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A comparison of carbon storage potential in corn- and prairie-based agroecosystems

by

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DOCTOR OF PHILOSOPHY

Majors: Sustainable Agriculture; Crop Production and Physiology

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We shall not cease from exploration, and the end of all our exploring will be to arrive where we started and know the place for the first time. –T.S. Eliot

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ABSTRACT

Increasing carbon (C) in the soil is important both for removing harmful C from the atmosphere and improving the health of the soil. In this dissertation, I set out to examine how planting and harvesting prairies on soils suitable for corn affected soil C storage potential when compared to corn-based systems. I addressed three questions designed to a) improve our understanding of the fundamental differences between how prairies and corn grow throughout the year, b) test how prairies and corn add C to the soil after establishment, and c) use our current understanding of prairie and corn growth and C and N dynamics to predict how SOC will change over the next 50 years. Measurements of fundamental differences showed corn produced more aboveground and overall biomass with faster growth rates that peaked later in the season than prairie. Duration of growth was shorter in corn than prairie. Corn allocated a much smaller proportion of its biomass belowground than prairie and produced much less root biomass than prairie. Corn biomass had higher N concentrations, but less efficient growth relative to these concentrations. Six years after establishment of the experiment, I found prairies had more root mass that was more recalcitrant and located at depths unfavorable to decomposition, but did not have greater amounts of labile C (POXC) or total SOC than corn-based treatments, nor greater amounts of total SOC than in the establishment year. However, it was important to note that prairies placed ~5 times more C belowground as root C than corn-based treatments. Simulations made over 50 years using the APSIM model showed that prairies had much larger increases in root C, fresh organic matter, and microbial biomass pools, while a corn-based system with a winter cover crop maintained these pools, and continuous corn and corn-soybean rotations lost C in these pools. However, all treatments lost C from the more stable C pool, resulting in an overall loss of SOC after 50 years. The lack of gain in soil C was attributed to a combination of C-saturated soils and rhizosphere-induced priming. However, the validity of these mechanisms needs more investigation.

CHAPTER 1. INTRODUCTION

1. Background

Deriving fuel from biological sources is an idea that has been popular as fossil fuel supplies are diminished, atmospheric carbon dioxide (CO_2) levels increase, and our nation desires to become more independent of foreign fuel sources. The Energy Independence and Security Act of 2007 required an increase in biofuel production from 17.8 billion liters to 136.3 billion liters of biofuel per year by 2022. Biofuel from non-edible sources was required to constitute 60% of this production. Thus, agronomists across the nation resolved to find the best biofuel feedstock production system to achieve these ambitious goals. The best production system was thought be the one most consistent with the original purposes of biofuels by having a high net energy yield, being environmentally resilient, and decreasing greenhouse gases in the atmosphere.

Tilman and colleagues (2006) found evidence that low-input high-diversity prairie systems could fit this description by producing more usable energy and greater greenhouse gas reductions than corn grain ethanol or soybean based biodiesel. However, prairie data in this study was site specific while corn and soybean data were drawn from national databases. Tilman and colleagues' study was challenged and defended (Russelle et al. 2007, Tilman et al. 2007), but no side-by-side comparisons of prairie- and corn-based biofuel systems were available to produce new data for the arguments.

In response to this void of knowledge, a comparison of biofuel systems (COBS) was established at the Iowa State University South Reynoldson Farm in the spring of 2008. COBS consists of prairie-based and corn-based cropping systems and was created with the central premise that cropping systems designed to produce large amounts of biomass, with high net energy return, can simultaneously create significant environmental benefits.

Seven years after the establishment of COBS, there have been some shifts in envisioning how prairies may fit into Midwestern United States agriculture. In 2011, the United States National Research Council investigated the potential economic and environmental effects of reaching the standards set by the Energy Independence and Security Act of 2007 and found that while the United States has the potential to reach the grain-based standards, the production mandate for cellulosic biofuels is not likely to be met by 2022. The United States can probably produce enough cellulosic feedstock, but enough commercially viable biorefineries do not yet exist for cellulosic biofuel production. However, one of the country's first commercial cellulosic biofuel refineries is currently being built ~20 miles from the COBS site. It will begin production with corn residue, but as the environmental feasibility of removing corn residue remains in question (Laird and Chang 2013), having information available on perennial biofuel crops such as prairies will be important.

Apart from biofuel production, there is rapidly increasing interest in incorporating prairies into maize production systems for conservation purposes. The STRIPS project (Science-based Trials of Rowcrops Integrated with Prairies) proposes strategically converting 10% of a row-crop field into prairie to gain a large suite of benefits such as a 95% reduction in sediment loss, a 90% reduction in phosphorus (P) loss, an 85% reduction in nitrogen (N) loss, a four-fold increase in plant diversity, and twice as many bird species (Iowa State University 2014). Prairie strips are currently being incorporated into the project's first field-trials and understanding how prairies function on non-marginal land and how this compares to the corn it replaced will be important in realizing all of the benefits prairie may provide.

Thus far at COBS, it has been found that corn systems have been highest yielding with respect to biofuel feedstock when grain was included (Jarchow et al. 2014), but lowest yielding when only corn stover and prairie biomass was compared (Nichols et al. *in press*). When cellulosic ethanol potentials (grain excluded) were compared over a five year period, the prairie treatments averaged 1300 L ha^{-1} yr^{-1} more than the corn treatments (Nichols et al. *in press*). The corn systems required 2-3 more N fertilizer than the prairie systems (Jarchow et al. 2014) and had 17 times larger losses of NO_3-N in subsurface drainage water (Daigh 2013).

A picture of how prairie- and corn-based systems compare to each other both economically and environmentally is developing, but some major gaps remain. One of these missing pieces is how prairies and corn affect soil carbon (C). I focused on C addition to the soil in the interest of removing C from the atmosphere and improving soil health through greater levels of soil C. The goal of my dissertation was to forward basic science of C cycling by establishing and comparing the potential for C storage in prairie- and corn-based agroecosystems.

2. Soil C storage

Atmospheric carbon dioxide (CO_2) emissions increased from 280 ppm at the turn of the 20th century to 400 ppm in 2014. Land use change mostly in the form of agriculture contributed to one-third of this rise, which has led to a 20% increase in radiative forcing since 1995 (Forster et al. 2007). Increases in radiative forcing have resulted in changes in the planet's climate, the direct effects of which are rising sea levels, decreases in snow and ice cover, melting glaciers, increasing ground instability in permafrost regions, increasing drought since the 1970's, more frequent heat waves, earlier timing of spring thaw events, northward shifts in plant and animal populations, increasing heat-related mortality, and changes in infectious disease vectors in the Northern Hemisphere (Rosenweig et al. 2007). As climate change continues to occur at the current rate, these changes will intensify, leading to a predicted decrease of 30% in species diversity, limited food resources due to agricultural failure, and loss of land to rising sea levels (Schneider et al. 2007). Strategies that can decrease atmospheric CO_2 levels and thus decrease radiative forcing are highly desirable.

Carbon sequestration by soils has been suggested as an option in mitigating rising CO_2 levels. Soils are the biggest reservoir of C next to the ocean, and at a 1 m depth, contain 7 times the content of C in the atmosphere. If agricultural soils were returned to their native SOM levels, this would offset 9-12% of annual anthropogenic emissions (Magdoff and Weil 2004).

In addition to the problems resulting from rising atmospheric CO_2 levels, increased C fluxes from the soil to the atmosphere have been detrimental to the soil. Carbon in the soil surface horizons is mostly present as a part of soil organic matter (SOM) and most often enters the soil as such. SOM serves many purposes that enable soil to function as a substrate for plant growth and an ecosystem base. SOM is the primary source of the nutrients N, P, and sulfur (S) and its decomposition and capacity for cation exchange regulate nutrient availability. Soil water retention and availability are also regulated by the ability of SOM to absorb H_2O. Association of organic matter with soil minerals promotes the formation of aggregates, providing soil structure for air and water exchange (Horwath 2008).

In the Midwestern United States, conversion of 99% of native prairie ecosystems to row-crop agriculture has resulted in the loss of 30-50% of SOM in these soils due to erosion and tillage induced increases of microbial metabolism of SOC (David 2009). This has contributed to an estimated loss of 55 Pg of C worldwide over the last 200 years (Amundson 2001) and a loss of 5 Gt in croplands of the United States (Lal 1998).

Table 1. A comparison of C gain measured directly or through C budgeting.

Method	**System**	**Gain (Mg C ha^{-1} y^{-1})**	**Depth (cm)**	**System Age (y)**	**Author**
Direct C Measurement	Restored Prairie	0.4	16	3-24	Matamala et al. 2008
	C4 native grasses	2.1	30	6-8	Omonde et al. 2006
	Restored Prairie	0.8	40	5	Gebhert et al. 1994
	Restored Prairie	1.1	300	5	Gebhert et al. 1994
	Grassland	0.6	10	2-40	McLauchlan 2006
	Restored Prairie	0.8	120	18	Kucharik et al. 2002
	Restored Prairie	0.0	25	2-6	Karlen et al. 1999
	Restored Prairie	0.0	15	10	Baer et al. 2000
	Restored Prairie	0.0	60	10	Camill et al. 2004
	Restored Prairie	0.0	35	4-16	Kucharik et al. 2007
	Switchgrass	0.8	30	11	Tufekcioglu 2003
	Forage Grass	0.8	15	5-12	Mensah et al. 2003
	No-till	0.6	<30	15-20	West and Post 2002
	No-till	0.9	120	1	Kucharik et al. 2002
C Budgeting	Restored Prairie	-3.9 to 1.4	120	18	Brye et al. 2002
	No-till	-.7 to 2.0	120	10	Brye et al. 2002
	Restored Prairie	-2.3 to 1.3	100	60	Kucharik et al. 2006
	Remnant Prairie	-1.4 to 1.9	100	--	Kucharik et al. 2006
	Restored Prairie	-.4 to 2.5	30	3	Guzman 2008
	Restored Prairie	-1.0 to 2.9	30	8	Guzman 2008
	Restored Prairie	-.9 to 5.3	30	13	Guzman 2008
	Remnant Prairie	-2.0 to 2.0	30	--	Guzman 2008
	No-till	-.8 to .4	30	3	Guzman 2008

Restoration of prairie systems has been acknowledged as a possible way to bring SOM levels back toward original levels. A study of restored prairie chronosequences from ages 2 to 24 years showed that 50% of lost C could be restored in 100 years (Matamala 2008), while a similar study resulted in a model that predicted original SOC levels would be met 55-75 years after restoration (McLauchlan et al. 2006). However, doubt over the ability of prairies to contribute to soil C remains. Several studies in the Midwestern United States have failed to find any increase in soil C after prairie establishment (Karlen et al. 1999, Baer et al. 2000, Brye and Kucharik 2003, Camill et al. 2004, Kucharik 2007). Rates of C accumulation derived in studies that directly measured changes in soil C over time (4 y maximum), in chronosequences, or in comparison to adjacent cultivated fields are shown in Table 1.

Direct measurements of SOC can give some indication of changes in soil C levels, but are often unable to capture differences between years because the changes are below detectable levels. Another way to determine to what extent a system is a sink or source of CO_2 is to create a budget that takes into account all gains and losses of C. This allows us to see not only in what direction a system is moving, but also what is contributing to the change and how one system functions differently from another system. When this more complete approach is used, the ability of cropped and prairie based systems to sequester C has been found to differ from rates determined through direct C measurement. Carbon gains found under budgeting approaches range from -3.9 Mg C ha^{-1} y^{-1} (Kucharik et al. 2006) to 5.3 Mg C ha^{-1} y^{-1} (Guzman and Al-Kaisi 2010) and are often found to be both negative and positive in a given system, depending upon the year of measurement (Table 1). Thus, when C losses are accounted for as well as C gains, it is no longer apparent that prairies or no-till cropping systems are sinks of C, let alone which system sequesters more C. In many cases, uncertainties in above and belowground production and respiration contribute to these changes in magnitude and direction (Cahill et al. 2009).

3. Dissertation

In the Midwestern United States, how much C prairie places and stores in the soil compared to how much C corn places and stores in the soil is still unknown. This knowledge is desired so we can design and manage systems for C sequestration and soil health improvement.

In this dissertation, I address three major questions:

1. What are the fundamental differences in how prairies and corn assimilate and allocate C and use N?
2. What evidence do we have of differences in soil C storage between prairie- and corn-based cropping systems six years after system establishment?
3. What differences will we see in prairie- and corn-based systems soil C storage 50 years from now?

Accordingly, the dissertation is divided into three chapters.

Chapter 1. Above- and belowground growth, biomass, and nitrogen use in maize and reconstructed prairie cropping systems.

Chapter 2. Root inputs drive carbon storage differences in corn- and prairie-based cropping systems.

Chapter 3. Predicted changes in soil organic carbon over fifty years in corn- and prairie-based cropping systems.

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CHAPTER 2. ABOVE- AND BELOWGROUND GROWTH, BIOMASS, AND NITROGEN USE IN MAIZE AND RECONSTRUCTED PRAIRIE CROPPING SYSTEMS

1. Introduction

In recent years, there has been increased interest in evaluating and comparing the characteristics of annual and perennial plants for producing both biofuel and food. Annual plants such as maize (*Zea mays*) and soybean (*Glycine max*) are already widely used as biofuel feedstocks, but the use of perennial species such as switchgrass (*Panicum virgatum*), *Miscanthus x giganteus*, and species found in prairie communities may create opportunities for the provision of more ecosystem services than are provided by annual plant systems (Tilman et al. 2006; Heaton et al., 2008; Jarchow and Liebman 2012a). Efforts are also being made to develop perennial grain crops that require fewer purchased inputs and that have fewer negative environmental impacts than annual species used for grain production (Glover et al. 2010; Pimentel et al. 2012).

The focus on identifying improved biofuel and food cropping systems for both productivity and ecological benefits has resulted in an amplified effort at predicting what effect these systems will have on biogeochemical processes and associated outcomes such as greenhouse gas emissions, nutrient leaching, soil erosion, and changes in soil organic matter (Fazio and Monti 2011; Taubert et al. 2012). However, at present such predictions are difficult to make due to a lack of information concerning differences in timing of growth and nutrient use in perennial and annual cropping systems, especially belowground. Studies quantifying differences between annual and perennial systems have tended to focus on aboveground cumulative biomass and nutrient concentrations, neglecting temporal patterns of above- and belowground growth and nutrient acquisition. Direct experimental comparisons of how annual and perennial plant systems grow throughout the year above and below the soil surface are needed to make comprehensive comparisons and support mechanistic models with which to accurately predict system-level processes that are dependent on the interaction of plants and the environment.

Maize and prairie plant communities provide a good opportunity for comparison of annual and perennial plant systems. Maize is the most widespread crop in the United States, with 39.3 million hectares planted in 2012 (USDA NASS), making it a relevant preeminent example of an annual plant system. Prairie species are native to many of the same areas in which maize is grown, as they previously occupied much of the same land. This offers a chance to compare annual and perennial plant systems developed (through breeding or evolution) for the same environmental conditions. Prairie vegetation is also under consideration as a biofuel cropping system that may complement the use of maize as a biofuel feedstock, further making comparisons pertinent (Tilman 2006; James 2010; Jarchow et al. 2014).

Previous comparisons of annual and perennial plant systems grown in the same environment have shown cumulative whole-plant biomass in annual systems to be greater than (Ward et al., 2011), less than (Warembourg and Estelrich 2001; Dohleman and Long 2009) or equal to (Ploschuk et al. 2005; Ward et al. 2011; Gonzalez-Paleo and Ravetta 2012) perennial systems. Length of growth period is one important trait that contributes to this final difference in biomass between plants (Yin et al. 2009). Studies that have measured the duration of growth in perennial and annual systems have found that perennial systems utilize more of the growing season than annual systems (Dohleman and Long 2009; Gonzalez-Paleo and Ravetta 2012; Jarchow and Liebman 2012a). Many of these studies also found that perennial plants allocate more biomass belowground than annual plants (Ploschuk et al. 2005; Warembourg and Estelrich 2001; Gonzalez-Paleo and Revatta 2012; Jarchow and Liebman 2012a).

