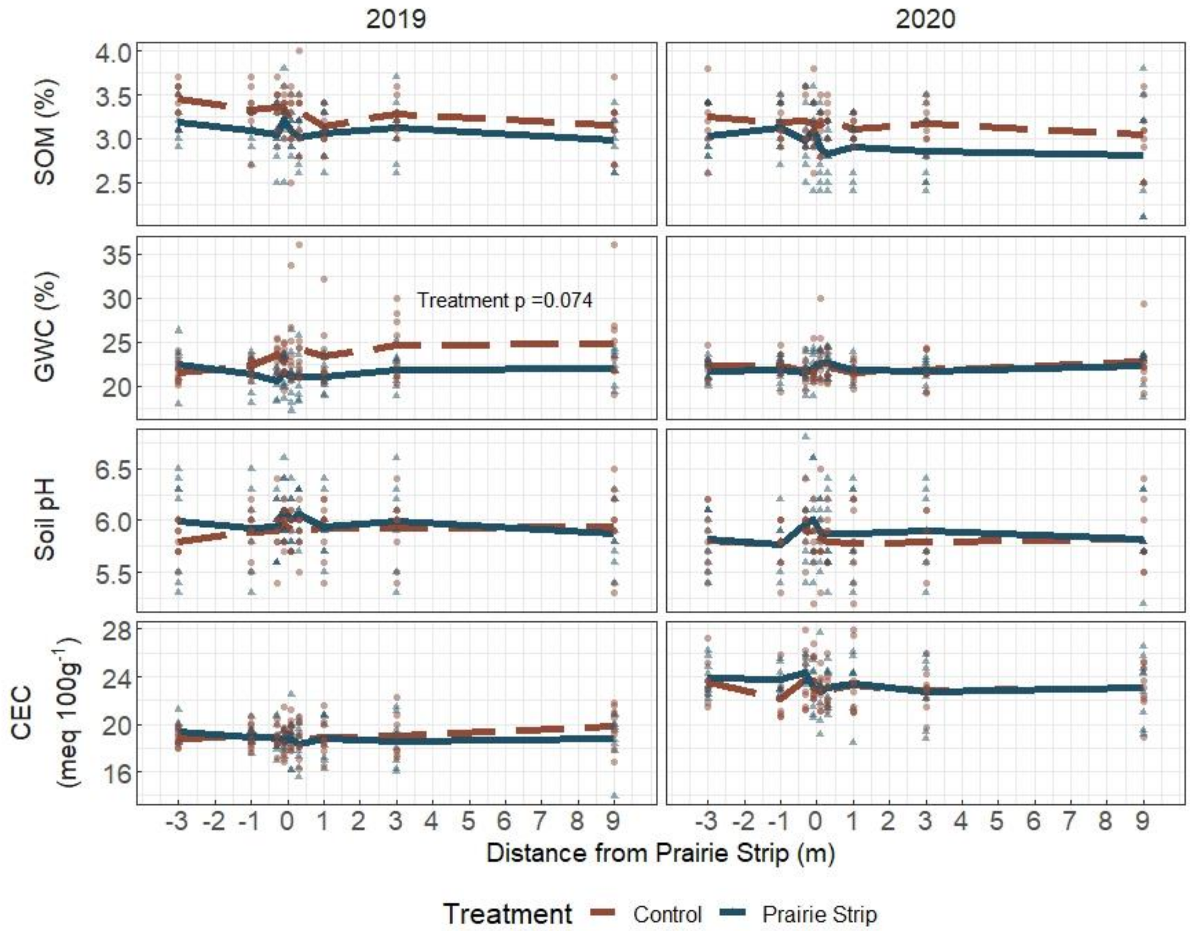

Figure S3.1 Soil properties within cropland adjacent to prairie strips in 2019 and 2020. Significant treatment or treatment × distance interaction and p-values are shown within graph panels (p< 0.1). Insignificant p-values are not shown. Abbreviations: SOM= soil organic matter, GWC= gravimetric water content, CEC= cation exchange capacity.

CHAPTER 4. PRAIRIE STRIPS INCREASE SOIL HEALTH THROUGH TIME WITH MINOR EFFECTS ON ADJACENT CROPLAND

Cole Dutter[1*], Jarad Niemi[2], Marshall McDaniel[1]

1 Iowa State University, Department of Agronomy
2 Iowa State University, Department of Statistics

* Corresponding author
Email: cdutter@iastate.edu
Address:
2531 Agronomy Hall
716 Farm House Lane
Ames, IA 50011
Phone: (515) 350-8286
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Keywords: Conservation Reserve Program, Chronosequence, Ecotone, Intercropping, On-farm research, STRIPS, Tea Bag Index

Abstract:

Prairie strips (PS) are a new conservation practice that has shown disproportional benefits relative to the space they remove from production: improved water quality, reduced sediment loss, nutrient retention, increased microbial functioning, and improved biodiversity. The soil health benefits of PS are just beginning to be explored, and accrual rates of these benefits are still unknown. We used a chronosequence of PS across Iowa, USA, to assess the effect of PS age on active and total soil organic carbon (SOC) and total nitrogen (TN), plant-available nutrients, soil properties, and soil functioning assessed through decomposition. We sampled in the Fall within the PS, 3 m upslope from the PS, 3 m downslope from the PS, and a control field without PS. All sites were in a maize (*Zea mays* L.)-soybean (*Glycine max* (L.) Merr.) rotation. We found that PS had a negligible effect on the adjacent cropland soil properties at a 3 m distance. PS were correlated with increased microbial biomass C under the prairie vegetation at a rate of 16 mg kg^{-1}

y^{-1}, increased and then reduced salt- extractable N over time, and increased organic matter and soil organic C by 0.04% y^{-1} and 0.03% y^{-1}. PS were correlated with reduced soil nitrate-N compared to control fields across all ages and increased ammonium-N by 4% y^{-1}under the PS. Early ages of PS were correlated with a decreased decomposition of materials with wide carbon-to-nitrogen ratios. PS were associated with increased soil C, retention of immobile plant-available nutrients, and a reduction in nitrate-N under the PS. Our findings indicate that PS improve soil health under the PS and has a negligible impact on cropland to ~3 m distance from the PS.

1. Introduction

Land managers have restored grasslands on marginal lands, or those typically with low productivity and vulnerable soils, to mitigate agriculture's environmental ills. These ills include rampant soil erosion (Thaler et al., 2022), loss of nearly half of soil organic matter (Davidson & Ackerman, 1993; Haas et al., 1957), and impaired waterways (Alexander et al., 2008). Grassland restoration in the United States is encouraged through the Conservation Reserve Program (CRP), established in 1985 and has been moderately successful in encouraging land managers to restore grasslands on marginal land (McGranahan et al. 2013; Skold, 1989; Vandever et al. 2021).

While successful at remedying these agricultural issues, grasslands are usually implemented in large contiguous swaths of land that preclude agricultural production and limit grower economic benefits. Alternatively, planting prairie strips (PS) that are >10 m wide (<25% of a given field) provides disproportional environmental benefits while allowing growers to continue cropping the field (Schulte 2017). For example, PS implemented for 4-6 years dramatically reduced nutrient and sediment loss from a catchment (Schulte et al., 2017; Zhou et al., 2014). More recent studies have demonstrated that longer-term implementation of PS, 12-13 years, can also affect the soil under and around the PS (CHAPTER 2; CHAPTER 3). The consistency of the PS effect on soils and how the effect changes with time since implementation remain unknown.

We can generate expectations on how PS might affect the soil under them over time by drawing from grassland restoration chronosequence studies. Generally, these studies report increases in pools of soil microbial biomass, labile resources (extractable or potentially mineralizable pools), and total organic matter with time since grassland restoration (Allison et al., 2005; Baer et al., 2002; Li et al., 2021). More specifically, microbial biomass and other more dynamic or rapid turnover pools tend to increase faster than pools like soil organic carbon (SOC) and nitrogen (N) (De et al., 2020; Li et al., 2021). However, there are key differences between these studies and PS. PS are typically composed of more diverse species mixtures than grasslands (Adler et al., 2009; Hirsh et al., 2013), and they are in narrow strips, which may affect their impact on soils through time.