Nitrogen (N) productivity, defined as the amount of biomass produced per unit of N contained in the biomass per unit of time (e.g. g biomass per g N per day), is a measure of N utilization efficiency by the plant (Ingestad, 1992). Quantifying N productivity is necessary to understand plant N use dynamics, which enhances our knowledge of individual plant physiological efficiency, plant community nutrient cycles, N leaching potential, N mineralization rates, and other environmental processes involving N (Weih et al. 2011). Few studies have compared N productivity between annual and perennial plants, although Ploschuk et al. (2005) found perennial bladderpod (*Lesquerella mendocina*) had higher plant N concentrations and less whole-plant biomass than annual bladderpod (*Lesquerella fendleri*).

Fertilization is a management option for perennial plants managed as crops. While the effect of N fertilizer is well documented in annual cropping systems, fewer studies have examined the effect of intentional N fertilization on herbaceous perennial communities. Nitrogen fertilization has been found to increase aboveground biomass and internal plant N concentrations in grassland systems (Reich et al. 2003; Heggenstaller et al. 2009; Jarchow and Liebman 2013), but the effects of N fertilization on root biomass production are mixed (Reich et al. 2003; Heggenstaller et al. 2009; Jarchow and Liebman 2012a). Intentional N fertilization has been found to differentially affect the phenology, growth rates, and species composition of prairie systems (Jarchow and Liebman 2012b, 2013). The response of reconstructed prairie systems to N fertilization is largely unknown, although this information is needed to predict how prairies will function within managed ecosystems with regard to productivity and biogeochemical processes.

The aim of this study was to quantitatively evaluate growth, biomass and N use dynamics in maize and reconstructed prairies systems in order to provide information useful to design resilient Midwestern cropping systems that support food and/or biofuel production. We sought to test two hypotheses. 1) When compared with prairie, maize should produce more biomass, over a shorter period of time, with a greater proportion allocated aboveground, and with an overall lower N productivity. 2) When compared with unfertilized prairie vegetation, N fertilization of prairie vegetation should result in more biomass produced over the same period of time, a greater proportion of which would be allocated aboveground, with an overall lower N productivity. Nitrogen-fertilized maize, reconstructed prairie, and N-fertilized reconstructed prairie were grown in a field plot experiment, and above- and belowground plant mass and N concentration were measured at regular intervals for two years. Empirical measurements were used to model plant growth and N dynamics.

2. Materials and Methods

2.1 Site Conditions and Experimental Design

We conducted the experiment in Boone County, IA, USA on the Iowa State University Agronomy and Agricultural Engineering Research Farm (41°55′N, 93°45′W). Soils at the site were primarily Webster silty clay loam (fine-loamy, mixed, superactive, mesic Typic Endoaquoll) and Nicollet loam (fine-loamy, mixed, superactive, mesic Aquic Hapludoll). The 60-year mean growing season precipitation 11 km from the site was 720 mm. Prior to initiation of the field experiment in 2008, the site was used for maize and soybean production and was planted with soybean in 2007. Soil sampling to 15 cm in November 2007 indicated mean soil pH was 6.7, mean organic matter concentration (via dry combustion analysis with a conversion factor of 1.724 from total carbon to organic matter [Schumacher 2002]) was 51 g kg^{-1}, mean extractable phosphorus concentration (via Bray-1 procedure) was 11 mg kg^{-1}, and mean extractable potassium (via Mehlich-3 procedure) was 141 mg kg^{-1}.

Experimental plots were 27 m x 61 m and were arranged as a spatially balanced complete block design (van Es et al. 2007) with four replicates of three treatments – continuous maize, reconstructed prairie, and N-fertilized reconstructed prairie. No tillage occurred in this experiment. Measurements were made in 2010 and 2011, during the third and fourth years after the experiment was established. Because the prairie treatments discussed here were components of a larger cropping-systems experiment, P and K were added in May 2008 to all treatments to ensure that sufficient P and K were available for annual-crop growth. Phosphorus was added at a rate of 78 kg P_2O_5 ha^{-1} (34 kg P ha^{-1}). Potassium was added at a rate of 146 kg K_2O ha^{-1} (121 kg K ha^{-1}). In 2009, P and K were added to the maize treatment at rates of 112 kg P_2O_5 ha^{-1} (49 kg P ha^{-1}) and 112 kg K_2O ha^{-1} (93 kg K ha^{-1}), respectively.

Both prairie treatments were sown on 19 May 2008 with the same custom seed mix obtained from Prairie Moon Nursery (Winona, MN, USA) that contained 31 species, including C_3 and C_4 grasses and leguminous and non-leguminous forbs (Table S1). All species were perennial and sourced from within 240 km of the experiment site. The composition of the seed mix by weight was 12% C_3 grasses, 56% C_4 grasses, 8% legumes, and 24% non-leguminous forbs. A detailed description of the prairie plant community compositions can be found in Jarchow and Liebman (2013). The fertilized prairie treatment received no fertilizer in 2008 (the establishment year), and was fertilized at a rate of 84 kg N ha^{-1} $year^{-1}$ in all subsequent years. Plots were fertilized on 29 March 2010 with ammonium nitrate (34% N) and 11 April 2011 with urea ammonium nitrate (32% N). This fertilizer rate was chosen because it was similar to the maximum rate of pre-planting N fertilization recommended for maize (Blackmer et al. 1997) and the expected N removal in the harvested biomass of perennial grasses grown in the area (Heggenstaller et al. 2009).

The maize hybrid used (Agrigold 6325 VT3) had a 104-day relative maturity and transgenes for glyphosate resistance, corn borer (*Ostrinia nubilalis*) resistance, and corn rootworm (*Diabrotica* spp.) protection. Maize was planted following standard practices (Abendroth et al. 2011) in rows spaced 76 cm apart at 79,500 seeds ha^{-1} on 6 May 2010 and 82,500 seeds ha^{-1} on 11 May 2011. In 2010, maize received 87 kg N ha^{-1} at planting and an additional 36 kg N ha^{-1} on 17 June; in 2011, maize received 87 kg N ha^{-1} at planting and an additional 56 kg N ha^{-1} on 29 June. Rates of N added after planting were based on results of late-spring tests of soil nitrate-N concentration (Blackmer et al. 1997). All N was applied as urea-ammonium nitrate (32% N). An unfertilized maize treatment was not included in the experiment because the effects of N fertilizer on maize are well known (Cerrato and Blackmer 1990; Sawyer et al. 2006; Kveryga et al. 2009).

2.2 Data Collection

Aboveground biomass was measured by clipping two 0.28-m^2 quadrats in each plot approximately every two weeks beginning at shoot emergence in April for the prairie treatments and in May for the maize, similar to methods used by Loecke et al. (2004). Dead litter was discarded and biomass was then dried at 60° C for at least 48 hours and weighed. Species identities were not assessed within the quadrats used for biomass collection, rather the species composition of both prairie treatments was determined by Jarchow and Liebman (2013) using a point intercept method (Jonasson 1988). In mid-August, eight 1-m^2 quadrats per plot were sampled by dropping a long pin into each quadrat 12 times and recording identity and number of contacts that each species had with the pin. More details can be found in Jarchow and Liebman (2013).

Belowground biomass was measured with an in-situ growth core approach (Neill 1992) to capture only those roots growing within the measurement year. After fall harvest in 2009 and 2010, eight 10.2-cm-diam soil cores were taken to 30 cm depth in each plot and brought to the laboratory. Holes created in the field were held open during the winter by capped 10.2 cm PVC piping. In the laboratory, cores were divided into 10 cm sections and virtually all roots were removed by hand. Soil was stored in intact cores at 30°C for the first year of the experiment and 4 °C in sealed plastic bags for second year of the experiment. The differences in storage conditions did not have an apparent effect on the outcome of the experiment. At the end of winter while plants were still dormant, the root-free soil was returned to its original location in the field in 10 cm depth increments. Soil was packed to imitate the surrounding bulk density, approximately 1.4 g cm^{-3}. Root-free zones were located randomly within prairie plots and at 20 cm from maize rows. Eight root-free areas were situated within each plot, allowing duplicate sampling at four time points throughout the growing season. Two 4-cm-diam soil cores were taken within each 10.2-cm-diam root-free area to a 30 cm depth at each root sampling date. Bulk soil was washed from the roots with water using a soil elutriator (Wiles et al. 1996), roots were dried at 60° C for 24 hours, non-root biomass was removed from the roots by hand, and roots were weighed.

In-situ growth cores have a few disadvantages. Belowground biomass measurements from in-situ cores capture only lateral roots, leading to overall root biomass values that are lower than measurements that may include vertical roots. The use of in-situ growth cores also contributes to lower belowground biomass values when compared to belowground biomass values derived from bulk root measurements of materials that may have accrued over multiple years. Root measurements were made to only 30 cm, but measurements of end-of-the-growing season root biomass to a 1 m depth from the same experiment showed the top 30 cm included the majority (60-80%) of root mass in a 1 m layer of soil (Jarchow et al. 2014). Despite these disadvantages, in-situ growth cores provide measurements that can be fairly compared among treatments.

After drying, all the above- and belowground plant samples were ground to 2 mm with a centrifugal mill and concentrations of carbon (C) and N were determined by combustion analysis at the Soil and Plant Analysis Laboratory at Iowa State University (Ames, IA, USA).

2.3 Data Analysis

A functional growth analysis approach (Hunt 1985) was used to analyze the data. A non-linear growth curve (Yin et al., 2003) was fitted to each replicate of aboveground biomass data:

$$w = w_{max}\left(1 + \frac{t_e - t}{t_e - t_m}\right)\left(\frac{t}{t_e}\right)^{\frac{t_e}{t_e - t_m}} \quad \text{with } 0 \leq t_m < t_e \qquad (1)$$

where w is weight; w_{max} is the maximum value of w, which is reached at t_e, the time growth ends; t is time; and t_m is the point at which the growth rate reaches its maximum value. Growth duration was defined as the length of the period in which plants were growing and was determined by subtracting the time of the first measurement from t_e. The parameters included in Eq (1) have a clear biological meaning and therefore are useful to compare growth of different cropping systems. Such an analysis has been used previously by Loecke et al. (2004), Heggenstaller et al. (2009), and Archontoulis et al. (2011). We selected Eq (1) among many others equations because it is flexible (it can take many shapes; Yin et al., 2003) and compared to other growth functions it can predict biomass decline after a certain time (see Archontoulis and Miguez (2013) for a comparison of 20 different growth functions).

Aboveground N concentrations were fit to a first order open compartment equation (Pinheiro and Bates 2001):

$$c_t = \frac{k_e k_a}{Cl(k_a - k_e)}[exp(-k_e t) - \exp(-k_a t)] \qquad (2)$$

where c_t is the concentration at time t, k_e is the elimination rate constant, k_a is the absorption rate constant, and Cl is clearance. For the purposes of our analyses, k_e was thought of not as an elimination constant, but as a dilution constant. The model can be interpreted as follows. The plant is a single compartment into which N is flowing through N uptake. As the plant takes up N, it is also growing and adding structural material at a faster rate than photosynthetically active tissue while increasing volume, leading to a dilution of N. The balance of the uptake rate (k_a) and dilution rate (k_e) determines the N concentration in the plant. Nitrogen concentration data are often evaluated as a function of aboveground biomass and fitted to a power function, aW^{-b}, where *a* and *b* are empirically derived constants and *W* is weight (Gastal and Lemaire 2002). Eq (2) refers to N concentration over time and includes a component for N uptake in addition to dilution, allowing comparison to our perennial systems, for which the classical N concentration equation was inappropriate due to an increase in N concentration early in the season. Root N concentrations were fit and predicted with splines.

Each model was fitted to achieve the lowest Akaike information criterion (AIC) and Bayesian information criterion (BIC) possible for that particular model. All model fits were visually assessed and deemed to be very good, with the exception of the first order compartment model for aboveground N concentration in fertilized prairie (Appendix A, Figs. S1-S6). The first order compartment model consistently underpredicted the N concentration that occurred in fertilized prairie early in the season by an absolute value of ~1% N concentration (Figs. S3, S4).

Mean parameters for equation 2 used to predict aboveground biomass can be found in Appendix A (Table S2). However, when compared to segmented fits that attempted to accommodate the rise and fall of N concentrations, the first order compartment model was still found to be the best possible fit.

Biomass and aboveground N concentrations were fitted, predicted, and compared statistically using the R package *nlme* (Pinheiro et al. 2013). Statistical comparison consisted of creating nonlinear mixed effects models and performing contrasts to determine significant parameter differences between treatments. Belowground N concentrations were predicted with splines in *nlme*. Statistical comparison outside of *nlme* was done by selecting the predicted values at specific times during the growing season and conducting analyses of variance followed by mean separations via Tukey's test using the *agricolae* package in R (de Mediburu 2014). Thermal units were used as the temporal scale instead of calendar days in all models. Thermal units make comparisons between years easier and indicate plant growth stage better than calendar days. (Abendroth et al. 2011). Thermal units were calculated similar to growing degree days, but a base temperature of zero was used for all cropping systems:

$$tu = \frac{T_{max}+T_{min}}{2} \qquad (3)$$

where tu is thermal units, T_{max} is the maximum daily temperature, and T_{min} is the minimum daily temperature.

3 Results

3.1 Vegetation and Climate

Although both prairie treatments were planted with the same seed mixture, N fertilization altered species composition and diversity, as reported by Jarchow and Liebman (2013). When measured as plant cover by functional group, the fertilized prairie treatment almost always had higher diversity. The unfertilized prairie treatment composition was characterized by greater cover of native C_4 grasses and legumes, whereas the fertilized prairie treatment composition was characterized by greater cover of native C_3 grasses and non-leguminous forbs (Fig. 1). In the unfertilized prairie, the dominant species by cover in August 2010 were big bluestem (*Andropogon gerardii)* (35.8%), Indiangrass (*Sorghastrum nutans)*(27.6%), and switchgrass (*Panicum virgatum)* (13.4%); in August 2011, they were big bluestem (40.0%), Indiangrass (29.6%), and Canada wildrye (*Elymus canadensis)* (10.0%). In the fertilized prairie, the dominant species by cover in August 2010 were Canada wildrye (45.4%), big bluestem (19.2%), and switchgrass (11.6%); in August 2011, they were Canada wildrye (29.6%), big bluestem (25.5%), and oxeye sunflower (*Heliopsis helianthoides)* (9.7%).

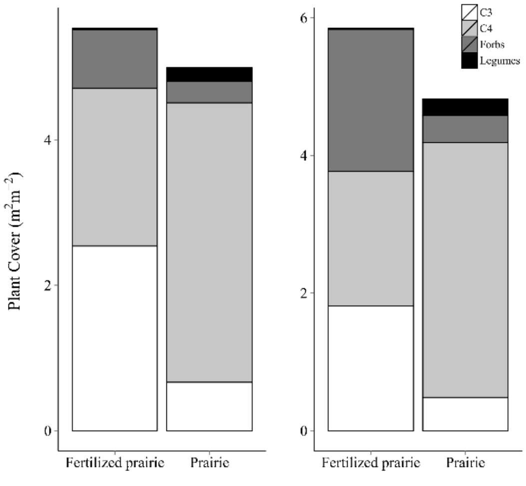

Figure 1. Plant cover of C_3 grasses (white), C_4 grasses (light grey), forbs (dark grey), and legumes (black) in the unfertilized and fertilized prairies in August of 2010 and 2011.

Growing season precipitation in 2010 and 2011 was 1160 mm and 610 mm, respectively. Summer flooding occurred briefly in 2010. The experiment site experienced below-freezing winter temperatures with intermittent snow cover. Temperature and precipitation patterns for 2010 and 2011 are shown in Fig. 2.

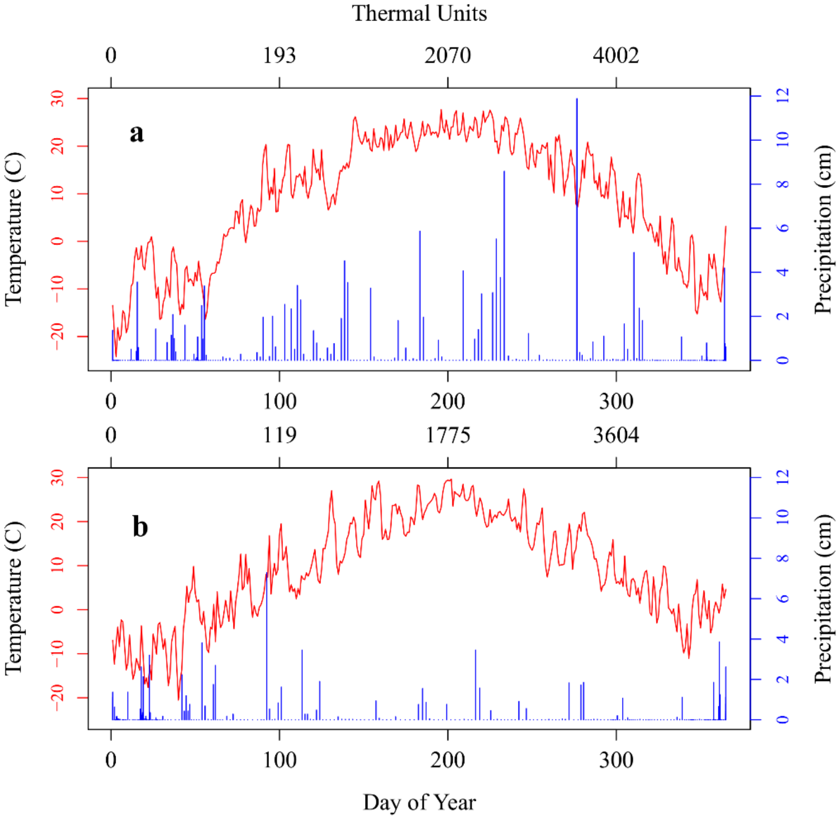

Figure 2. Daily temperature and precipitation at the experimental site, also displayed by thermal units (top axis; thermal units, T_b=0°C) for (a) 2010 and (b) 2011. Lines are temperature, corresponding with the left y-axis. Bars are precipitation (mm), corresponding with the right y-axis.

3.2 Biomass

In both years, maize produced ca. 1.25 times as much aboveground maximum biomass (w_{max}) as N-fertilized prairie and twice as much aboveground maximum biomass as unfertilized prairie (Fig. 3a, b; Table 1). Fertilization of prairie led to 1.4 (2011) to 1.7 (2010) times more aboveground maximum biomass compared with the unfertilized prairie treatment. Unfertilized prairie had the greatest belowground maximum biomass, with over twice as much belowground biomass as fertilized prairie both years and 6.5 and 8 times as much biomass as maize in 2010 and 2011, respectively (Fig. 3c, d). Whole-plant (above- plus belowground) biomass trends

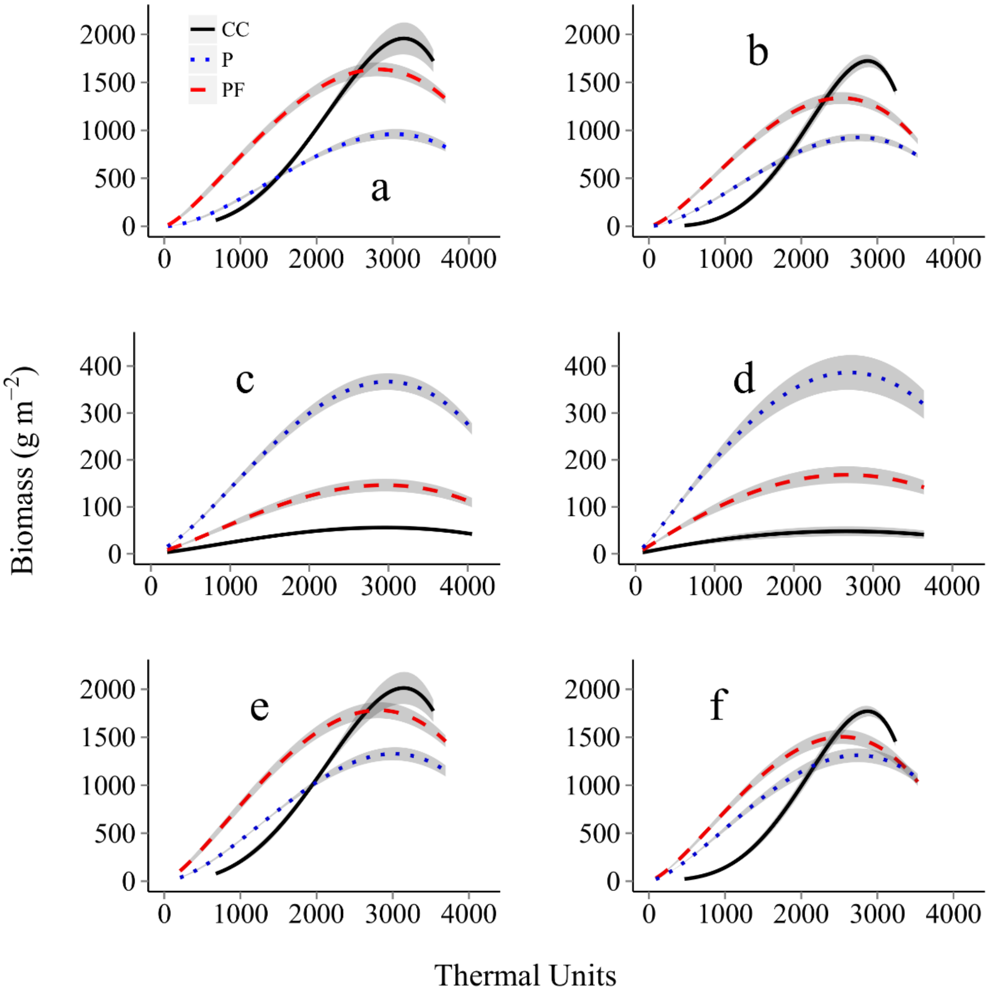

Figure 3. Biomass (a) aboveground 2010, (b) aboveground 2011, (c) belowground 2010, (d) belowground 2011, (e) total 2010, and (f) total 2011. Lines are predictions from Eq. 1. Solid line is maize, dashed line is fertilized prairie, and dotted line is unfertilized prairie. Grey shading represents one standard error of the mean. Eq (1) goodness of fit is provided in figs S1,2.

followed the same patterns seen for aboveground biomass, although the differences were not as great (Fig. 3e, f). Whole-plant maize biomass was 1.2 times more than fertilized prairie biomass and 1.4 times more than unfertilized prairie biomass.

3.3 Biomass Allocation

As the season progressed, the proportion of biomass allocated aboveground increased in all treatments except for fertilized prairie in 2010, for which the proportion remained relatively constant (Fig. S7, Table 2). In maize, especially in 2011, root biomass was more than 50% of the whole-plant biomass at the beginning of the growing season, but decreased to less than 5% of the whole-plant biomass by the end of the growing season (Fig. S7b, Table 2). Fertilized prairie differed between the two years: in 2010, root biomass comprised about 10% of whole-plant biomass, whereas in 2011, root percentage was closer to 20% (Fig. S7c, d, Table 2). Unfertilized prairie had the greatest proportion of plant biomass in roots, ranging between 40% and 69% of whole-plant biomass (Fig. S7e, f, Table 2).

Table 1. Mean parameters of the beta growth function (Eq. 1) for w_{max} (maximum dry weight), t_m (moment of maximum growth), t_e (moment growth ends), and growth duration for the beta growth curve used to predict aboveground (above), belowground (below), and total plant biomass for maize, unfertilized prairie, and fertilized prairie in 2010 and 2011.

Year		Treatment	w_{max} ($g\ m^{-2}$)				t_m (thermal units)				t_e (thermal units)				growth duration (thermal units)		
2010	Above	Maize	1958.8	(166.4)	A	a	2104.8	(80.6)	A	a	3140.1	(10.2)	A	a	2463.1	(10.2)	c
		Unfertilized Prairie	961.7	(53.2)	A	c	1329.9	(111.8)	A	b	3014.7	(27.4)	B	b	2964.7	(27.4)	a
		Fertilized Prairie	1637.0	(72.7)	A	b	807.5	(113.0)	A	c	2797.4	(29.9)	C	b	2747.4	(29.9)	b
	Below	Maize	55.8	(4.3)	B	c	806.3	(2.6)	B	a	2953.0	(0.3)	A	a	2746.0	(0.3)	b
		Unfertilized Prairie	367.0	(17.8)	B	a	1026.5	(25.5)	B	a	2985.9	(6.1)	B	a	2778.9	(6.1)	a
		Fertilized Prairie	146.3	(13.4)	B	b	834.3	(10.6)	B	a	2952.2	(3.4)	C	a	2745.2	(3.3)	b
	Total	Maize	2011.4	(166.5)	-	a	2079.1	(81.5)	-	a	3140.3	(10.3)	-	a	2625.5	(84.1)	b
		Unfertilized Prairie	1327.6	(67.4)	-	c	1250.1	(86.8)	-	b	3009.2	(22.1)	-	b	2964.7	(27.4)	a
		Fertilized Prairie	1782.5	(83.6)	-	b	809.9	(103.5)	-	c	2809.0	(26.4)	-	c	2584.9	(84.4)	b
2011	Above	Maize	1729.5	(65.6)	A	a	2110.3	(46.5)	A	a	2877.2	(30.6)	A	a	2409.2	(30.6)	b
		Unfertilized Prairie	926.7	(38.7)	A	c	1130.0	(34.5)	A	b	2754.0	(17.3)	B	b	2688.0	(17.3)	a
		Fertilized Prairie	1338.0	(62.1)	A	b	843.9	(67.3)	A	c	2526.4	(30.3)	C	c	2460.4	(30.3)	b
	Below	Maize	47.9	(10.5)	B	c	124.5	(12.7)	B	b	2657.2	(1.6)	A	b	2566.2	(1.5)	a
		Unfertilized Prairie	386.6	(37.2)	B	a	500.9	(85.4)	B	a	2695.1	(22.7)	B	a	2604.1	(22.7)	a
		Fertilized Prairie	168.3	(17.8)	B	b	245.1	(29.0)	B	ab	2665.2	(6.1)	C	ab	2574.2	(6.1)	a
	Total	Maize	1771.5	(56.6)	-	a	2081.6	(48.1)	-	a	2879.1	(31.9)	-	a	2435.1	(46.4)	a
		Unfertilized Prairie	1310.4	(72.2)	-	c	962.6	(31.9)	-	b	2741.0	(10.7)	-	b	2638.0	(60.1)	a
		Fertilized Prairie	1504.7	(74.4)	-	b	793.2	(61.5)	-	c	2533.2	(28.6)	-	c	2484.5	(60.2)	a

Different uppercase letters indicate significant differences between aboveground and belowground components within a year.
Different lowercase letters indicate significant differences among treatments within a biomass fraction within a year.
Standard error of the mean is in parentheses.

Table 2. Mean root to shoot ratios and N root to shoot ratios of maize, fertilized prairie, and unfertilized prairie at the beginning (677 thermal units), middle (2104 thermal units) and end (3532 thermal units) of the 2010 and 2011 growing seasons.

			Thermal Units								
Ratio of	**Year**	**Treatment**	**677**			**1957**			**3237**		
Root to Shoot	2010	Maize	0.30	(0.097)	ab	0.05	(0.004)	b	0.03	(0.003)	C
		Unfertilized Prairie	0.55	(0.067)	a	0.41	(0.018)	a	0.38	(0.015)	A
		Fertilized Prairie	0.09	(0.009)	b	0.09	(0.005)	b	0.09	(0.006)	B
	2011	Maize	0.77	(0.248)	a	0.05	(0.013)	c	0.03	(0.007)	C
		Unfertilized Prairie	0.69	(0.052)	ab	0.45	(0.028)	a	0.42	(0.029)	A
		Fertilized Prairie	0.17	(0.021)	b	0.13	(0.011)	b	0.14	(0.011)	B
Nitrogen Root to Shoot	2010	Maize	0.07	(0.020)	b	0.03	(0.002)	c	0.05	(0.004)	C
		Unfertilized Prairie	0.28	(0.040)	a	0.38	(0.014)	a	0.97	(0.050)	a
		Fertilized Prairie	0.04	(0.010)	b	0.09	(0.003)	b	0.27	(0.016)	b
	2011	Maize	0.24	(0.066)	ab	0.03	(0.005)	c	0.04	(0.007)	c
		Unfertilized Prairie	0.36	(0.026)	a	0.44	(0.034)	a	0.80	(0.052)	a
		Fertilized Prairie	0.09	(0.014)	b	0.12	(0.014)	b	0.25	(0.018)	b

Different letters indicate significant differences among treatments within years and thermal units. Standard error of the mean is in parentheses.

3.4 Crop Growth Rates and Parameters

Absolute crop growth rates are illustrated in Fig. 3 and the times when these rates were achieved are shown in Fig. 5, with the moment of maximum growth (t_m) displayed as the peak growth rate and the moment growth ended (t_e) displayed where the lines reach a y-axis value of 0. For aboveground biomass, fertilized prairie had the earliest moment of maximum growth, 877 thermal units before unfertilized prairie and 1282 thermal units before maize when averaged over the two years (Table 1). Fertilized prairie also had the earliest end of growth, 124 thermal units before unfertilized prairie and 347 thermal units before maize when averaged over the two years.

Unfertilized prairie had the longest duration of growth in aboveground biomass in both years with 501 and 279 more thermal units than maize in 2010 and 2011, respectively, and 218 and 228 more thermal units than fertilized prairie in 2010 and 2011, respectively. Fertilized prairie had a greater duration of growth than maize in 2010, but the fertilized prairie and maize did not differ in 2011(Fig. 5a,b; Table 1).

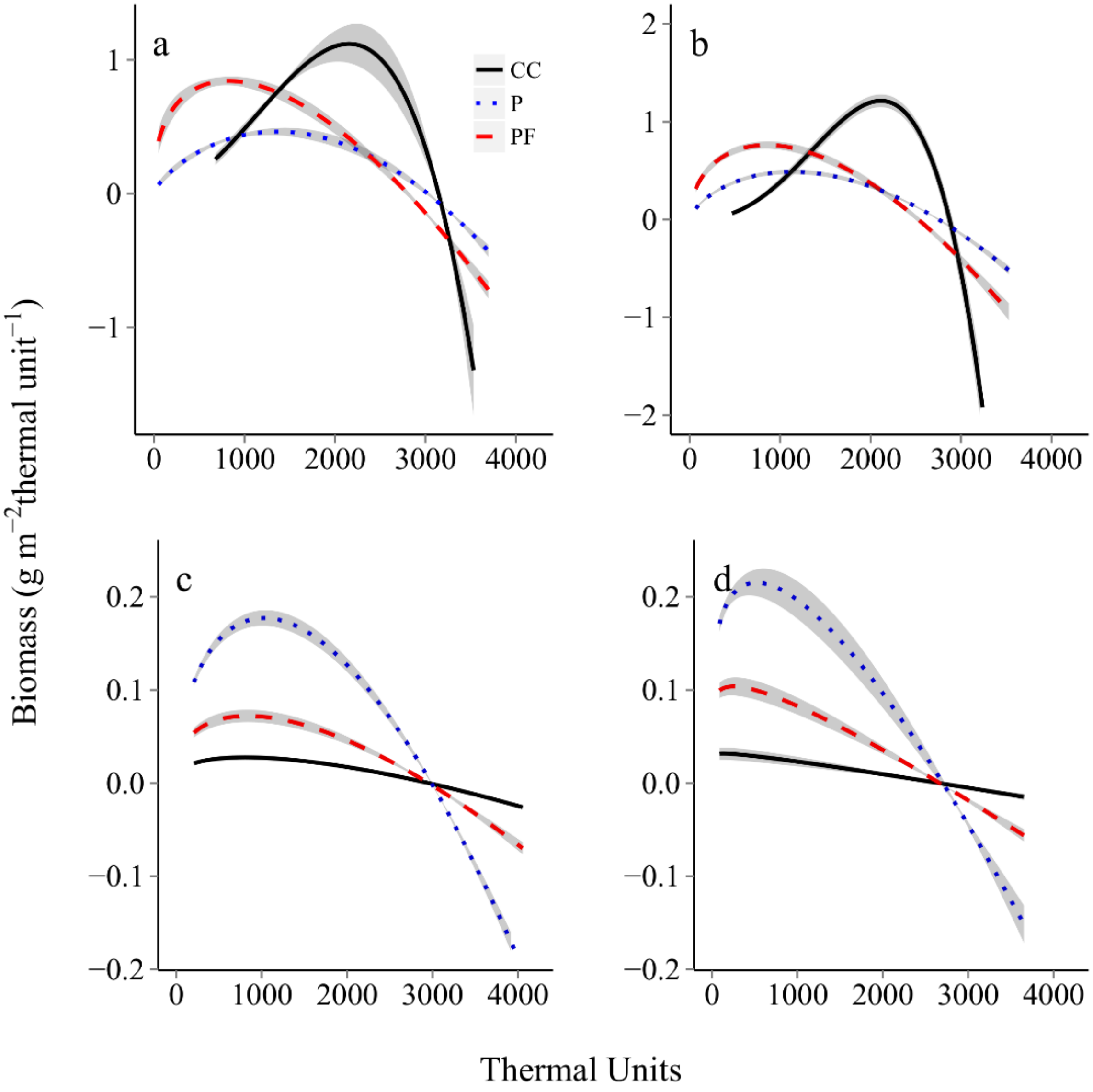

Figure 4. Simulated absolute growth rates (g m^{-2} thermal unit^{-1}) in (a) aboveground biomass in 2010, (b) aboveground biomass in 2011, (c) belowground biomass in 2010, and (d) belowground biomass in 2011. Solid line is maize, dashed line is fertilized prairie, and dotted line is unfertilized prairie. Grey shading represents one standard error of the mean.