Monitoring changes in soil under PS through time is key to understanding the belowground dynamics of prairie restoration but is also important within the recent context of increased interest in soil health and C sequestration as an additional source of grower income (Karlen et al., 2021; Keenor et al., 2021). Additionally, with recent work showing PS can affect the adjacent cropland soils after 12-13 years (CHAPTER 2, CHAPTER 3) and somewhat the crops (CHAPTER 2), it remains unknown whether this PS effect on nearby soils occurs immediately after implementation and how it might change through time. Prairie strips affect cropland by reducing nitrate and increasing P and K upslope (CHAPTER 2). Additionally, PS increase microbial biomass C and N underneath and alter potential enzyme activity after 12-13 years both underneath and adjacent to the PS (CHAPTER 3). These prior studies have all taken place at the same PS site and only incorporated older PS. There have not been any studies on PS in a broader context, nor on the accrual rates of such benefits.

We used a chronosequence approach to explore whether the PS effect soil health under the PS and in the adjacent cropland, extend beyond the original experiment, and examine any trends through time. While chronosequences can have their drawbacks (Johnson & Miyanishi, 2008), when sites are appropriately collected and paired with controls, they are an effective way to monitor changes in soil properties through time, especially when funding or other limitations preclude long-term monitoring at one site (Baer et al., 2002; Kucharik, 2007). We monitored PS-induced changes in labile C and N pools, total C and N pools, plant-available nutrients, static soil properties such as pH and cation exchange capacity, and microbial community function measured via decomposition over a 2-to-13-year chronosequence. Our primary objectives were to quantify the PS effect through time on 1) soil properties under the PS and 2) soil properties in the cropland adjacent to the PS (3 m upslope and downslope). Results from this study will improve our understanding of how PS affect soil health under and around them.

2. Materials and Methods

2.1. PS chronosequence site descriptions and experimental design

Sites selected for this paired catchment chronosequence study were located in Iowa, USA, and covered four of seven major landforms in Iowa (Figure 4.1). All sites were in a maize (Zea mays L.)-soybean (*Glycine max* (L.) Merr.) rotation that is common in the Iowan landscape. Each site was sampled in a single year, except the three oldest (NSNWR) sites, which were sampled in 2019 and 2020 (Chapter 2, Chapter 3).

2.2. Soil sampling and decomposition substrate placement

Soil sampling occurred at each site in early October, post senescence but before crop harvest. Soils were sampled along three transects within the PS catchment that ranged from 23 to 293 m apart within the PS catchment, and each transect consisted of three sampling positions (under the PS, 3 m upslope from the PS, 3 m downslope from the PS). Control fields without PS were sampled at three locations of similar hillslope positions and similar watershed contributing areas as the PS samples. Eight soil cores were collected with a 2 cm diameter soil probe at each sampling location to 15 cm depth. Soil cores for each location were composited and stored on ice in a cooler until returned to the laboratory. The soils were sieved (<2 mm) and subdivided for analysis.

About 15 g was weighed and dried at 105°C for 24 h to get gravimetric water content (GWC). To measure microbial biomass C and N, twin replicates from each soil were weighed to ~ 5 g. One replicated was fumigated with $CHCl_3$. Both replicates were extracted with 25 ml of 0.5 M K_2SO_4, non-purgeable organic carbon, and total nitrogen were measured with a Shimadzu TOC-L analyzer (Shimadzu Corporation, Kyoto, Japan) and compared between each replicate (Brookes et al., 1985; Vance et al., 1987). The C and N in the salt-extracted but unfumigated samples are hereafter referred to as salt-extractable organic C (SEOC) and organic N (SEON). A 5 g amount of soil was extracted with 25 ml of 0.5 M K_2SO_4, and extracts were measured for ammonium-N and nitrate-N using a Synergy™ HTX Multi-Mode Microplate Reader (BioTek Instruments, Winooski, VT, USA) with Gen5™ software. The remaining soil was dried and sent to a commercial lab for analysis.

Dried soils were analyzed for plant-available nutrients as assessed with local soil fertility methods. Soil test phosphorus, hereafter just referred to as Phosphorus, was extracted with 2 g per 20 ml of Mehlich III extract and analyzed on an ICP-OES 7300 Machine (Perkin Elmer, Waltham, MA, USA). Potassium, Calcium, and Magnesium were extracted using a Mehlich III extraction, 2 g soil to 20 ml extractant, and were read on an ICP-OES 7300 Machine (Perkin

Elmer, Waltham, MA, USA). Sulfur was extracted with a Monocalcium Phosphate extraction, 10 g soil to 25 ml of extractant, and read on an ICP-OES 7300 Machine (Perkin Elmer, Waltham, MA, USA). Zinc was measured using a diethylenetriaminepentaacetic acid extraction, 10 g soil to 20 ml extractant, and read using an ICP-OES 7300 Machine (Perkin Elmer, Waltham, MA, USA). Soil organic matter (SOM) was measured using loss on ignition for 2 hours at 360 ℃ using a Blue M oven and TSI weighing system. Sixty-six of 216 soil samples with a pH >6.6 were acid fumigated before the SOC analysis. SOC and TN analysis was performed using a ThermoFinnigan Delta Plus XL mass spectrometer attached to a GasBench II with a CombiPal autosampler.

Decomposition materials consisting of green tea (*Camellia sinensis* (L.) Kuntze), red tea (*Aspalathus linearis* (Burm. f.) R. Dahlgren), and birch (*Betula spp*.) tongue depressors were deployed at each of the sampling locations in early June (Keuskamp et al., 2013; Middleton et al., 2021). Both green and red tea was packaged in nylon mesh bags (mesh size 0.25 mm); the birch sticks were encased in nylon mesh (1 mm). The tea was buried at a depth of 5 cm, the 15 cm long birch sticks were buried vertically, and >2cm of soil covered the top of the stick. The tea was collected at 7- and 100-day intervals. The birch tongue depressors were collected at 60- and 100-day intervals. Upon collection, tea was extracted from the tea bag and weighed. After collecting the birch sticks, the sticks were oven dried at 50℃, then weighed for dry mass. Tea bags were placed in a muffle furnace to get ash content. The final weights of both tea and birch stick were used to calculate a % mass loss for each substrate.

2.3. Data handling and statistical analysis

For comparison between PS and control catchments, data from each sampling location (PS, 3 m upslope, 3 m below, control) at each site were averaged to create a single value. The samples from the PS catchments (PS, 3 m upslope, 3 m below) were then converted to a raw difference from the control for each site. The resulting differences were then analyzed via a mixed linear model. The fixed effects were the age of PS (Age; a continuous variable from 2 to 13), distance from PS (Distance; with categorical variables of PS, 3 m upslope, 3 m below), and an Age × Distance interaction. The random effect was the site (n = 15). Both sample years were analyzed since each PS site year was connected with the corresponding control site year. Thus, the sample year would not affect the response to the PS age. The unknowns were estimated via residual maximum likelihood (REML) using the software defaults in lme4 (Bates et al., 2015) and emmeans (Lenth, 2021). The results of this analysis are interpreted as follows: an Age effect constitutes a change across all sample distances with time, a Distance effect constitutes an effect at one or more sample distances, and an Age x Distance effect constitutes an age effect at one or more sample distances.

3. Results

The chronosequence consisted of 18 site-years, each with a paired control catchment, with years since implementing PS: 2 (n=2), 3 (n=3), 4 (n=1), 5 (n=2), 6 (n=2), 7 (n=1), 8 (n=1), 12 (n=3), and 13 (n=3) years (Table 4.1). Selected sites ranged in age from the second year to 13 years since prairie establishment, and approximately half of the sites were commercial farms (Table 4.2). NSNWR sites had smooth brome (Bromus inermis L.) cover for ~before the PS establishment, whereas, to our knowledge, the other farms had been cropped previously (Table 4.2). At five sites, the location of the PS catchment was randomly chosen; at ten sites, the location of the PS treatment was not randomly chosen but chosen by the farmer based on their preference (Table 4.2).