Belowground, moments of maximum growth differed very little among treatments, with the only significant difference being a 377 thermal unit lag by unfertilized prairie compared with maize in 2011 (Table 1). This pattern was also true for end of growth in roots, for which unfertilized prairie root growth ended 38 thermal units after maize. Belowground growth duration was significantly different only between the unfertilized prairie and the other two treatments in 2010, when unfertilized prairie roots grew for 34 more thermal units than fertilized prairie and 33 more thermal units than maize (Fig. 5c,d; Table 1).

Moments of maximum growth occurred earlier belowground than aboveground in maize and unfertilized prairie in both years (Fig. 5, Table 1). Average differences in above- and belowground moments of maximum growth were 1642 thermal units for maize and 466 thermal units in unfertilized prairie. The moment of maximum growth occurred earlier aboveground than belowground by 27 thermal units in 2010 for fertilized prairie. In 2011, the belowground fertilized prairie moment of maximum growth occurred 598 thermal units earlier than the aboveground moment of maximum growth. The moment that growth ended did not differ significantly between above and belowground components in any of the treatments (Table 1).

3.5 Nitrogen Concentration in Shoots and Roots

Aboveground tissue N concentration initially increased in both prairie treatments, then decreased through the rest of the growing season to a minimum of 0.33-0.49% (Fig. 6). Aboveground tissue N concentration in maize decreased throughout the season to a minimum of 0.86%. Belowground tissue N concentration remained relatively stable throughout the growing season for all treatments (Fig. 6). Tukey tests comparing treatment N concentrations at early, middle, and late growth periods showed maize had the highest aboveground N concentration followed by fertilized prairie, then unfertilized prairie in both years above- and belowground, with the exception of no difference between belowground maize and fertilized prairie N concentrations in 2011 (Table 3). Aboveground N concentrations dropped below belowground levels first in unfertilized prairie, then in fertilized prairie, then in maize (Fig. 6).

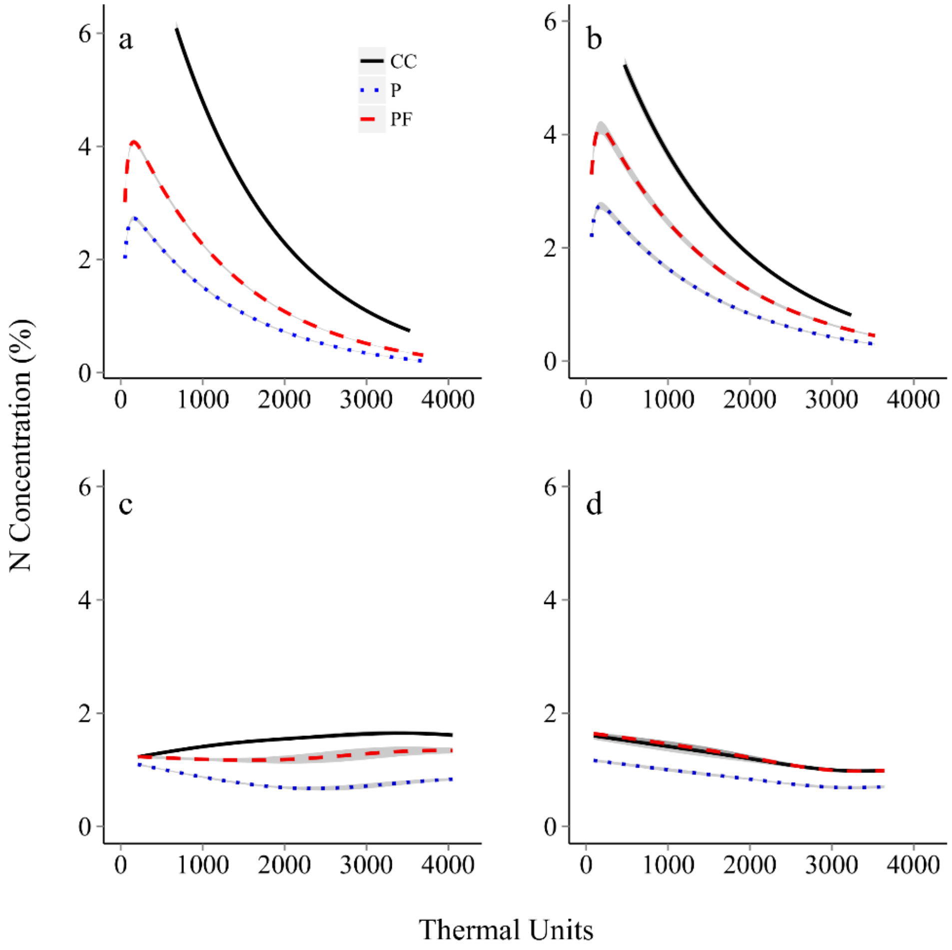

Figure 5. Nitrogen concentrations (%) during (a) aboveground 2010, (b) aboveground 2011, (c) belowground 2010, and (d) belowground 2011. Lines are predictions from Eq. 2 (aboveground) and spline fits (belowground). Solid line is maize, dashed line is fertilized prairie, and dotted line is unfertilized prairie. Grey shading represents one standard error of the mean. Goodness of fit of Eq. 2 is provided in figs S3,4.

Table 3. Mean N concentrations (%) in the aboveground (above) and belowground (below) biomass at the beginning (677 thermal units), middle (1957 thermal units) and end (3237 thermal units) of the 2010 and 2011 growing seasons for maize, unfertilized prairie, and fertilized prairie.

			Thermal Units							
Year		**Treatment**	**677**			**1957**			**3237**	
2010	Above	Maize	6.09	(0.12)	a	2.37	(0.05)	a	0.92	(0.02) a
		Unfertilized Prairie	1.92	(0.03)	c	0.75	(0.01)	c	0.29	(0.01) c
		Fertilized Prairie	2.87	(0.03)	b	1.12	(0.01)	b	0.43	(0.01) b
	Below	Maize	1.34	(0.02)	a	1.54	(0.01)	a	1.65	(0.04) a
		Unfertilized Prairie	0.96	(0.01)	c	0.69	(0.02)	c	0.75	(0.04) c
		Fertilized Prairie	1.20	(0.02)	b	1.18	(0.07)	b	1.31	(0.09) b
2011	Above	Maize	4.54	(0.12)	a	1.92	(0.05)	a	0.81	(0.02) a
		Unfertilized Prairie	2.02	(0.05)	c	0.85	(0.02)	c	0.36	(0.01) c
		Fertilized Prairie	3.05	(0.08)	b	1.29	(0.04)	b	0.54	(0.02) b
	Below	Maize	1.48	(0.09)	a	1.20	(0.07)	a	0.99	(0.01) a
		Unfertilized Prairie	1.06	(0.03)	b	0.84	(0.02)	b	0.70	(0.02) b
		Fertilized Prairie	1.52	(0.04)	a	1.22	(0.04)	a	0.99	(0.04) a

Different letters indicate significant differences among treatments within years and thermal units. Standard error of the mean is in parentheses.

3.6 Nitrogen Productivity

Nitrogen productivity (amount of biomass produced per unit N present in the biomass per thermal unit) was consistently higher in the reconstructed prairie systems (in both above and belowground tissues) than maize (Fig. 6). Tukey tests comparing N productivity at early, middle, and late growth periods showed all treatments to be different in all components, except in 2011 for belowground fertilized prairie and maize (Table 4). N productivity increased throughout the growing season in all treatments aboveground. In 2010, unfertilized prairie belowground N productivity showed a peak in N productivity midway through the growing season, whereas fertilized prairie remained steady and maize had a slight decrease. In 2011, all treatments had increasing belowground N productivity until plateauing later in the season. Nitrogen productivity for whole-plant biomass reflected aboveground patterns (Fig. 7).

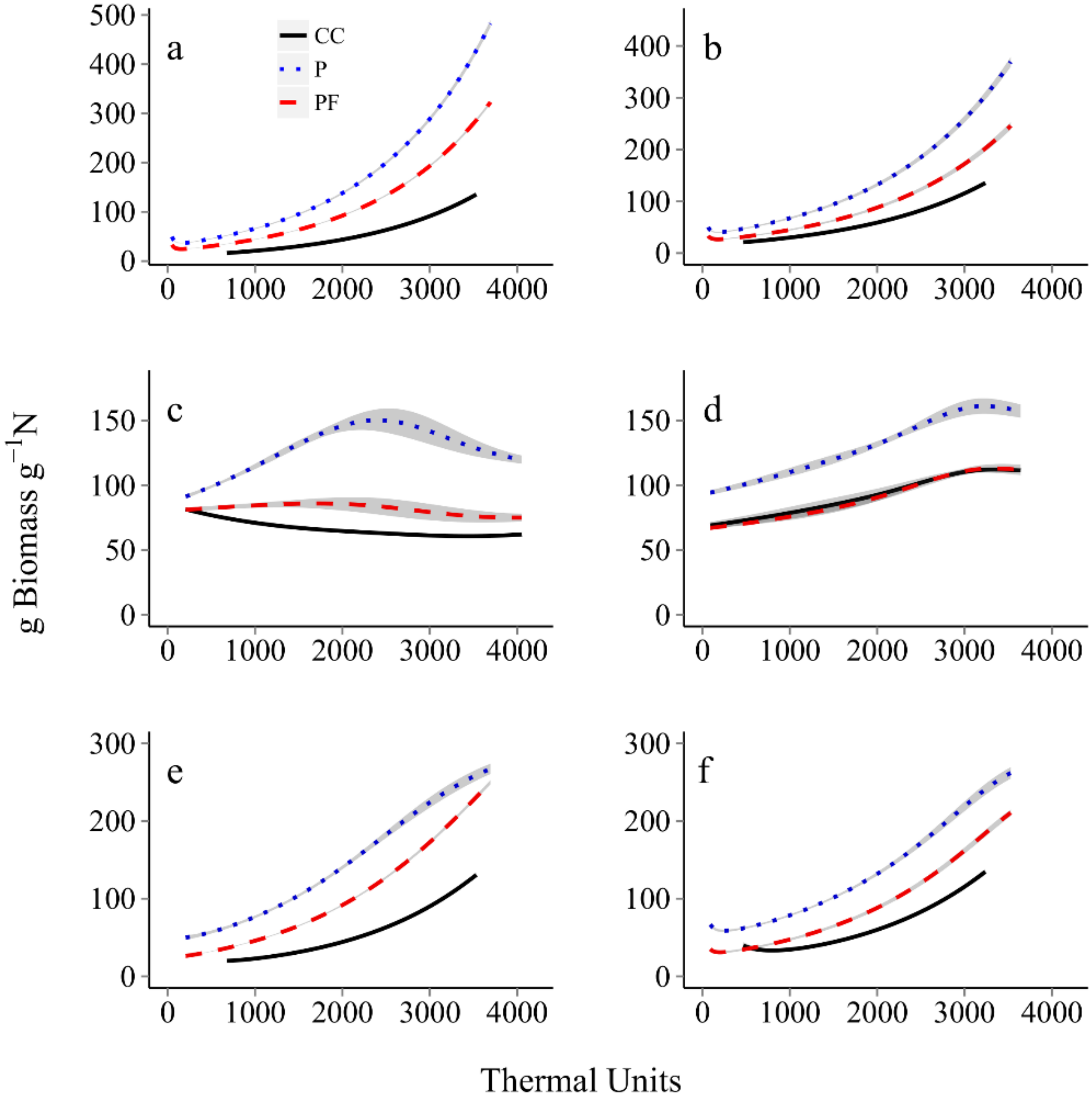

Figure 6. Nitrogen productivity (g biomass g N^{-1}thermal unit^{-1}) in (a) aboveground biomass in 2010, (b) aboveground biomass in 2011, (c) belowground biomass in 2010, (d) belowground biomass in 2011, (e) total biomass in 2010, and (f) total biomass in 2011. Lines are predictions of data generated by Eqs 1 and 2. Solid line is maize, dashed line is fertilized prairie, and dotted line is unfertilized prairie. Grey shading represents one standard error of the mean.

Table 4. Mean N productivity (g biomass g N^{-1}°C-d^{-1}, or g of biomass produced per g of N present in the plant per thermal unit) in the aboveground (above) and belowground (below) biomass at the beginning (677 thermal units), middle (1957 thermal units) and end (3237 thermal units) of the 2010 and 2011 growing seasons for maize, unfertilized prairie, and fertilized prairie.

Year		Treatment	Thermal Units								
			677			1957			3237		
2010	Above	Maize	16.4	(0.3)	c	42.3	(0.9)	c	10.9	(2.2)	c
		Unfertilized Prairie	52.0	(0.8)	a	133.8	(2.0)	a	344.4	(5.1)	a
		Fertilized Prairie	34.8	(0.4)	b	89.5	(0.9)	b	230.5	(2.4)	b
	Below	Maize	74.6	(1.1)	c	64.8	(0.6)	c	60.9	(1.4)	b
		Unfertilized Prairie	104.2	(1.1)	a	145.0	(4.1)	a	135.6	(8.6)	a
		Fertilized Prairie	83.2	(1.6)	b	85.7	(4.9)	b	77.6	(5.6)	b
2011	Above	Maize	24.3	(0.7)	c	57.3	(1.6)	c	135.6	(3.7)	c
		Unfertilized Prairie	54.4	(1.4)	a	128.5	(3.2)	a	303.8	(7.6)	a
		Fertilized Prairie	36.2	(1.1)	b	85.6	(2.5)	b	202.3	(5.9)	b
	Below	Maize	74.9	(4.0)	b	91.9	(4.9)	b	111.5	(0.9)	b
		Unfertilized Prairie	104.1	(2.7)	a	130.6	(2.4)	a	157.3	(5.1)	a
		Fertilized Prairie	72.3	(1.8)	b	89.8	(2.8)	b	112.0	(4.1)	b

Different letters indicate significant differences among treatments within years and thermal units. Standard error of the mean is in parentheses.

3.7 Nitrogen Allocation to Roots and Shoots

Belowground N mass in maize was consistently low in 2010 and quickly decreased to a small proportion in 2011 (Fig. S8, Table 2). The proportion of N mass allocated belowground in fertilized prairie increased over the growing season in both years. Unfertilized prairie had the greatest proportion of belowground N mass and also showed an increase in this proportion over the growing season (Fig. S8, Table 2).

4 Discussion

4.1 Comparison of biomass and biomass allocation patterns

Our results for within-growing-season growth patterns and dry matter allocation to roots and shoots were consistent with end-of-season findings by Jarchow and Liebman (2012a). However, our study provides additional knowledge concerning patterns of dry matter accumulation over time, data that can be used to calibrate and improve dynamic simulation models for maize and reconstructed prairies (see Chapter 3). It is well documented in the literature that simulation models suffer from lack of data on root dynamics and root to shoot ratio, further underlining the importance of this study (Zhao et al. 2014).

The different growth patterns between maize and prairies are explained by growth behavior (annual versus perennial). Maize as an annual crop invested in fecundity over vegetative structure survivorship and allocated energy to seed production and the required support structures. In contrast, reconstructed prairie as a perennial species invested in vegetative structure survivorship over fecundity and allocated energy to deep, spreading, long-lived root systems (DeHaan 2004).

The addition of N fertilization on reconstructed prairies resulted in more whole-plant biomass than the unfertilized prairie, a greater proportion of which was allocated aboveground (Table 1, 2, Fig. 3, 4). Our results agree with relevant findings by Reich et al. (2003) and Jarchow and Liebman (2013c). Generally, a limiting resource (e.g., N) will result in allocation that favors the part of the plant most able to overcome this limitation (Hunt 1986). Adding N fertilizer to prairie systems most likely shifted resource limitation from N acquisition belowground to light interception aboveground, resulting in a greater proportion of biomass aboveground and a greater whole-plant biomass. However, the difference in biomass amounts and allocation may also be due to differences in species composition, as fertilized prairie had more C_3 grasses and forbs than did the unfertilized prairie treatment (Fig. 1).

Reconstructed prairie biomass and maize stover are potential sources for bioenergy production in the Midwestern US. For bioethanol production two factors are important: amount of biomass and conversion factor. Maize stover has been found to have similar ethanol conversion and gross caloric ratios as C_4 prairie grasses, but higher ratios than C_3-C_4-legume mixtures similar to the prairie examined in this study (Jarchow et al. 2012c). When maize grain was also considered, maize had almost twice the estimated ethanol yields as C_4 prairie grasses (Jarchow et al. 2012c). James et al. (2010) also found maize to be more profitable than prairie, but used prairie biomass yields that were lower than those measured in this study. Jarchow et al. (2012c) found C_3 prairie grasses to have lower ethanol conversion and gross caloric ratios than C_4 prairie grasses. In the present study, although fertilized prairie produced more harvestable biomass than unfertilized prairie, the greater proportion of C_3 prairie grasses found in the fertilized prairie compared to the unfertilized prairie may indicate a less favorable bioenergy feedstock composition in the fertilized prairie.

An environmental advantage of greater biomass production is the potential for greater additions to soil organic matter (SOM) stocks through above- and belowground detritus. Soil organic matter is the primary source of soil C and the nutrients N, P, and sulfur (S) and its decomposition and capacity for cation exchange strongly affect nutrient availability. Soil water retention and availability are also regulated by the ability of SOM to absorb water. Association of organic matter with soil minerals promotes the formation of aggregates, providing soil structure for air and water exchange (Horwath 2008). In the present experiment, maize produced more biomass than the prairie treatments, but most of this production was aboveground where it was harvested and removed from the system. In contrast, the two prairie treatments provided more biomass towards SOM input. Indeed, data from the same study site show that prairies placed more C in the soil as roots, had more C in roots at greater depths that are less favorable to decomposition, and had C in root material that was more chemically resistant to decomposition (Jarchow et al. (2014); see Chapter 2).

4.2 Growth timing and parameters

Both prairie treatments exhibited their highest aboveground growth rates in the beginning of the growing season (Table 1, Fig. 5). DeHaan et al. (2004) observed perennial sorghum emerging four weeks earlier than annual sorghum. As temperatures warm in the spring, many prairie species are able to respond immediately. High growth rates in maize occur during the reproductive stage, when the grain develops. This period of rapid growth often coincides with optimum maize growing temperatures and a rapid accumulation of thermal units (Abendroth et al. 2011).

Aboveground growth stopped in prairie treatments before it ended in maize (Table 1, Fig. 5). This conflicts with descriptions from Gonzalez-Paleo and Ravetta (2012), in which the extensive rooting systems of perennials allowed for continued activity while annual species lost photosynthetic capabilities and began the process of senescence. However, despite an earlier end date for prairie growth, the earlier beginning date of growth meant that both prairie treatments had longer growth duration than maize. This longer duration has been shown to lead to greater use of solar radiation (Gonzalez-Paleo and Ravetta 2012), a greater potential for photosynthate production (DeHaan 2004), and in the case of the perennial grass *Miscanthus x giganteus*, greater biomass production than maize (Dohleman and Long 2009).

Growth duration and rates have important environmental implications. Longer growth duration in prairies means vegetative cover and plant activity at times when maize systems have bare soil, mainly early in the year. Surface cover protects the soil from the erosive effects of spring rain and shades the soil, preventing warming. Roots take up nutrients that may otherwise be leached, preventing loss to waterways (Huggins et al. 2002). In the soil, respiration and root exudation activate and encourage microbial communities, leading to different processes in the prairie at times when maize soil communities are functioning without support or competition from plants (de Graff et al. 2009; Denef et al. 2009).

4.3 Nitrogen concentration, productivity, and allocation

According to Lambers and Poorter (1992), leaves of fast growing species (annuals) generally have higher N concentration than those of perennial species. Our results confirm this general perception and provide the relative difference between maize and prairies (Table 3, Fig. 6). Most of the N found in aboveground tissues is in the chloroplasts, thus higher N concentrations indicate greater leaf photosynthetic capacity (or canopy radiation use efficiency; Sinclair and Muchow 1999). Fast-growing species also have higher N absorption rates to support higher growth rates when compared with slow-growing species (Lambers and Poorter 1992). Fertilized prairie also had faster growth and higher N concentrations than unfertilized prairie (Table 1, 3, Fig. 5, 6). When comparing all of these treatments, the system receiving the greatest amount of N fertilizer consistently had the highest N concentration, a result consistent with findings by Heggenstaller et al. (2009) and Reich et al. (2003). All of these relationships held true even with the under-prediction of prairie N concentration produced by equation 2.

An interesting finding from this study is that the belowground N concentrations were relatively constant over time and changed very little compared to aboveground N in all cropping systems (Table 3, Fig. 6). Adams and Wallace (1985) and Wilson et al. (2013) found that root N concentrations increased in the roots of monoculture grasses near the end of the season, indicating a recycling of N (N transfer from above to below). However, our study did not show this to be necessarily true in perennial mixtures of more than 30 species.

Unfertilized prairie had the greatest N productivity both above and belowground (Table 4, Fig. 7) compared to the other treatments. This means unfertilized prairie produced the most biomass relative to the amount of N available in the plant, showing a high efficiency of the use of internal N. This was unexpected considering that plants that grow more slowly are often shown to have a low rate of photosynthesis, large losses of photosynthates, and large investments in non-photosynthetic tissue, characteristics that would lead to less efficient growth (Lambers and Poorter 1992). Despite the possibility of these constraints, unfertilized prairie was able to produce a fair amount of aboveground biomass and the most belowground biomass of all the treatments (Table 1, Fig. 3).

Nitrogen root to shoot ratios reflected a combination of the changes in biomass combined with changes in plant N concentration (Fig. S8, Table 2). As more biomass was allocated to aboveground tissues, aboveground plant N concentrations decreased, resulting in a shift of the greater proportion of N in the plant from aboveground to belowground, where N concentrations stayed relatively stable despite an increase in root biomass (Fig. 6).

Nitrogen concentrations, N productivity, and N allocation in plants all have important biogeochemical implications. Nitrogen is harmful to the environment when lost to waterways, to the atmosphere in forms that are later deposited to non-target ecosystems, or to the atmosphere as nitrous oxide (N_2O), a greenhouse gas. Additions of N fertilizer lead to more of these particular losses (Vitousek et al. 1997). In this study, maize had higher N concentrations and lower N productivity, indicating greater need for N fertilization, lower efficiency of N use, and higher potential for N loss than prairies.

Plant N concentration and N requirements affect the value of a biofuel feedstock. Higher N concentrations reduce the conversion efficiency of biomass to biofuel, especially in thermochemical processes (Wilson et al. 2013). Meeting higher N requirements through fertilization leads to greater production costs. While maize had the greater energy potential when compared to the prairie plants by Jarchow (2012c), this study found maize also had the highest N concentrations and greatest need for N fertilization.

This study provided quantitative data on above- and belowground growth dynamics for three Midwestern production systems (maize, reconstructed prairie, and fertilized reconstructed prairie). These data enhance our knowledge of temporal growth and plant N dynamics, especially belowground, and can be used to calibrate simulation models to help design resilient food and fuel production systems. Choices between annual and perennial plant systems for food and fuel production are dependent upon the desired traits of the crop and will likely be based on some tradeoffs (Jarchow et al. 2012a). If priorities focus solely on biomass production, an annual species like maize will perform best. However, if lower N needs and higher root production are important, perennial systems such as reconstructed prairie will perform best. A compromise between the two systems would be a more managed perennial system like fertilized prairie, which uses less N than maize, but produces more biomass than unfertilized prairie.

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6 Appendix A

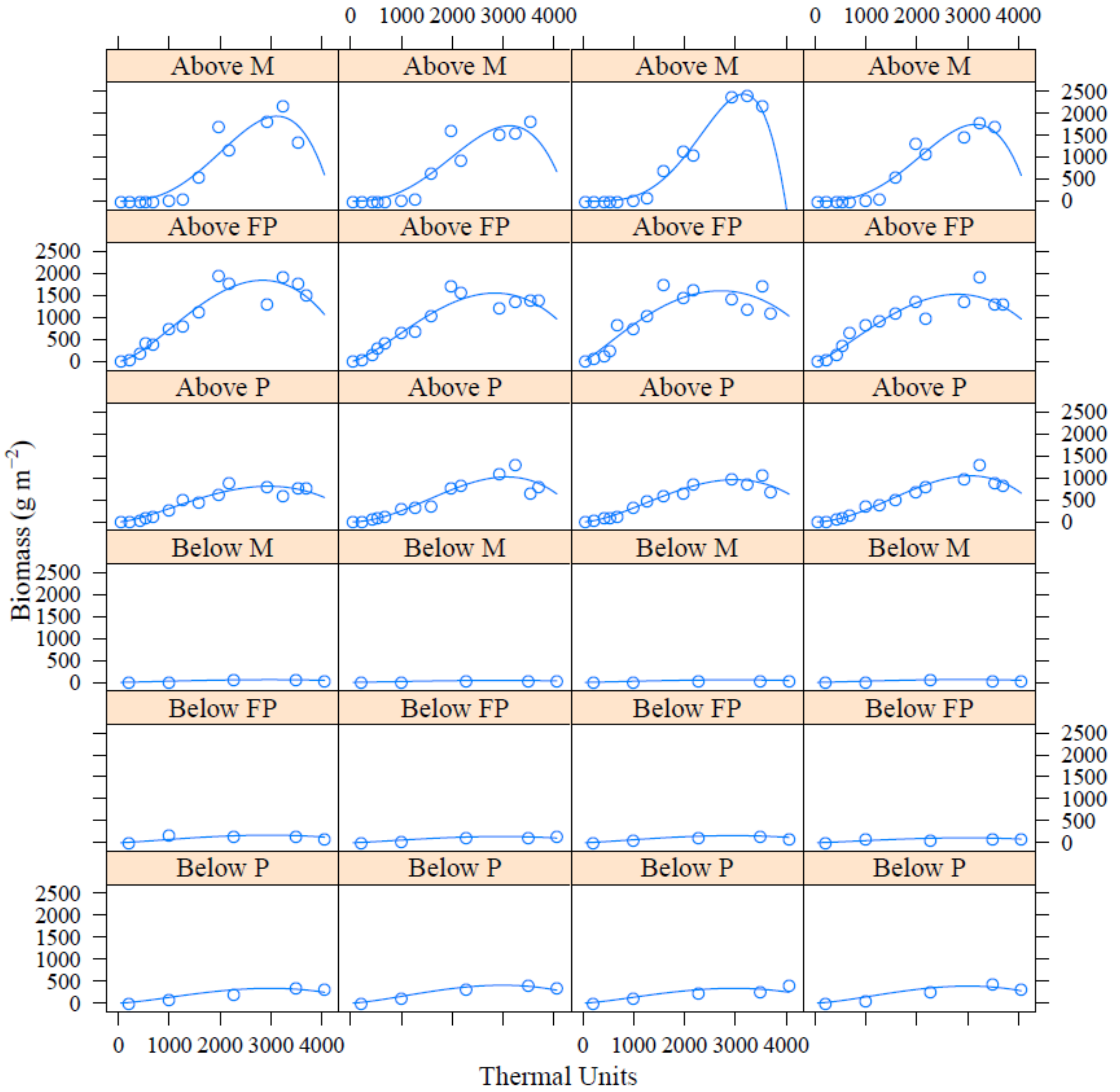


Figure S1. Fits of the beta growth model to replicate measurements of above and belowground biomass in 2010. Letters represent cropping treatments, M is maize, P is prairie, and FP is fertilized prairie. Predicted values falling outside the sampling time range were not used.

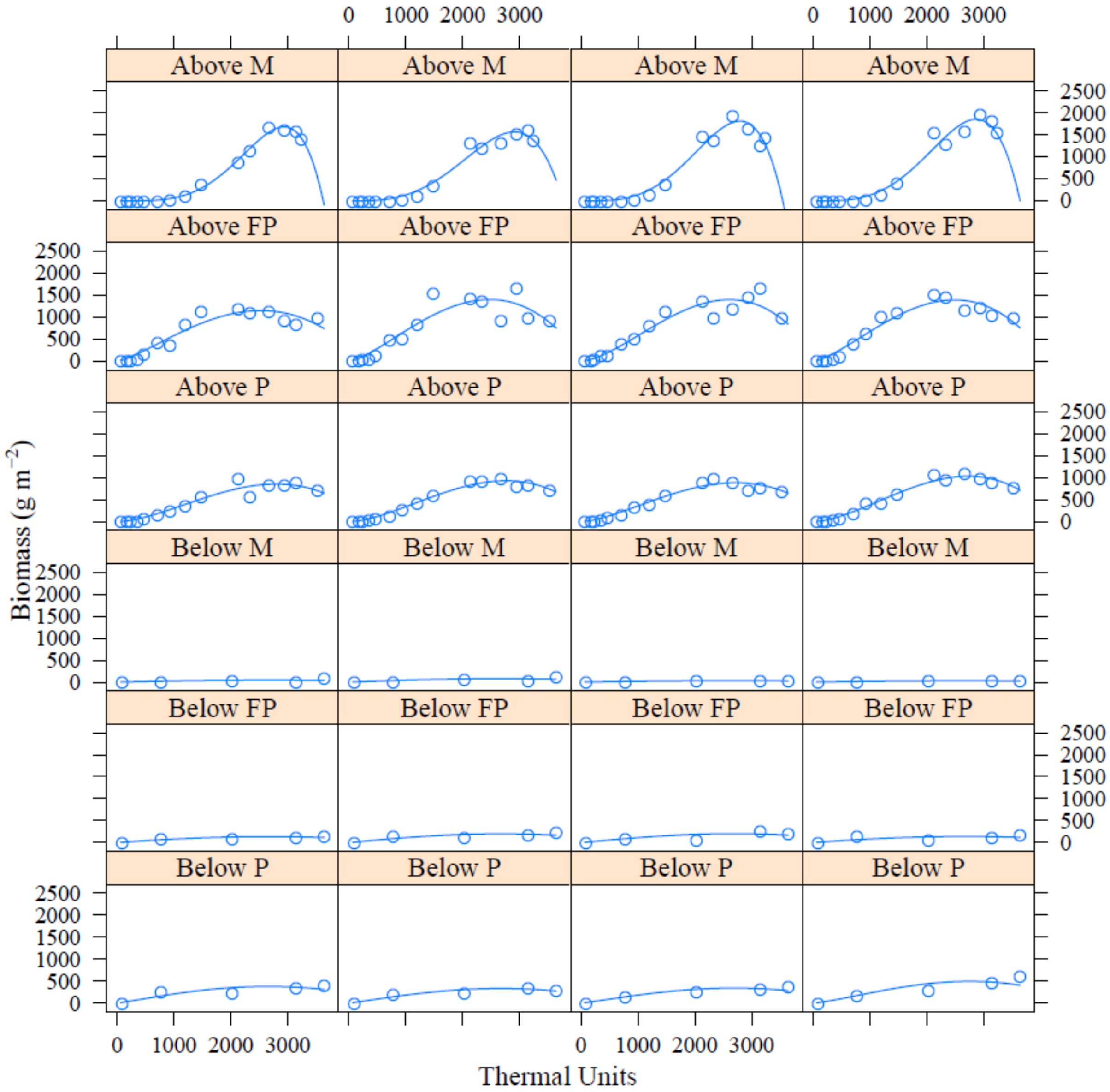


Figure S2. Fits of the beta growth model to replicate measurements of above and belowground biomass in 2011. Letters represent cropping treatments, M is maize, P is prairie, and FP is fertilized prairie. Predicted values falling outside the sampling time range were not used.