3.1. Descriptive statistics across all sites and climate context

The sites selected across the state of Iowa, USA, ranged in climate, soil texture, and soil properties (Table 4.1). Each site consisted of paired catchments that ranged from 0.84 to 85 ha. Mean annual precipitation ranged from 923 to 1160 mm of rainfall, with the mean being 967 mm (Table 4.1). The mean annual temperature ranged from 7.9 to 10.2 ℃ (Table 4.1). Soil texture ranged from 23 to 32% clay and 18 to 40% sand (Table 4.1). The means for sand and clay were both 26%. Soil pH across all sites ranged from 5.7 to 7.5, with a mean of 6.4 (Table 4.1). Soil organic matter ranged from 1.7 to 4.0%, with a mean of 3.0% (Table 4.1). Additionally, this study had low CVs across all of the soils. Soil organic matter, cation exchange capacity, and percent sand were the largest three CVs at 22, 22, and 30, respectively (Table 4.1).

3.2. PS effects on dynamic carbon, nitrogen, and nutrient pools

The PS had strong effects on dynamic soil variables through time, but these effects were mostly under the PS rather than the adjacent soil (Table 4.3). PS had no effect under the PS or in the adjacent cropland on magnesium, calcium, or sulfur. Salt-extractable organic C (SEOC) decreased under the PS by 20 mg kg^{-1} and decreased 3 m downslope from the PS by 21 mg kg^{-1} compared to the control (Figure 4.2). PS had marginally lower SEOC under the PS and downslope from the PS compared to upslope from the PS (Table 4.3). Regardless of age, soil nitrate-N decreased under the PS by 8.6 mg N kg^{-1} compared to the control catchments, and PS had reduced nitrate-N by 11 mg N kg^{-1} and 10 mg N kg^{-1}compared to upslope and downslope from the PS, respectively (Table 4.3; Figure 4.3). PS had a marginal effect on zinc (Zn) upslope and downslope from the PS; Zn decreased upslope from the PS by 1 mg kg^{-1} and downslope from the PS by 0.7 mg kg^{-1} compared to the control catchments. PS had marginally lower Zn than downslope from the PS (Table 4.3; Figure 4.3).

Microbial biomass C (MBC) increased underneath the PS by 16 mg C kg^{-1} y^{-1}(Table 4.3; Figure 4.2). MBC increased under the PS by 8 mg C kg^{-1} y^{-1} compared to upslope from the PS and 7 mg C kg^{-1} y^{-1} compared to downslope from the PS. PS had a marginal effect on microbial biomass N (MBN) underneath the PS compared to the control locations ($p = 0.07$); MBN increased under the PS by 1.4 mg C kg^{-1} y^{-1} (Figure 4.2). Salt-extractable organic N (SEON) increased underneath the PS by 1.2 mg kg^{-1} and decreased SEON with time since implementation under the PS by 0.2 mg kg^{-1} y^{-1} compared to the control catchments. SEON increased under the PS with time since implementation by 0.2 mg kg^{-1} y^{-1} compared to upslope and downslope from the PS (Table 4.3; Figure 4.2). Ammonium-N increased under the PS with time since implementation by 0.06 mg N kg^{-1} y^{-1} compared to the control catchments. Ammonium under the PS increased with time since implementation by 0.04 mg N kg^{-1} y^{-1} compared to upslope from the PS and by 0.06 mg N kg^{-1} y^{-1} compared to downslope from the PS (Table 4.3; Figure 4.3). Phosphorus (P) decreased upslope from the PS by -37 mg kg^{-1} and P increased with time since implementation upslope from the PS by 4 mg kg^{-1} y^{-1} compared to the control catchments (Figure 4.3). Potassium (K) decreased upslope from the PS by -181 mg kg^{-1}, and K increased with time since implementation by 26 mg kg^{-1} y^{-1} under the PS and 22 mg kg^{-1} y^{-1} upslope from the PS compared to the control catchments. Potassium increased with time since implementation by 4 mg N kg^{-1} y^{-1} underneath the PS compared to upslope and downslope from the PS (Table 4.3; Figure 4.3).

3.3. Prairie strips age effects on static soil properties

Prairie strips strongly affected the static soil variables, but these were mainly isolated under the PS (Table 4.3). PS had no effect under the PS or in the adjacent cropland on soil water holding capacity, cation exchange capacity, or total N. Soil organic matter (SOM) increased with time since implementation by 0.04% y^{-1} under the PS compared to the control catchments

(Figure 4.4). SOM increased with time since implementation by 0.03% y^{-1} under the PS compared to upslope and downslope from the PS (Table 4.3). Soil organic C (SOC) increased with time since implementation by 0.03% y^{-1} under the PS compared to the control catchments (Figure 4.4). SOC increased with time since implementation by 0.04% y^{-1} under the PS compared to upslope and downslope from the PS (Table 4.3). Soil pH decreased with time since implementation by 0.03 y^{-1} under the PS compared to the control catchments. Soil pH decreased with time since implementation by 0.02 y^{-1} under the PS compared to upslope from the PS and 0.01 y^{-1} compared to downslope from the PS (Table 4.3; Figure 4.4).

3.4. Prairie strips age effects on decomposition

Prairie strips had minimal effect on the decomposition of substrates. PS had a marginal effect on the decomposition of the 60-day birch stick under the PS (Table 4.3; Figure 4.5). PS decomposed 0.3% y^{-1} more than upslope and downslope from the PS. PS age had a marginal effect on decomposition at all PS catchment locations for the late red tea substrate (100 day). PS decreased decomposition upslope from the PS by 8% (Figure 4.5).

4. Discussion:

Our results suggest some soil health indicators saw improvement across time under the PS – comparable to studies on large swaths of grassland restoration (Baer et al., 2002; De et al., 2020; Li et al., 2021). We also found some minor soil health impacts within 3-m of the PS in the adjacent cropland soil.

4.1. PS effects on soil health underneath the PS

Labile organic C was affected by the presence of PS but not by the time since PS implementation (PS age). Prairie strip soil started with a lower concentration of labile organic C than the control (Table 4.3; Figure 4.2). This reduction in labile organic C could be attributed to the rapid incorporation of soil microorganisms and plants (Fischer et al., 2010; Kuzyakov &

Jones, 2006). Nitrate-N availability under the PS averaged ~9 mg kg^{-1} less than the control locations regardless of PS age (Figure 4.3). This might indicate that PS reduce excess soil nitrate quickly after implementation. However, this finding contradicts Baer et al. (2002), who found that nitrate decreased over time with prairie reconstruction in the top 10 cm, but not in the 10- 20 cm depth. A previous study also found that PS reduced nitrate in groundwater and vadose zone within the first two years of implementation (Zhou et al., 2010). Thus, our finding that PS reduce soil nitrate underneath them in that timeframe is reasonable.