Table S2. Mean parameters for equation 2 used to model N concentration in aboveground biomass in 2010 and 2011.

Year	**Treatment**	**Cl (%N)**		**k_e (%N thermal unit $^{-1}$)**		**k_a (%N thermal unit $^{-1}$)**	
2010	Maize	-9.310	(0.012)	-7.077	(0.004)	-5.596	(0.037)
	Unfertilized Prairie	-8.400	(0.013)	-7.374	(0.004)	-2.877	(0.038)
	Fertilized Prairie	-8.763	(0.006)	-7.255	(0.002)	-3.963	(0.019)
2011	Maize	-9.263	(0.029)	-7.372	(0.006)	-4.210	(0.018)
	Unfertilized Prairie	-8.350	(0.028)	-7.179	(0.006)	-3.650	(0.017)
	Fertilized Prairie	-8.821	(0.032)	-7.279	(0.007)	-3.939	(0.020)

Standard error of the mean is in parentheses.

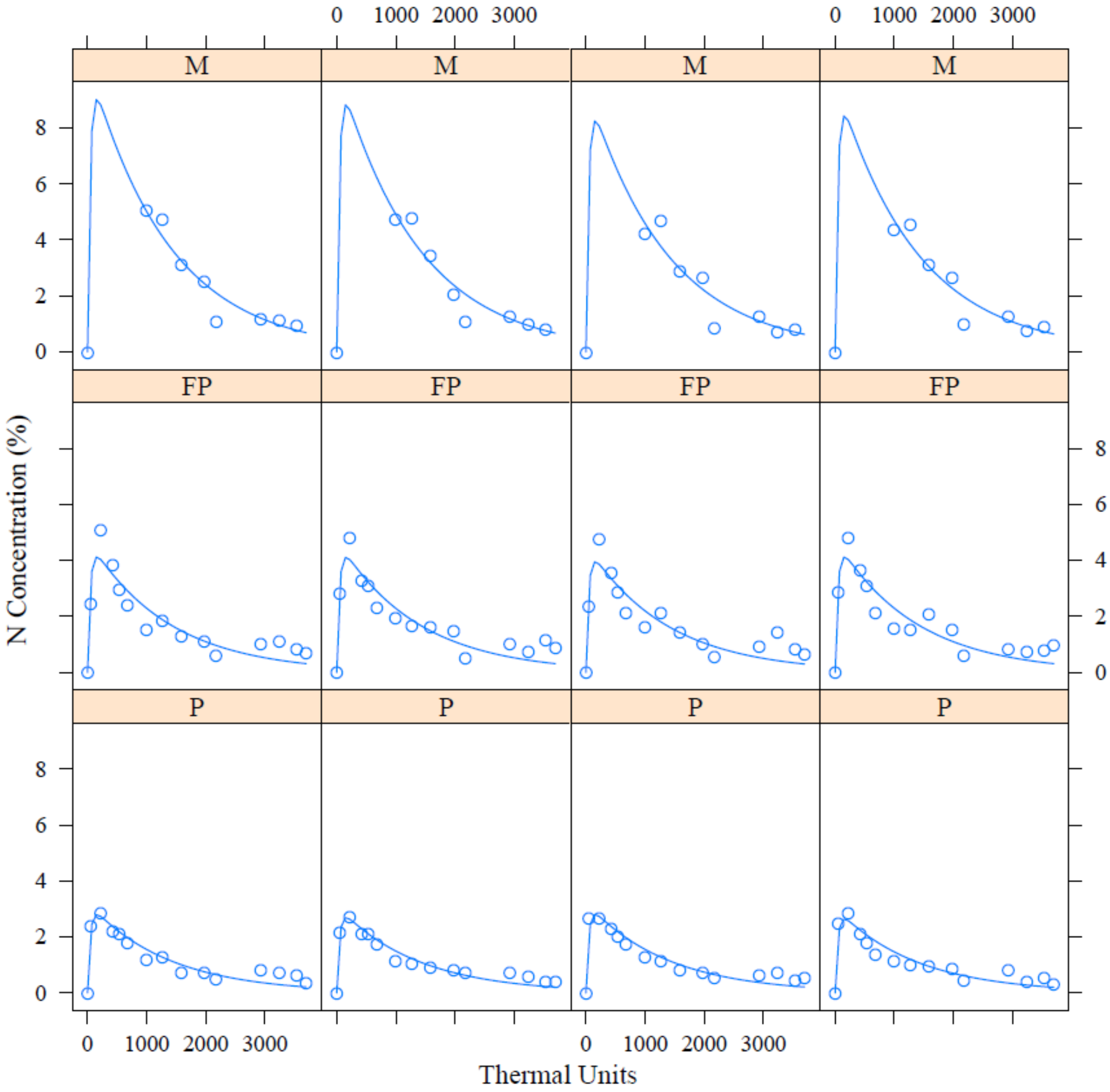


Figure S3. Fits of the first order compartment model to replicate measurements of aboveground biomass in 2010. Letters represent cropping treatments, M is maize, P is prairie, and FP is fertilized prairie. Predicted values falling outside the sampling time range were not used, including values under 677 thermal units in the maize treatment.

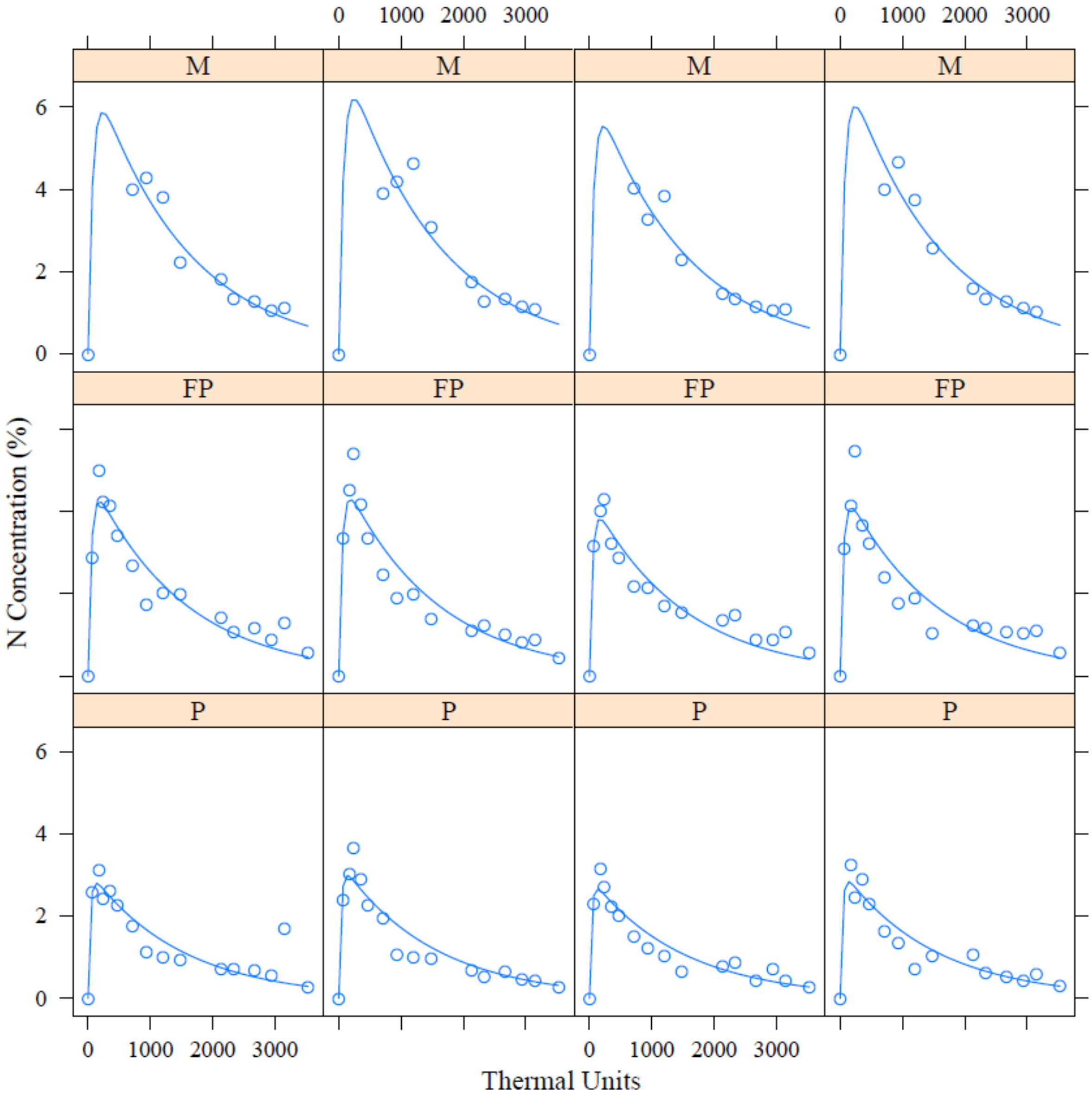


Figure S4. Fits of the first order compartment model to replicate measurements of aboveground biomass in 2011. Letters represent cropping treatments, M is maize, P is prairie, and FP is fertilized prairie. Predicted values falling outside the sampling time range were not used, including values under 468 thermal units in the maize treatment.

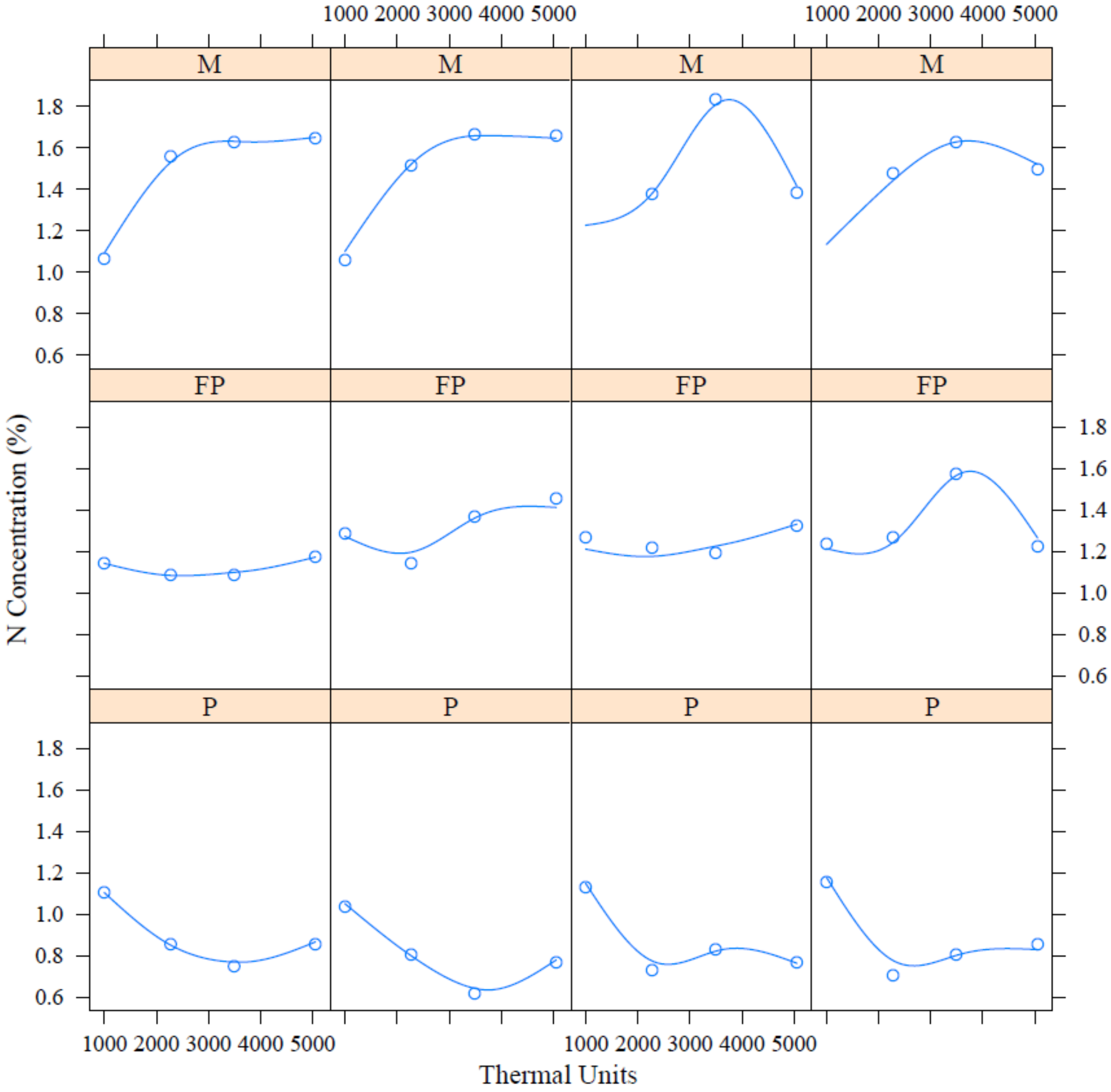


Figure S5. Fits of splines to replicate measurements of belowground biomass in 2010. Letters represent cropping treatments, M is maize, P is prairie, and FP is fertilized prairie.