Over time, microbial biomass C increased under the PS (Figure 4.2). MBC is a sensitive biological indicator due to its ability to respond to management (Insam, 2001). Microbial biomass is important for nutrient cycling and accumulation of soil organic C (Ma et al., 2018). Prairie strips increase MBC by increasing root inputs to SOM (Bach & Hofmockel, 2015), plant litter (Jin et al., 2010), and increased moisture content (Wiesmeier et al., 2013). This finding is corroborated by other findings correlating MBC and time since restoration (Allison et al., 2005). Microbial biomass N (MBN) responded marginally to the presence of PS and PS age (Figure 4.2). This is somewhat expected because prairies tend to be N limited, especially since these PS were not fertilized (Owensby et al., 1970; Risser & Parton, 1982). Labile organic N within the PS decreased over time after starting with a higher concentration than the control fields (Figure 4.2). This decline in labile organic N may be due to the increased microbial biomass coupled with N-limitation, causing tighter cycling of N. This may also indicate a change in the plant litter C:N ratio. Nitrogen limitation can change the percent N of the plant litter that accumulates on the soil (Owensby et al., 1970), and plant litter can influence the labile N portions of the soil (Rosenqvist et al., 2010). This reduction in labile organic N is contrary to other studies' findings, in which dissolved organic N increased with grassland restoration (Yang et al., 2022). Prairie strip age did influence ammonium-N (Table 4.3; Figure 4.3). Ammonium built up under the PS at a rate of ~0.1 mg kg^{-1} y^{-1}. While this may seem inconsequential, it is equivalent to ~4% of the base concentration per year on average. This increase in ammonium corresponding to a reduction in SEON may indicate that the SEON is mineralized by the microbiome and building up in the soil as ammonium. This increase in ammonium with PS age is corroborated by Baer et al. (2002). Phosphorus (P) was significantly correlated with time since PS implementation (Table 4.3). Early PS had far less (~35 mg kg^{-1}) Mehlich III P than the control locations (Figure 4.3) and increased at a rate of ~ 4 mg kg^{-1} y^{-1}. The three-year-old strips heavily influenced this initial reduction and may be an artifact of nutrient management decisions in adjacent cropland or nutrient management decisions in the control fields. Potassium (K) followed the same trend as P, and initial K concentrations in PS are ~175 mg kg^{-1} less than the control locations (Figure 4.3). Three-year-old PS again strongly influenced this trend, which suggests that both initial concentrations for P and K were due to nutrient management decisions during PS establishment or nutrient management in control fields. Potassium did accumulate under the PS at a rate of 26 mg kg^{-1} y^{-1}. This trend was confirmed through another chronosequence that found K depleted through the cultivation of grasslands (Jiao et al., 2012). Organic matter increased under PS at a rate of 0.04% per year faster than in the control locations. Soil organic C also followed this trend under PS, accumulating at a rate of ~0.03% per year faster than the control (Figure 4.4). This finding aligns with many previous studies (Burke et al., 1995; Gebhart et al., 1994, De et al., 2020). Total N (TN) was not affected by the presence of PS or time since PS implementation (Table 4.3). Our study did see a general but insignificant increase in TN through time compared to the control (Figure 4.4). A possible explanation for the lack of significance is that N fertilization can increase TN concentrations in cropland (Chen et al., 2011; Jagadamma et al., 2007), and all control fields received N fertilizer during the maize portion of the crop rotation, whereas the PS were unfertilized. Thus, the control fields may have had elevated TN concentrations due to this fertilization, thus obscuring the increased TN within the PS. Soil pH was affected by the interaction of PS and the age of PS. The soil pH under the PS decreased with age at ~0.03 per year relative to the control, more slowly than the pH decline in the adjacent cropland (Table 4.3; Figure 4.4). This effect was likely due to the increased return of base cations through plant litter and a lack of N fertilization within the PS. Soil water holding capacity and cation exchange capacity were not affected by the PS. Decomposition is a good indication of soil biological activity and soil functioning (Hu et al., 2021; Middleton et al., 2021; Sinsabaugh et al., 1993). The moderate decomposition (60 day) of birch sticks was affected by the age of the PS (Figure 4.5). Compared to adjacent cropland, this reduction in percent mass loss indicated a limitation of nutrients during the season, such as N or P (Sinsabaugh et al., 1993). The moderate timeframe of birch decomposition increased at a rate of 0.3% y^{-1}. The increased decomposition in the older PS suggests that the PS are less nutrient limited than younger PS. Even though the N limitation may be present, there is evidence of a tighter and well-balanced nutrient cycle in the older PS. Secondarily, this increase in decomposition in older PS may indicate a shifting and better-established fungal community (Hu et al., 2021).

4.2. PS effect on nearby cropland soil health

Prairie strip effects on the nearby cropland soil health were negligible. SEOC was marginally reduced downslope from the PS (Figure 4.2). This finding is corroborated by a previous study that found prairie strips reduce dissolved organic export from catchments compared to 100% cropland (Smith et al., 2014). This effect may be caused by a reduction in runoff from the PS (Smith et al., 2014) or the microbial biomass within the PS being highly efficient in incorporating SEOC and not allowing much ‘spillover’ of labile C from the PS (Fischer et al., 2010). PS reduced P upslope from the PS, which may be due to nutrient management decisions for the control catchments. However, the accumulation of P upslope from the strip has previously been reported (Figure 4.3; Chapter 2). This effect is likely due to the perennial vegetation reducing P-laden sediment export (Syversen et al., 2001; Syversen & Borch, 2005). Potassium was reduced upslope from the PS, but this too was likely due to nutrient decisions made within the control catchments (Figure 4.3). Zinc near PS was ~1 mg kg^{-1} less than the control location and did not significantly change with PS age. PS effect on Zn may be due to nutrient management decisions or increased plant uptake of Zn (Figure 4.3). Late red tea decomposition (100 day) was marginally affected by age (Figure 4.5). Decomposition of red tea was also reduced by 8% compared to the control catchments, indicating that PS influences nutrient availability upslope from the PS (Sinsabaugh et al., 1993).

5. Conclusion

Prairie strips are a new management practice to facilitate soil health restoration within actively cropped fields. Many benefits of the ecosystem-scale benefits of PS have already been demonstrated (Schulte et al., 2017). We examined how PS affect soil health over time in sites throughout Iowa, USA. We found that PS are associated with multiple benefits, some of which are instantaneous and others that accrue over time. However, PS generally do not affect the soil health in the adjacent cropland. Prairie strips and time since prairie strip implementation seemed to affect microbial biomass C, salt-extractable organic C and N, organic matter, and percent SOC under the PS. Prairie strips also influenced soil nitrate-N availability, P and K accumulation, and soil pH under the PS. Simultaneously, soil function was also minimally influenced by the presence of PS. Overall, PS correlated with improved soil health through time. Future research should examine nutrient dynamics during the growing season and the optimal timeframe to leave PS in place to maximize soil health benefits before returning the land to production.

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Tables and Figures

Table 4.1 Site abbreviations, time since prairie strip (PS) implementation, soil properties, and climate for each site.

Site	Time Since Implementing PS (years)	Sample Size per PS catchment (n)	Soil Series	Soil pH	Soil Organic Matter (%)	Cation Exchange Capacity (meq/ 100 g)	Soil Water Holding Capacity (%)	% Clay	% Silt	% Sand	Mean Annual Precipitation† (mm)	Mean Annual Temperature† (℃)
CLY	2	12	Nicollet	5.9	2.3	19	67	25	38	38	939	9.8
MCB	2	12	Tama	6.7	3.5	22	89	27	51	21	939	9.8
NYK	3	12	Clearfield	6.3	3.4	29	85	28	54	18	937	10.2
RDM	3	12	Lawler	6.5	4.0	26	83	32	49	19	1065	9.1
STN	3	12	Tama	6.0	3.5	26	72	31	50	18	1160	9.6
SMI	4	12	Clarion	5.9	3.7	34	69	32	40	27	946	8.2
GUT	5	12	Webster	7.5	2.1	26	62	23	37	40	971	9.1
RHO	5	12	Downs	6.7	2.3	22	81	23	50	27	939	9.8
ARM	6	12	Marshall	6.5	2.9	21	78	25	51	24	937	9.6
MCN	6	12	Arispe	6.1	3.4	24	91	27	52	21	972	9.4
SLO	7	12	Readlyn	6.3	2.4	19	61	20	38	41	960	9.2
ROD	8	12	Festina	7.0	1.7	10	73	23	52	25	977	7.9
BW2	12, 13	24	Ladoga	6.2	3.0	23	78	26	52	22	923	9.6
BW5	12, 13	24	Ladoga	6.2	2.9	22	79	24	52	24	923	9.6
INT	12, 13	24	Ladoga	5.7	3.2	26	78	24	52	24	923	9.6
Median				6.30	3.02	22.9	78.1	25	51	24	939	9.58
Mean				6.37	2.96	23.3	76.4	26	48	26	967	9.37
Standard Deviation				0.48	0.65	5.21	9.07	3.61	6.18	7.69	64	0.61
CV%				7.58	22	22	12	14	13	30	6.64	6.47

Table 4.2 Site abbreviations, time since prairie strip (PS) implementation, management history, and farm type for each site.

Watershed	Age	Tillage Prior to Implementation	Crop Prior to Implementation	Prior CRP Enrollment	Randomized Strip Implementation	Farm Type
CLY	2	N/A	N/A	N/A	N	Commercial
MCB	2	None	Soybeans	None	N	Commercial
NYK	3	None	Maize	None	N	Research
RDM	3	Yes	Maize	None	N	Commercial
STN	3	None	Soybeans	None	N	Commercial
SMI	4	Strip-Till	Soybeans	None	N	Commercial
GUT	5	None	Soybeans	None	N	Commercial
RHO	5	Yes	Maize	None	Y	Research
ARM	6	None	Soybeans	None	N	Research
MCN	6	Yes	Soybeans	None	Y	Research
SLO	7	None	N/A	None	N	Commercial
ROD	8	None	N/A	None	N	Commercial
BW2	12 & 13	None	Smooth Brome	N/A	Y	Research
BW5	12 & 13	None	Smooth Brome	N/A	Y	Research
INT	12 & 13	None	Smooth Brome	N/A	Y	Research

Table 4.3 Analysis of variance of measured parameters, rates of change, and associated figures.

Parameter	**Time Since Implementation (df =1)**		**Location* (df =2)**		**Time x Location (df =2)**		Rate of Change (per Location)			Units	Figure
	F-Statistic	**p-value**	**F-Statistic**	**p-value**	**F-Statistic**	**p-value**	Within the PS	3 m Upslope	3m Below		
Dynamic Soil Properties											
Microbial Biomass C	2.53	0.132	0.39	0.680	4.89	**0.013**	**15.7**	6.90	6.54	mg kg^{-1} yr^{-1}	2
Microbial Biomass N	0.18	0.678	0.17	0.844	2.07	0.141	1.40	-0.03	0.16	mg kg^{-1} yr^{-1}	2
Salt-extractable Organic C	0.90	0.356	2.73	0.079	0.50	0.612	1.90	1.11	1.37	mg kg^{-1} yr^{-1}	2
Salt-extractable Organic N	0.02	0.888	7.80	**0.002**	3.15	0.055	**-0.20**	0.11	0.18	mg kg^{-1} yr^{-1}	2
Nitrate-N	0.04	0.848	4.98	**0.013**	0.25	0.780	-0.20	0.02	0.12	mg kg^{-1} yr^{-1}	3
Ammonium-N	0.09	0.764	0.51	0.605	2.79	0.074	**0.06**	-0.06	-0.04	mg kg^{-1} yr^{-1}	3
Phosphorus	5.04	**0.029**	0.32	0.725	0.56	0.576	3.82	**3.92**	3.55	mg kg^{-1} yr^{-1}	3
Potassium	10.84	**0.003**	0.09	0.913	4.07	**0.026**	**26.4**	**22.1**	21.27	mg kg^{-1} yr^{-1}	3
Zinc	0.43	0.518	2.51	0.096	0.88	0.426	0.05	0.05	0.03	mg kg^{-1} yr^{-1}	3
Static Soil Properties											
Organic Matter	0.08	0.786	0.80	0.459	7.96	**0.001**	**0.04**	-0.01	0.00	%	4
Soil Organic C	0.19	0.670	0.27	0.766	4.46	**0.022**	**0.03**	0.01	0.00	%	4
Total N	0.25	0.627	0.06	0.943	1.41	0.263	0.00	0.00	0.00	%	4
Soil pH	1.96	0.177	0.06	0.938	3.31	**0.049**	**-0.03**	-0.06	-0.05	pH	4
Water Holding Capacity	0.89	0.370	1.14	0.331	1.44	0.251	0.62	-0.06	0.15	%	4
Cation Exchange Capacity	0.33	0.575	0.49	0.618	0.27	0.768	0.08	0.17	0.07	meq 100g^{-1} soil	4
Decomposition of Manufactured Substrates											
7-Day Green Tea	0.39	0.550	0.66	0.522	0.44	0.645	-0.02	-0.10	-0.27	%	5
7-Day Red Tea	0.98	0.347	0.65	0.529	0.18	0.835	-0.61	-0.55	0.11	%	5
60-Day Birch Stick	2.79	0.122	2.87	0.072	2.70	0.083	2.17	1.50	0.01	%	5
100-Day Green Tea	0.84	0.380	0.17	0.843	0.26	0.775	-0.04	-0.26	-0.30	%	5
100-Day Red Tea	3.35	0.093	0.65	0.529	0.11	0.899	0.79	0.69	-0.80	%	5
100-Day Birch Stick	0.84	0.374	0.32	0.726	0.33	0.720	2.65	1.92	1.26	%	5

† Underlined values are significant (<0.1) and bolded values (<0.05).