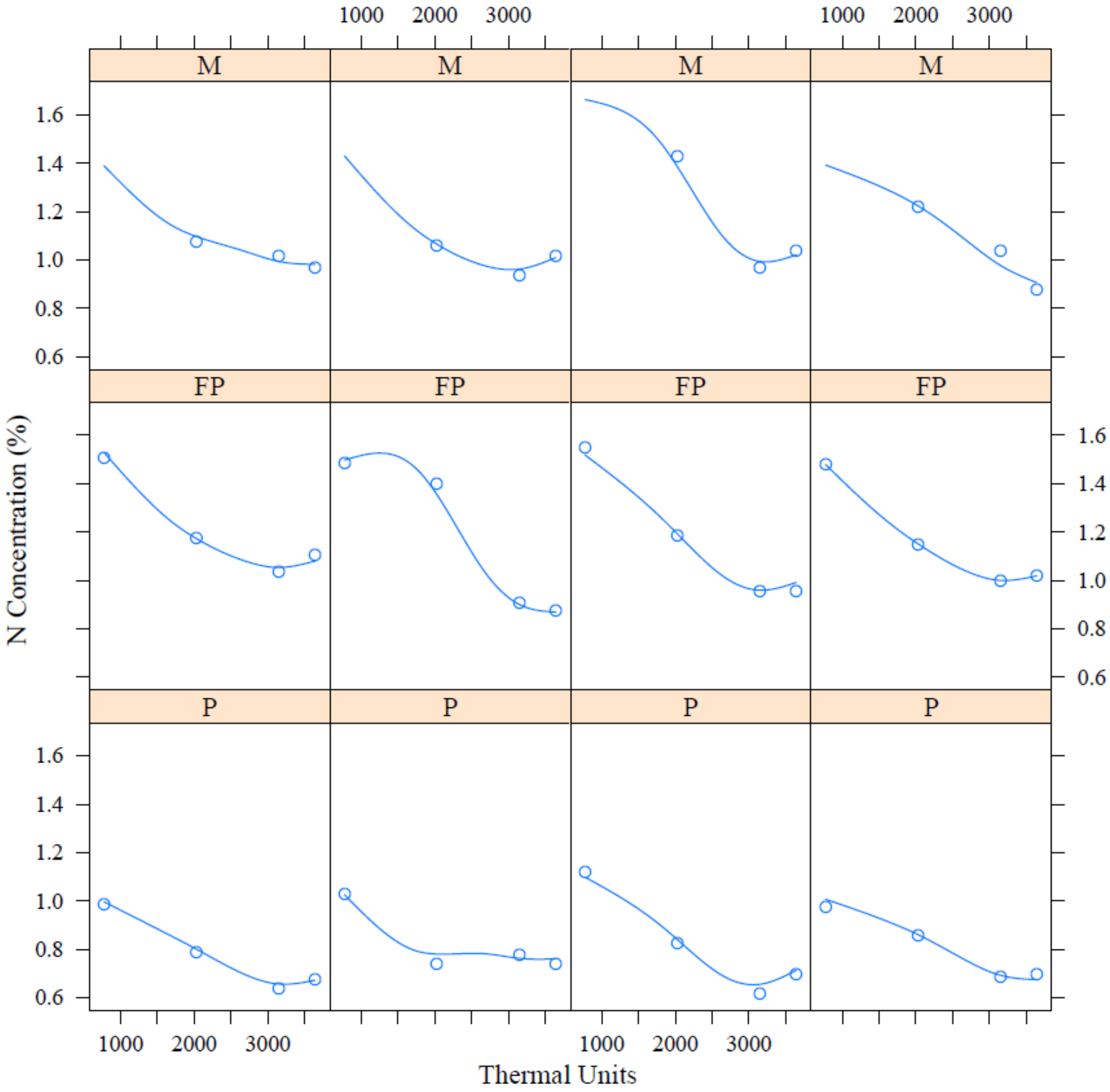


Figure S6. Fits of splines to replicate measurements of belowground biomass in 2011. Letters represent cropping treatments, M is maize, P is prairie, and FP is fertilized prairie. Missing values in maize treatments are due to not enough biomass sample for N content analysis.

CHAPTER 3. ROOT-INPUTS DRIVE C STORAGE POTENTIAL DIFFERENCES IN CORN- AND PRAIRIE-BASED CROPPING SYSTEMS

1 Introduction

High soil carbon (C) content is a crucial property of a highly productive soil. Soils high in C have a greater capacity for cation exchange, can retain more water, have better aggregation (Horwath 2007), have bigger and more active microbial communities, and provide plant-growth inducing compounds (Arshad and Frankenburger 1998). Carbon that is in the soil is C that is absent from the atmosphere, where it contributes to harmful levels of CO_2. Plants have the ability to remove C from the atmosphere through photosynthesis, but the extent to which this C is stored in the soil is often difficult to determine.

Carbon-rich soils in the Midwestern United States developed over thousands of years under perennial mixes of C3 and C4 grasses, legumes, and forbs known as prairies. However, conversion of 99% of this native ecosystem to row-crop agriculture in the last 150 years has resulted in the loss of 30-50% of the organic matter in these soils due to erosion and tillage-induced increases of microbial metabolism (David 2009).

The potential to restore soil C through the reconstruction of prairie systems is unclear because measuring changes in soil C is inherently difficult. Prairie soil C changes found under budgeting approaches range from -3.9 Mg C ha^{-1} y^{-1} (Brye et al. 2002) to 5.3 Mg C ha^{-1} y^{-1} (Guzman and Al-Kaisi 2010) and are often found to be both negative and positive in a given system, depending upon the year of measurement (Brye et al. 2002, Kucharik et al. 2006, Guzman and Al-Kaisi 2010). Thus, when C losses are accounted for as well as C gains, it is no longer apparent that prairies or no-till cropping systems are sinks of C, let alone which system sequesters more C. In many cases, uncertainties in above and below ground production and respiration contribute to these changes in magnitude and direction (Cahill et al. 2009). Directly measuring changes in soil C on an annual basis is rarely an option because annual changes in soil C are small relative to the soil C background, and therefore undetectable.

Carbon in the soil has many different forms and is contained in many different C pools, usually classified by the time C is expected to stay in each pool. Roots are routinely removed from soil before C quantification and are often not considered a part of the soil C pool in agricultural systems. But some perennial grass and forb roots live for over 10 years and maintain a root form even beyond that. Even as roots turn over, the root C pool remains present as long as the aboveground portion is living. This represents a C pool with a residence time that varies only in response to management decisions.

The aim of our project was to compare C storage potential between corn- and prairie-based systems. We chose to focus on the root C pool and hypothesized that greater root additions in the prairie would lead to a higher C storage potential than in the corn-based systems. We further hypothesized that the perennial behavior of prairies would result in roots that were more persistent than those of the annual roots found in the corn-based systems.

2 Methods

2.1 Site Conditions and Experimental Design

We conducted the experiment in Boone County, IA, USA on the Iowa State University Agronomy and Agricultural Engineering Research Farm (41°55′N, 93°45′W). Soils at the site were primarily Webster silty clay loam (fine-loamy, mixed, superactive, mesic Typic Endoaquoll) and Nicollet loam (fine-loamy, mixed, superactive, mesic Aquic Hapludoll). The 60-year mean growing season precipitation 11 km from the site was 720 mm. Prior to initiation of the field experiment in 2008, the site was used for maize and soybean production and was planted with soybean in 2007. Soil sampling to 15 cm in November 2007 indicated mean soil pH was 6.7, mean organic matter concentration (via dry combustion analysis with a conversion factor of 1.724 from total C to organic matter [Schumacher 2002]) was 51 g kg^{-1}, mean extractable phosphorus concentration (via Bray-1 procedure) was 11 mg kg^{-1}, and mean extractable potassium (via Mehlich-3 procedure) was 141 mg kg^{-1}.

Experimental plots were 27 m x 61 m and were arranged as a spatially balanced complete block design (van Es et al. 2007). Five cropping systems were studied: a corn-soybean rotation with annual grain removal (hereafter corn-soybean rotation), continuous corn with annual grain and stover removal (hereafter continuous corn), continuous corn with grain and stover removal and rye used as a winter cover crop (hereafter continuous corn with rye), reconstructed multispecies prairie with annual aboveground biomass removal (hereafter unfertilized prairie), and N-fertilized reconstructed multispecies prairie with annual aboveground biomass removal (hereafter fertilized prairie). All of the treatments were managed without tillage. Conventional farm machinery was used for planting, fertilization, crop protection, and harvest operations. Herbicides were not used in the prairie systems except for a small number of spot treatments for Canada thistle (*Circium canadense*) control, and the timing and frequency of herbicide use in the annual cropping systems varied among treatments. Nutrient management also varied among all treatments (Table 1).

Both prairie treatments were sown on 19 May 2008 with the same custom seed mix obtained from Prairie Moon Nursery (Winona, MN, USA) that contained 31 species, including C_3 and C_4 grasses and leguminous and non-leguminous forbs (Table S1). All species were perennial and sourced from within 240 km of the experiment site. The composition of the seed

Table 1. N fertilizer amount and date applied for all COBS treatments.

	2008		**2009**		**2010**		**2011**		**2012**		**2013**	
Treatment	Date Applied	Amount (kg N ha^{-1})	Date Applied	Amount (kg N ha^{-1})	Date Applied	Amount (kg N ha^{-1})	Date Applied	Amount (kg N ha^{-1})	Date Applied	Amount (kg N ha^{-1})	Date Applied	Amount (kg N ha^{-1})
Continuous Corn	15-May	72.8	7-May	84	6-May	87.4	11-May	87.4	11-May	87.4	17-May	89.6
	24-Jun	100.8	17-Jun	84	17-Jun	35.8	29-Jun	56	12-Jun	112	28-Jun	112
Corn with Rye	15-May	72.8	7-May	84	6-May	87.4	11-May	87.4	11-May	87.4	17-May	89.6
	24-Jun	100.8	17-Jun	134.4	17-Jun	81.8	29-Jun	134.4	12-Jun	134.4	28-Jun	89.6
Grain Corn	15-May	72.8	7-May	84	6-May	87.4	11-May	87.4	11-May	87.4	17-May	89.6
	24-Jun	100.8	17-Jun	56	17-Jun	17.9	29-Jun	39.2	12-Jun	134.4	28-Jun	115
Fertilized Prairie	No N fertilizer		17-Apr	84	29-Mar	84	11-Apr	84	28-Mar	84	26-Apr	84

mix by weight was 12% C_3 grasses, 56% C_4 grasses, 8% legumes, and 24% non-leguminous forbs. A detailed description of the prairie plant community compositions can be found in Jarchow and Liebman (2013). The fertilized prairie treatment received no fertilizer in 2008 (the establishment year), and was fertilized at a rate of 84 kg N ha^{-1} $year^{-1}$ in all subsequent years. This fertilizer rate was chosen because it was similar to the maximum rate of pre-planting N fertilization recommended for maize (Blackmer et al. 1997) and the expected N removal in the harvested biomass of perennial grasses grown in the area (Heggenstaller et al. 2009). Fertilization timing can be found in Table 1.

The maize used was a 104-day relative maturity hybrid with transgenes for glyphosate resistance, corn borer (*Ostrinia nubilalis*) resistance, and corn rootworm (*Diabrotica* spp.) protection (Agrigold 6325 VT3). Maize was planted following standard practices (Abendroth et al. 2011) in rows spaced 76 cm apart at 79,500 seeds ha^{-1} on 6 May 2010 and 82,500 seeds ha^{-1} on 11 May 2011. Fertilizer rates and types can be found in Table 1. Rates of N added after planting were based on results of late-spring tests of soil nitrate-N concentration (Blackmer et al. 1997). All N was applied as urea-ammonium nitrate (32% N). An unfertilized maize treatment was not included in the experiment because the effects of N fertilizer on maize have been extensively studied and modeled, with N fertilization leading to greater biomass and higher grain yields (Cerrato and Blackmer 1990; Sawyer et al. 2006).

2.2 Data Collection

2.2a Soil Collection

Soil cores were taken to 1 m depth in all plots each year over a six year period using a hydraulic soil probe (Giddings Machine Co., Windsor, CO, USA) after all crops were harvested.

Sampling occurred by replicate block from 31 October-25 November 2008, 9-11 November 2009, 25-28 October 2010, and 28-31 October 2011, 16-17 October 2012 and 7-11 October 2013.

In 2008, two cores were taken per plot. A 0-30 cm fraction was taken with a 10.2 cm internal diameter soil probe; the 30-100 cm fractions of the cores was taken within the same hole as the 0-30 cm fraction, but with a smaller soil probe. In Blocks 1 and 4, the internal diameter of the core was 6.0 cm. In Blocks 2 and 3, the internal diameter of the core was 5.2 cm.

In 2009 and 2010, four cores were taken per plot. The 0-30 cm fraction of the cores were taken with a 10.2 cm internal diameter soil probe; the 30-100 cm fraction of the cores were taken directly below the 0-30 cm fraction with a 5.1 cm internal diameter probe. In 2011-2013, four cores were taken per plot, and the entire core was taken with a 5.1 cm internal diameter probe. Soil cores were ultimately divided into three or five depth increments. In 2008, depth increments were 0-30 cm, 30-60 cm, and 60-100 cm. In 2009-2013 depth increments were 0-5 cm, 5-15 cm, 15-30, cm, 30-60 cm, and 60-100 cm. Following division and extraction from the field, soil cores were stored at 5°C until processing was initiated.

2.2b Roots

Root extraction from the soil began by washing the soil samples in wire mesh tubes (0.28 mm mesh) for 3 h in an elutriator (Wiles et al., 1996). Roots were removed from the remaining soil by suspending the air-dried sample in water and collecting the roots, which floated, with sieves followed by manually removing any remaining non-root material that was present in the samples. Any plant crowns that were present in the samples were removed and were not considered to be root biomass. Roots were then dried at 70°C for at least 4 h before being weighed. All above- and belowground biomass samples were ground to 2 mm with a centrifugal mill and concentrations of C and N were determined by combustion analysis in a CN analyzer (LECO Corporation, St. Joseph, MI) at the Soil and Plant Analysis Laboratory at Iowa State University (Ames, IA, USA).

Each year before roots were washed, 60-100 g of root-free soil was removed from each depth increment, air-dried, and archived in airtight containers at room temperature. In 2008 and 2013, this soil was ground on a roller-mill and organic C content was determined by first removing inorganic C with an acid treatment followed by catalytic oxidation and CO_2 measurement with NDIR in an Elementar TOC Cube at Brookside Laboratories, Inc. (New Bremen, Ohio).

In 2012, soil was ground with mortar and pestle and analyzed for permanganate oxidizable carbon (POXC) as described by Culman et al. (2012) and http://lter.kbs.msu.edu/protocols/133. Briefly, 2.5 g of soil were shaken for 2 minutes with a $KMnO_4$ solution and then allowed to settle for 10 minutes and then the supernatant was extracted. Permanganate oxidizable C led to reduction of the $KMnO_4$ which was detected in the supernatant by a spectrophotometer set at 550 nm.

2.3 Data Analysis

Root mass for the entire meter depth was calculated by summing together the root mass for each depth increment of an entire core and whole core root masses between treatments were compared within each year using contrasts within a linear mixed effect model in R. Treatment differences within depths and depth differences within treatments were also made for POXC using contrasts within a linear mixed effects model in the R package *nlme* (Pinheiro et al. 2013). Treatment differences within depths within years and differences between treatments within depths within years for root biomass were also made with contrasts with linear mixed effects models, but proc glimmix in SAS (SAS Institute, 2011) was used.

Because root mass in 2008 was measured at three increments (0-30 cm, 30-60 cm, and 60-100 cm) instead of five increments (0-5 cm, 5-15 cm, 15-30 cm, 30-60 cm, and 60-100 cm), 2008 root mass for 2008 0-5 cm, 5-15 cm, and 15-30 cm was estimated by multiplying the average 2009-2013 proportion by the 2008 0-30 cm increment. No important comparisons were made using this estimated data, but the data was used as a starting point for graphing C:N ratios in different depth increments and fitting curves to root accumulation. C:N ratios were compared between treatments within years within depths and between years within treatments within depths using proc glimmix in SAS.

Root mass measured at the end of the each growing season was subset by depth increment and each subset was fit by both a logistic model and a linear model for each plot. Logistic models and linear models were compared against each other using Akaike's Criterion (AIC) and the model with the lowest AIC was chosen. The AIC was not vastly different for any of the comparisons, but the logistic model had the best fit for every depth (Appendix Figure 1). Model fits and comparisons were done using the R package *nlme* (Pinheiro et al. 2013).

The first derivative of the logistic model was used to calculate the daily rate of accumulation over the entire year. Parameters from the logistic model were used to predict both amount and rate of accumulation for each day for each depth in each plot of the experiment. These predictions were averaged for each treatment and plotted. The annual mean rate was calculated by averaging accumulation rates across each growing season for each depth in each plot. Comparisons of rates between treatments within depths and within years and comparisons of rates between depths within treatments within years were made with proc glmmix in SAS.