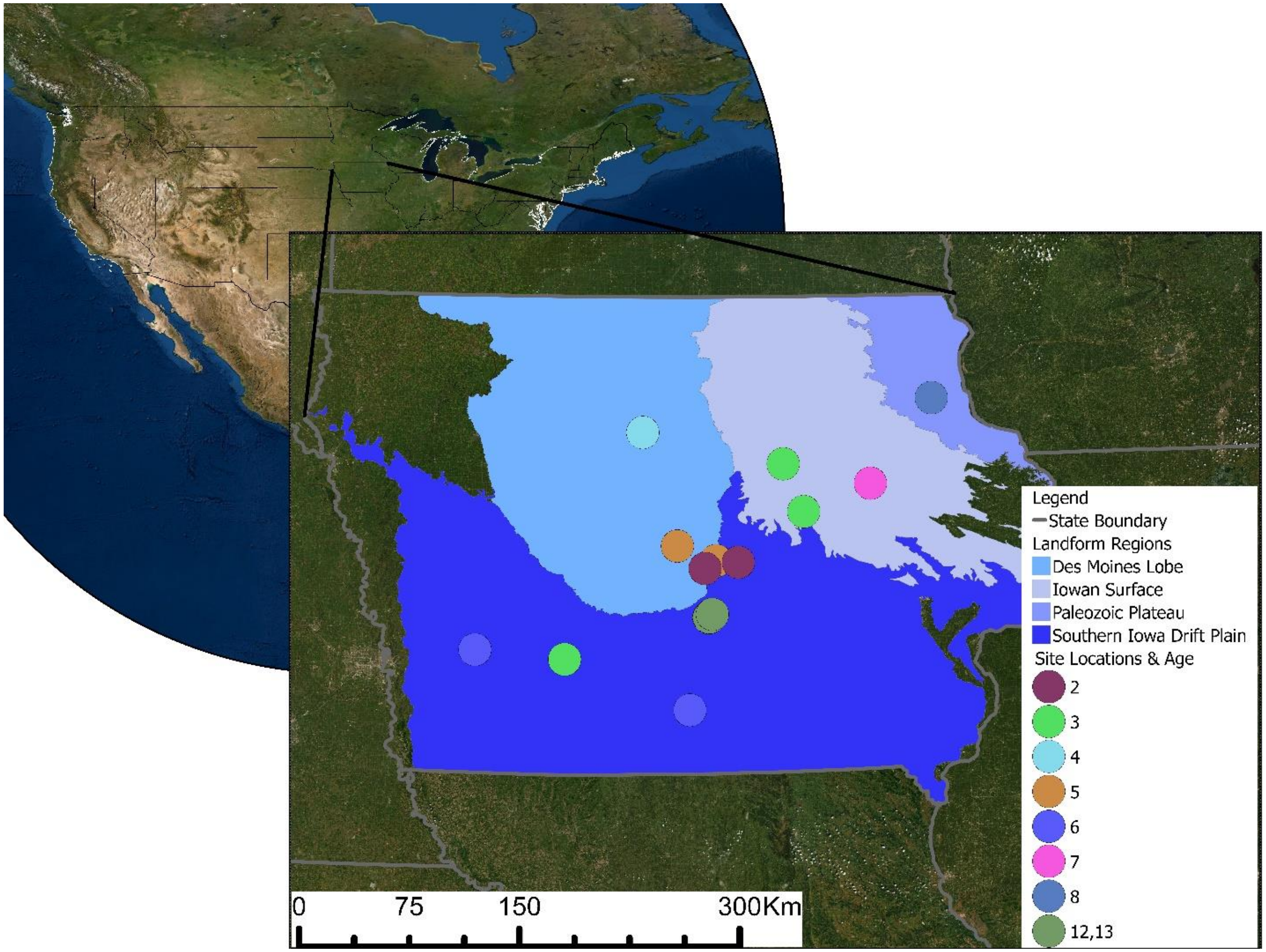

Figure 4.1 Map of sample locations within four landform regions in Iowa, United States. The Des Moines Lobe, Iowan Surface, Paleozoic Plateau, and Southern Iowa Drift Plain are sampled landform regions.

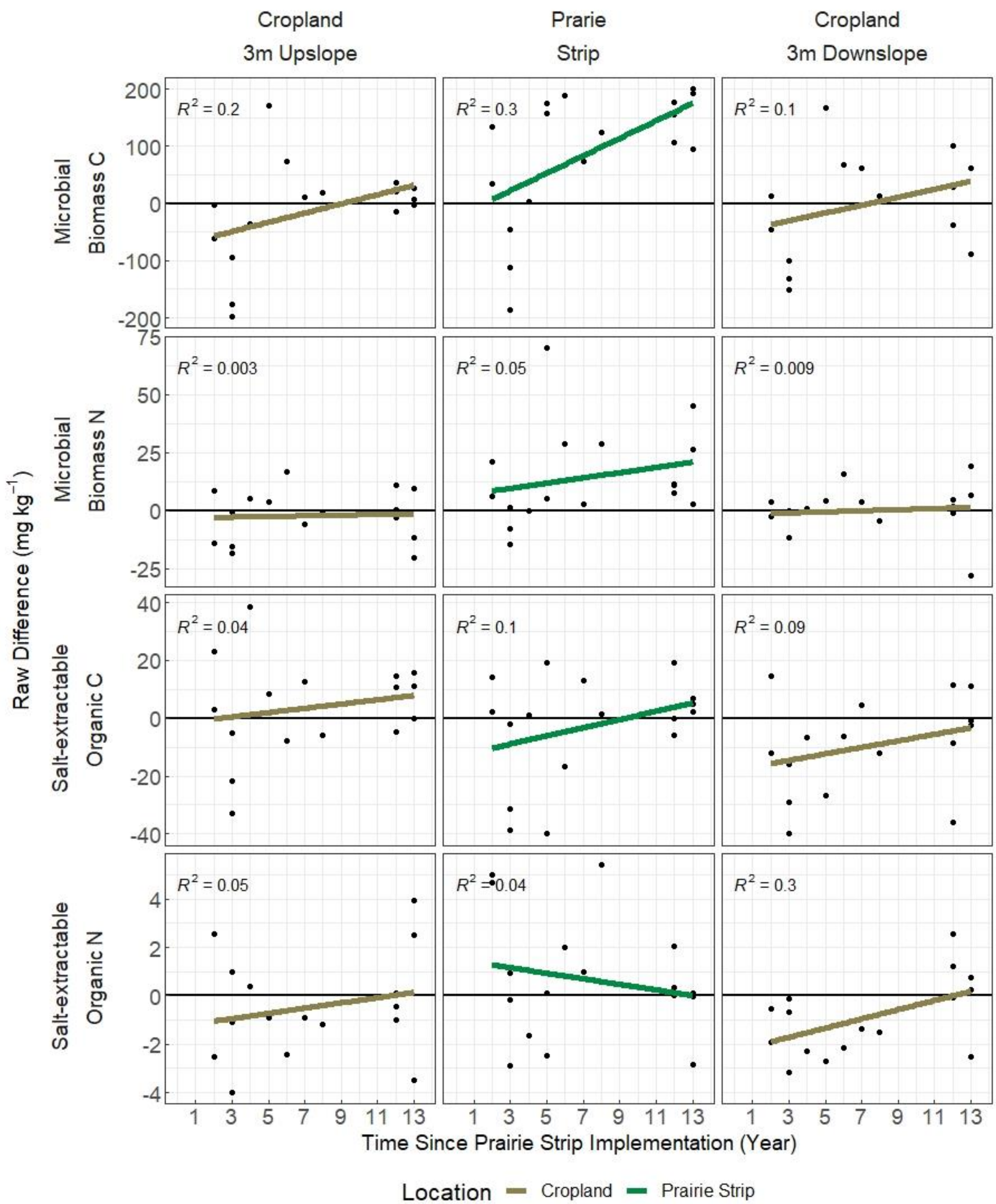

Figure 4.2 Dynamic soil carbon (C) and nitrogen (N) pools from prairie strip sites ranging from 2 years to 13 years of implementation. ’Raw Difference’ values are the difference between the prairie strip treatment locations (3 m Upslope, within the Prairie Strip, and 3 m Downslope) and the control catchments. The regression lines represent the linear regression where the unknowns are estimated via residual maximum likelihood (REML). R^2 values are given for each regression.

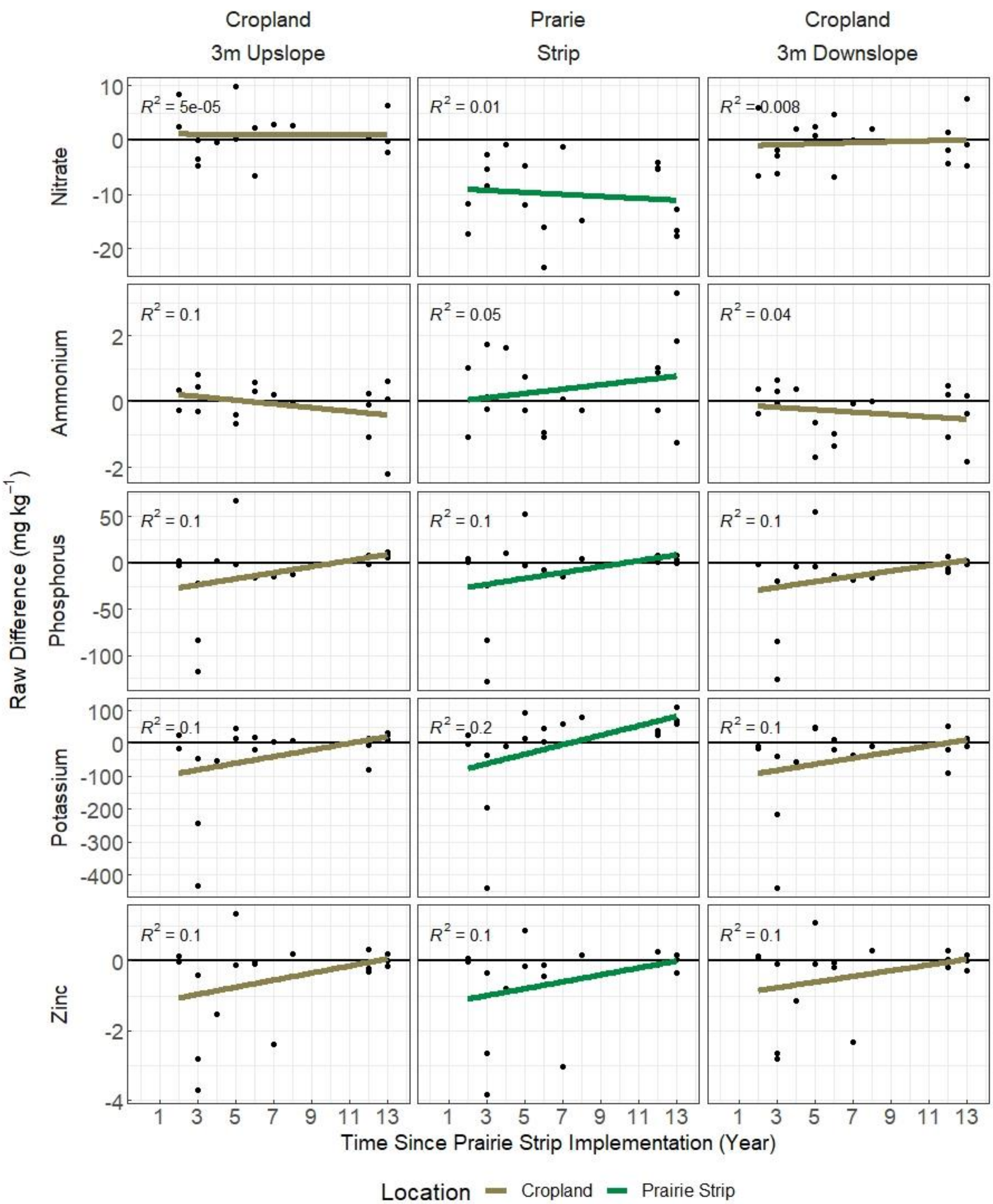

Figure 4.3 Dynamic plant-available nutrients from prairie strip sites ranging from 2 years to 13 years of implementation. 'Raw Difference' values are the difference between the prairie strip treatment locations (3 m Upslope, within the Prairie Strip, and 3 m Downslope) and control catchments. The regression lines represent the linear regression where the unknowns are estimated via residual maximum likelihood (REML). R^2 values are given for each regression.

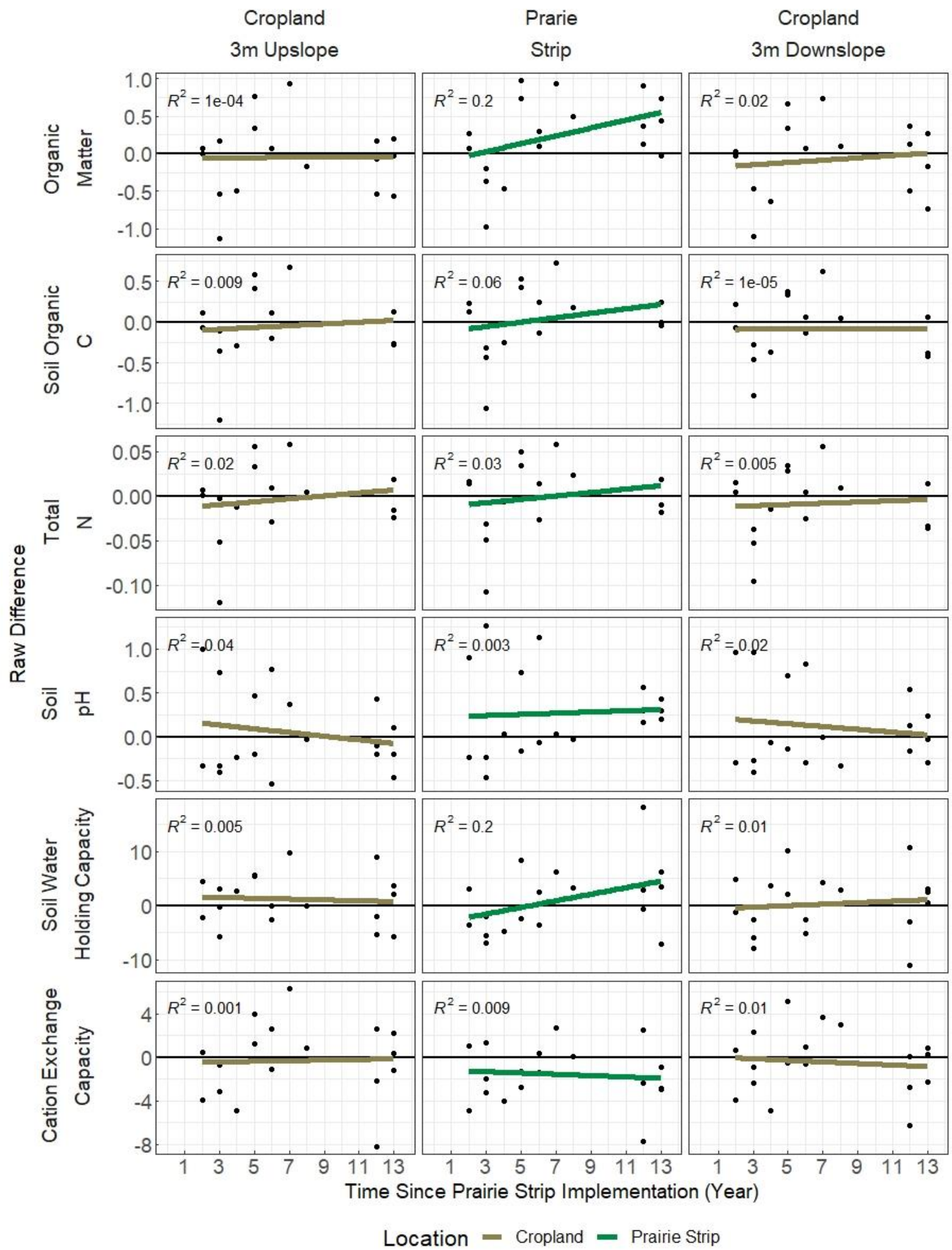

Figure 4.4 Static soil properties from prairie strip sites ranging from 2 years to 13 years of implementation. 'Raw Difference' values are the difference between the prairie strip treatment locations (3 m Upslope, within the Prairie Strip, and 3 m Downslope) and the control catchments. The regression lines represent the linear regression where the unknowns are estimated via residual maximum likelihood (REML). R^2 values are given for each regression.

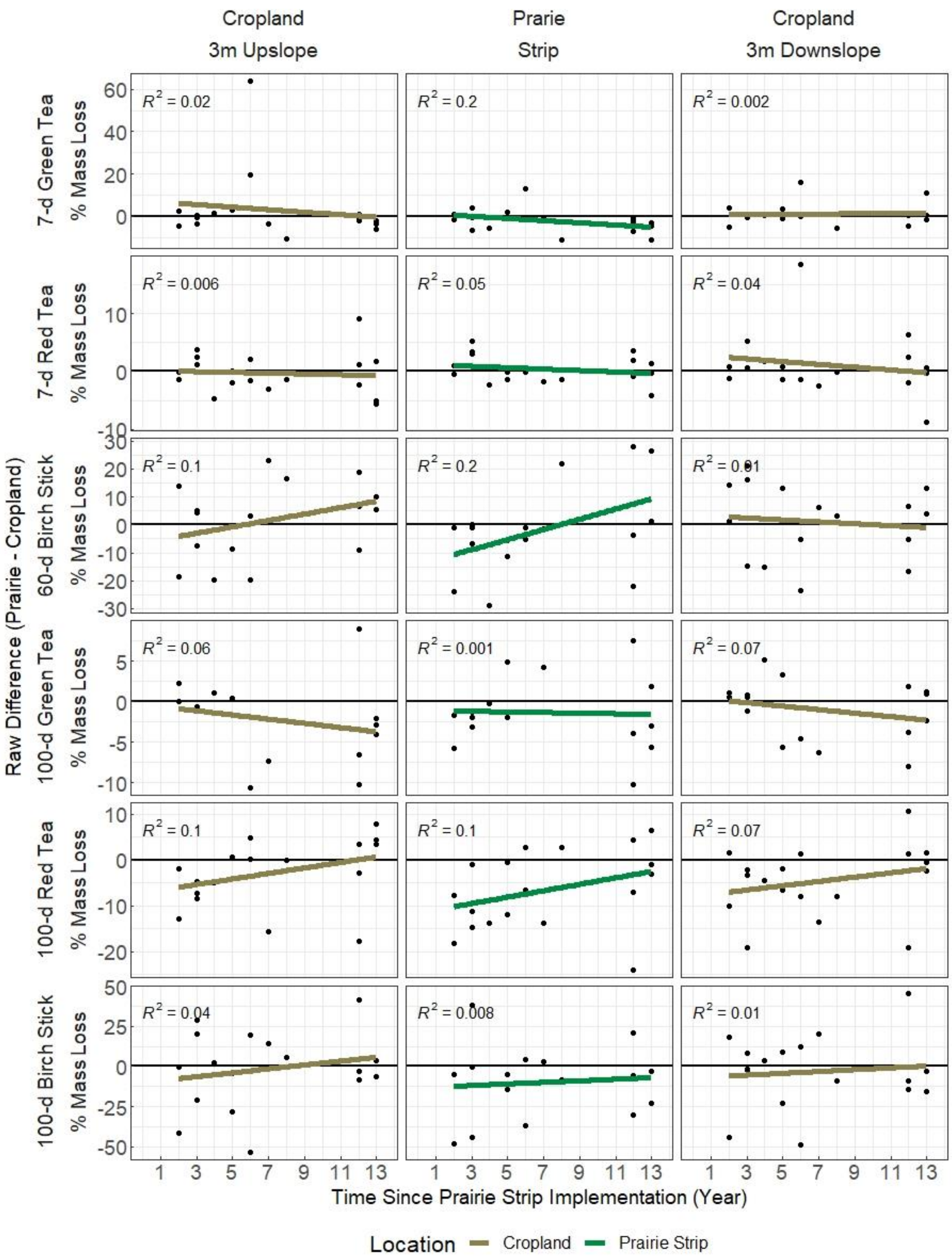

Figure 4.5 Substrate decomposition (% mass loss) from prairie strip sites ranging from 2 to 13 years of implementation. 'Raw Difference' values are the difference between the prairie strip treatment locations (3 m Upslope, within the Prairie Strip, and 3 m Downslope) and the control catchments. The regression lines represent the linear regression where the unknowns are estimated via residual maximum likelihood (REML). R^2 values are given for each regression.

CHAPTER 5. GENERAL CONCLUSIONS

Previous research has demonstrated that prairie strips (PS) have *disproportionate* environmental benefits, especially for water quality and biodiversity. However, their impact on soils underneath the PS and the adjacent crop health and cropland soils had remained a mystery. **My overarching goal was to answer the question: how do PS affect soils underneath and in the adjacent cropland?** Both scientists and producers had driven this larger, general inquiry that served as the fundamental basis for all three studies outlined in my Ph.D. Dissertation. Two non-related events in Midwest US agriculture further amplified the need to answer this question. First, the rapid growth in implementing PS, and the addition of it to the 2018 Farm Bill, meant the practice was being rolled out on more and more farms across the nation. Second, the emerging carbon (C) markets have created a frenzy of companies wanting to track changes in soil C and soil health more generally. The answers to my overarching question are important at a fundamental, basic science level, and practical level.

In CHAPTER 2, I showed that PS had little effect on adjacent crop yields. There was a slight PS effect decreasing leaf greenness in maize. However, this did not translate to significantly decreased crop yields in these years – nor did a 12-year history of yield records from cropland adjacent to the PS show much difference. The PS did, however, affect adjacent soils, especially plant-available nutrients and soil moisture in one year.

In CHAPTER 3, I followed up on this finding and showed that PS affect not just plant-available nutrients but also soil C, nitrogen (N), microbial biomass, and activity measured as potential enzyme activity (PEA). This PS effect on the soil biology and chemistry underneath the PS and adjacent soil highly depends on the cropping year. It is unknown whether this complex interaction was driven by the management that varies from maize to soybean phases of a rotation or the specific weather conditions of that year. The weather in 2019, when the crop was soybeans, was particularly wet during the spring, PS dried down the adjacent soils, and this also coincided with greater PEA, particularly hydrolytic enzymes. The next year in maize, less difference in PEA in general, but PS increased the PEA of the oxidative enzyme used to degrade lignin. There are subtle ways that PS affects adjacent soil biota and their activity. What this means for adjacent soil health and crop productivity is unknown and warrants further investigation.

In CHAPTER 4, I showed that PS are correlated with improved soil health over time compared to 100% cropland fields. Some effects of PS were instantaneous, while others accrued over time. Labile C and N were reduced across all PS ages, while microbial biomass, soil C, ammonium, phosphorus (P), and potassium accrued under the PS over time. PS effect on the adjacent cropland was negligible. Although, I did find that PS did reduce labile C under the PS and accumulated P upslope from the PS.

PS outperformed cropland on several metrics, including microbial biomass C and N, reduction of inorganic N both in Summer and Fall, elevated hydrolytic enzyme activity, and reduced oxidative enzyme activity. PS also had several effects on the adjacent cropland, including reduced soil organic C (SOC), reduced inorganic N when the cropland was unfertilized, accumulated phosphorus and potassium upslope from the PS, and elevated hydrolytic enzyme activity in the unfertilized soybean. Depending on the year, PS affects potential enzyme activities, both under the PS and in the adjacent cropland. PS affected leaf greenness in maize, but crop yield was only marginally affected by the PS to a distance of 9 m.

Long-term sustainability of soil while maintaining production is a serious concern in agriculture today. Prairie strips could be rotated through a field, regenerating soil while maintaining production. For this to occur, a timeline must be established to maximize the soil health benefits of PS. A chronosequence illustrated that microbial biomass C (MBC), soil organic matter (SOM), and SOC increased, but nitrate-N decreased under the PS. Due to the linear patterns, the chronosequence did not elucidate the optimal length of time that PS should be left in place to optimize the soil health benefits. Additional data from older prairie strips (> 14 years) are needed to identify any asymptote on benefit accrual.

Recommendations for Future Research

Do PS decrease adjacent soil organic carbon?

In CHAPTER 3, I found that PS catchments had decreased soil organic C downslope of the PS (up to 0.3 m). SOC depletion next to the PS was an unexpected result of this experiment. Mechanisms for this depletion must be further explored across various sites. It is yet to be known whether the reduction of labile C (CHAPTER 4) contributes to the depletion of SOC.

Does cropland decrease the PS effect on C and N?

This study focused on the PS effect on the cropland and ignored any effect that the cropland might have on the PS. The PS samples were taken from the center of the PS to reduce the cropland effect on measured parameters. It remains to be known whether PS benefits accrue under the PS or if there is a cropland influence on the PS side of the ecotone. Utilizing a transect approach extending from the edge of the PS toward the center of the PS would elucidate the distance from the cropland that C and N benefits (MBC, MBN, SOM, SOC, TN) accrue.

How do multiple prairie strips affect crops and soils?

Previous research showed that strips of prairie that occupied 10% of a catchment provided *disproportionate* environmental benefits. Current recommendations to producers are to plant around <25% of their field. However, there are multiple configurations of how a PS can be laid out. This flexibility is a benefit of the PS management practice. It remains an open question whether multiple PS, perhaps even in close proximity to each other, can have compounding effects on the soil underneath the PS and in the adjacent cropland.

What happens when we rotate a prairie strip?

Why concentrate all the soil health benefits under <25% of the field? The idea of rotating PS, "spread the benefits," so to speak, has been brought up by scientists and producers alike. This is only feasible if we think about farming on a longer-term scale (10-20 years). It would require planning and some effort to 'terminate' a PS and rotate it back into cropland. Furthermore, we do not have a clear idea of what happens to soils formerly under PS but now converted to cropland. How long the soil health benefits might remain or be lost is unknown. This topic is particularly relevant as enrollment in Conservation Reserve Program can fluctuate with grain prices and even global political events (e.g., the Russia-Ukraine war).