3 Results

3.1 Aboveground Biomass

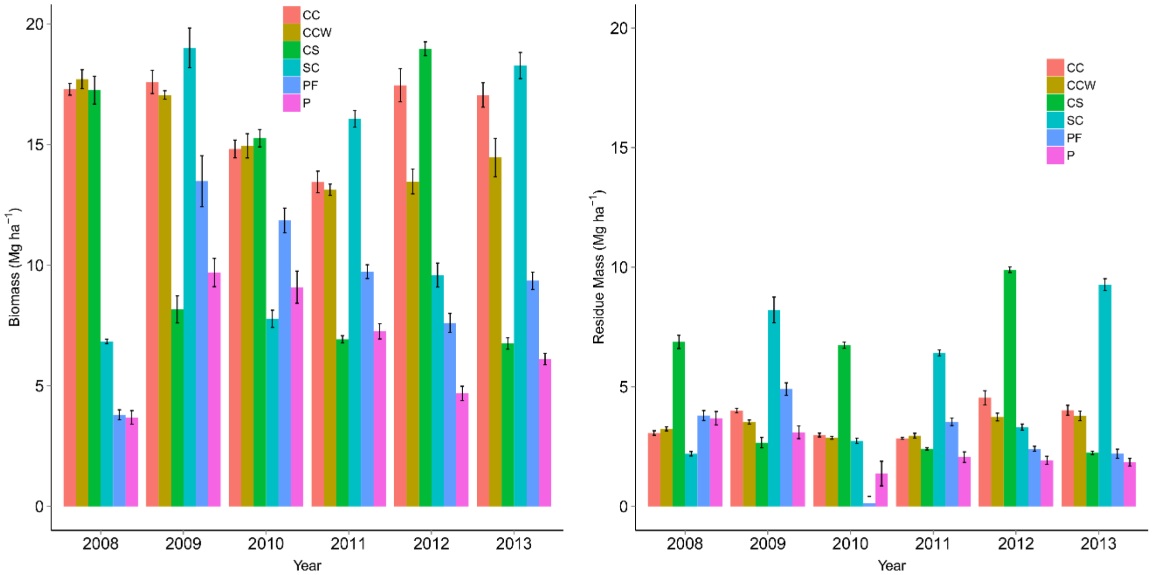


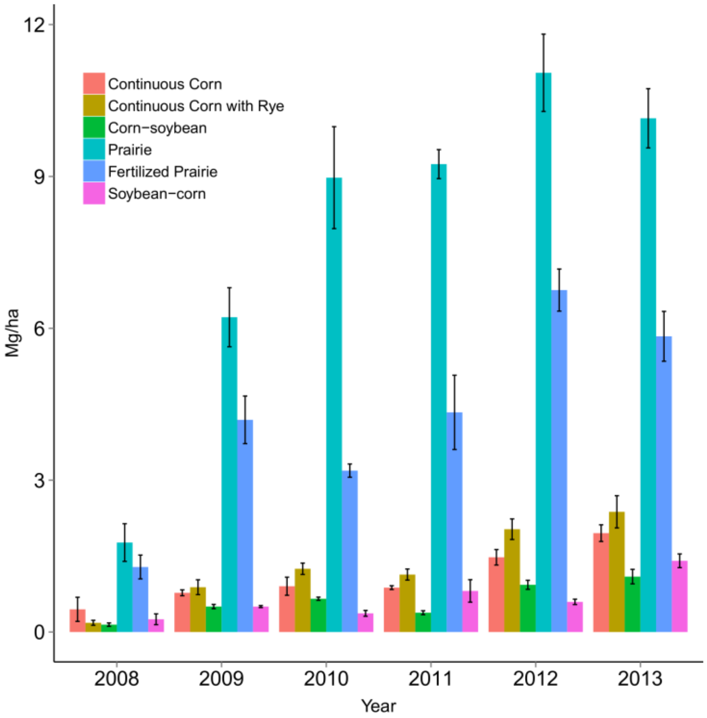
Figure 1. Aboveground biomass (left) and residue remaining on the field (right) at COBS in 2008-2013. Treatments are continuous corn (CC), continuous corn with winter cover crop (CCW), corn-soybean rotation (CS), soybean-corn rotation (SC), fertilized prairie (PF), and unfertilized prairie (P).

Over six years, corn yields averaged 16.3 Mg biomass ha^{-1}, 8.85 Mg ha-1 of which was grain. Over six years, soybeans averaged 7.67 Mg biomass ha^{-1}, 3.0 of which was grain. After the establishment year, between 2009-2013 unfertilized prairie averaged 7.37 Mg biomass ha^{-1} and fertilized prairie averaged 10.4 Mg biomass ha^{-1} (Fig. 1). Rye averaged 1.22 Mg biomass ha^{-1} (Table 1). Continuous corn treatments left an annual average of 3.46 Mg ha^{-1} of reside on the surface, corn of the corn-soybean treatment left an annual average of 7.9 Mg ha^{-1} of residue and soybean left an annual average of 2.60 Mg ha^{-1} of residue. The prairie treatments left an annual average of 2.58 Mg ha^{-1} of residue (Fig. 1).

Table 2. Winter rye above- and belowground biomass and C and N tissue composition at COBS in 2009-2013. One standard error is in parentheses.

Year	Aboveground Mass (Mg/ha)		Belowground Mass (Mg/ha)		Aboveground %C		Aboveground %N		Belowground %C		Belowground %N	
2009	0.37	(0.07)	0.06	(0.01)	39.19	(0.59)	3.47	(0.13)	33.13	(1.25)	1.26	(0.02)
2010	1.18	(0.08)	1.56	(0.14)	39.28	(0.14)	2.15	(0.06)	35.07	(0.55)	1.67	(0.03)
2011	1.53	(0.13)	2.09	(0.31)	40.91	(0.10)	1.52	(0.08)	32.31	(0.42)	1.05	(0.07)
2012	2.50	(0.07)	1.87	(0.19)	39.16	(0.12)	1.78	(0.07)	32.78	(0.25)	0.98	(0.02)
2013	0.50	(0.05)	0.94	(0.04)	38.84	(0.15)	3.31	(0.21)	30.79	(0.56)	1.34	(0.05)

3.2 Root Biomass



Year	Treatment	Mass $(Mg\ ha^{-1})$		
2008	CS	0.45	(0.24)	c
	CC	0.18	(0.05)	c
	CCW	0.15	(0.03)	c
	P	1.77	(0.37)	a
	PF	1.28	(0.23)	b
	SC	0.25	(0.11)	c
2009	CS	0.77	(0.06)	c
	CC	0.89	(0.15)	c
	CCW	0.50	(0.04)	c
	P	6.22	(0.58)	a
	PF	4.19	(0.47)	b
	SC	0.50	(0.02)	c
2010	CS	0.90	(0.18)	c
	CC	1.25	(0.11)	c
	CCW	0.66	(0.03)	c
	P	8.98	(1.01)	a
	PF	3.19	(0.13)	b
	SC	0.37	(0.06)	c
2011	CS	0.88	(0.04)	c
	CC	1.14	(0.11)	c
	CCW	0.38	(0.04)	c
	P	9.24	(0.29)	a
	PF	4.34	(0.73)	b
	SC	0.81	(0.22)	c
2012	CS	1.48	(0.15)	cd
	CC	2.03	(0.20)	cd
	CCW	0.93	(0.09)	c
	P	11.05	(0.76)	a
	PF	6.75	(0.42)	b
	SC	0.60	(0.05)	d
2013	CS	1.95	(0.16)	d
	CC	2.37	(0.32)	cd
	CCW	1.09	(0.14)	c
	P	10.15	(0.59)	a
	PF	5.84	(0.49)	b
	SC	1.41	(0.14)	cd

Figure 2 and Table 3. Root pool mass to a 1 meter depth. Error bars and parentheses in table denote one standard error of the mean. Different letters in the table denote significant differences between treatments within years.

Prairie treatments had more root pool mass than corn-based treatments every year of the study. From 2009-2013, unfertilized prairie had an average of 2 times more root pool biomass than fertilized prairie. By 2013, unfertilized prairie had almost 6 times more root pool biomass than an average of the row crop treatments and fertilized prairie had 3.5 times more root pool biomass than an average of the row crop treatments. In 2012 and 2013, continuous corn treatments that had a winter rye cover crop (CCW) had significantly more root pool biomass than experimental plots that were in the soybean year of the corn-soybean rotation (Fig. 2).

3.3 Root Pool Mass Accumulation

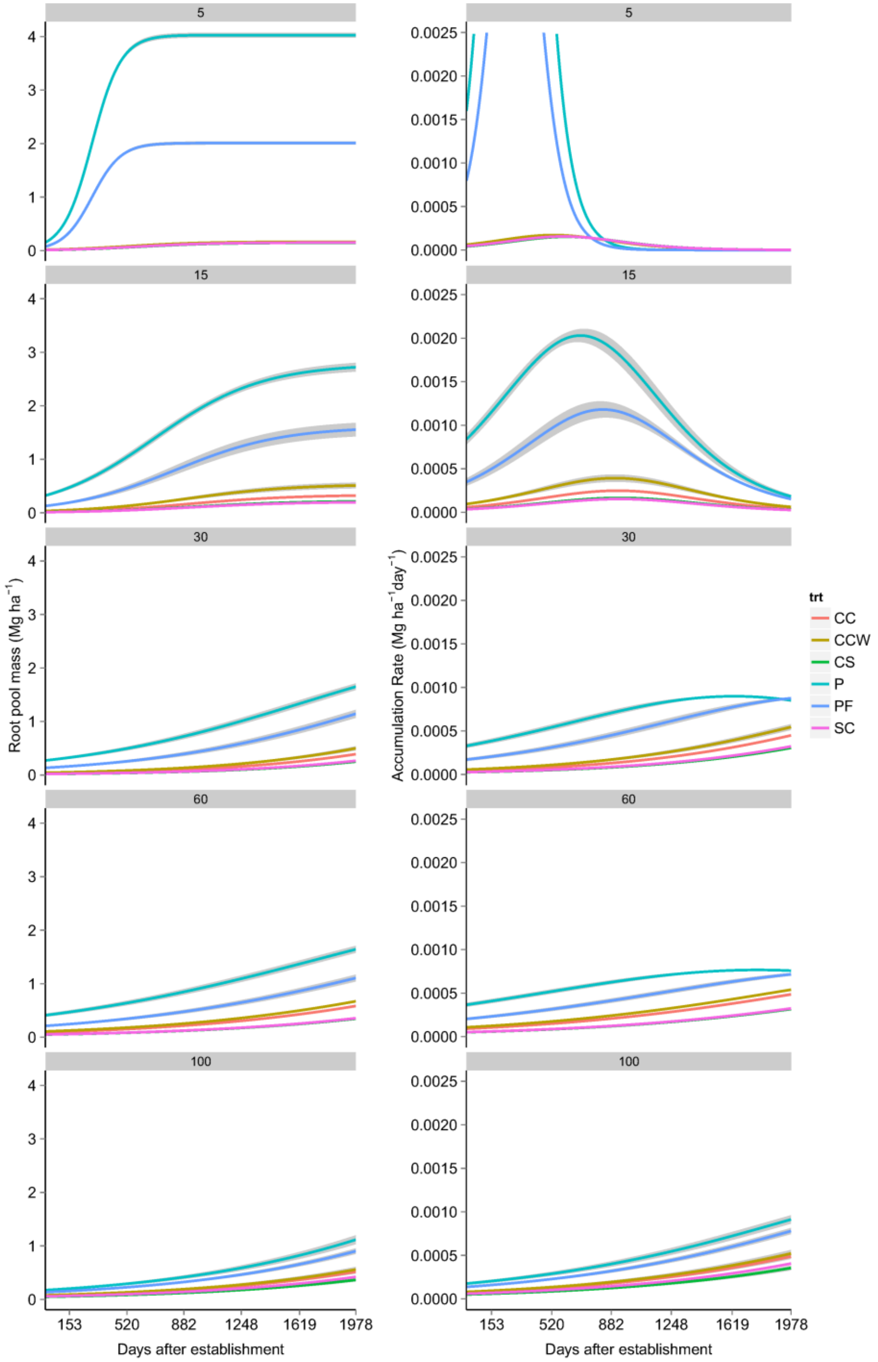


Figure 3. Root pool mass accumulation (left) and root pool mass accumulation rates (right) at 0-5 cm (5), 5-15 cm (15), 15-30 cm (30), 30-60 cm (60), and 60-100 cm (100) across days after establishment. Each x-axis tick mark is day that roots were sampled (153 is 2008, 520 is 2009, 882 is 2010, 1248 is 2011, 1619 is 2012 and 1978 is 2013). . Treatments are continuous corn (CC), continuous corn with winter cover crop (CCW), corn-soybean rotation (CS), soybean-corn rotation (SC), fertilized prairie (PF), and unfertilized prairie (P).Shading represents standard error.

Table 4. Means, standard errors, and comparisons of root pool accumulation rates. Differences in uppercase letters indicate significant differences between treatments within depths within years (read left and right). Differences in lowercase letters indicate significant differences between depths within treatments within years (read up and down).

		Rate of accumulation averaged across each growing season (g m^{-2} day^{-1})																	
Year	Depth	CC			CCW			CS			SC			PF			P		
2008	0-5	0.007	a	C	0.008	a	C	0.006	a	C	0.006	a	C	0.205	a	B	0.411	a	A
	5-15	0.007	a	C	0.012	a	C	0.005	a	C	0.004	a	C	0.044	b	B	0.102	b	A
	15-30	0.005	a	C	0.006	a	C	0.003	a	C	0.003	a	C	0.019	c	B	0.036	c	A
	30-60	0.010	a	C	0.012	a	C	0.006	a	C	0.007	a	C	0.025	c	B	0.058	a	A
	60-100	0.008	a	B	0.009	a	B	0.006	a	B	0.007	a	B	0.015	c	AB	0.019	a	A
2009	0-5	0.015	a	C	0.016	a	C	0.013	a	C	0.014	a	C	0.315	a	B	0.632	a	A
	5-15	0.016	a	C	0.025	a	C	0.010	a	C	0.009	a	C	0.087	b	B	0.177	b	A
	15-30	0.007	a	C	0.010	a	C	0.005	a	C	0.005	a	C	0.029	c	B	0.051	c	A
	30-60	0.015	a	C	0.017	a	C	0.009	a	C	0.009	a	C	0.036	c	B	0.084	d	A
	60-100	0.012	a	B	0.013	a	B	0.008	a	B	0.009	a	B	0.021	c	AB	0.027	e	A
2010	0-5	0.013	a	A	0.013	b	A	0.013	a	A	0.013	a	A	0.011	d	AB	0.021	d	A
	5-15	0.024	a	D	0.038	a	C	0.016	a	D	0.015	a	D	0.117	a	B	0.197	a	A
	15-30	0.012	a	C	0.016	b	C	0.007	a	C	0.008	a	C	0.042	bc	B	0.067	c	A
	30-60	0.020	a	C	0.024	ab	C	0.012	a	C	0.012	a	C	0.047	b	B	0.090	b	A
	60-100	0.016	a	BC	0.018	b	BC	0.011	a	C	0.013	a	C	0.030	c	AB	0.037	d	A
2011	0-5	0.005	a	A	0.004	c	A	0.005	a	A	0.005	a	A	0.000	c	AB	0.000	e	A
	5-15	0.022	a	D	0.034	a	C	0.015	a	D	0.013	a	D	0.093	a	B	0.131	a	A
	15-30	0.018	a	C	0.024	b	C	0.012	a	C	0.012	a	C	0.058	b	B	0.082	b	A
	30-60	0.027	a	C	0.032	b	C	0.015	a	C	0.016	a	C	0.056	b	B	0.068	c	A
	60-100	0.023	a	C	0.025	b	BC	0.017	a	C	0.019	a	C	0.041	b	AB	0.051	d	A
2012	0-5	0.001	c	A	0.001	c	A	0.001	b	A	0.001	b	A	0.000	c	A	0.000	d	A
	5-15	0.012	b	D	0.019	b	C	0.008	b	D	0.008	b	D	0.048	b	B	0.061	b	A
	15-30	0.028	a	D	0.036	a	C	0.018	a	E	0.019	ab	DE	0.074	a	B	0.089	a	A
	30-60	0.034	a	B	0.040	a	B	0.020	a	C	0.021	ab	C	0.058	b	A	0.041	c	B
	60-100	0.033	a	D	0.035	a	CD	0.023	a	D	0.027	a	D	0.056	b	B	0.068	b	A
2013	0-5	0.000	b	A	0.000	b	A	0.000	b	A	0.000	b	A	0.000	e	A	0.000	c	A
	5-15	0.005	b	B	0.008	b	B	0.004	b	B	0.003	b	B	0.019	d	A	0.023	b	A
	15-30	0.041	a	D	0.051	a	C	0.028	a	E	0.029	a	E	0.086	a	A	0.087	a	A
	30-60	0.041	a	B	0.046	a	B	0.025	a	C	0.026	a	C	0.052	c	A	0.022	b	C
	60-100	0.045	a	C	0.049	a	C	0.033	a	D	0.038	a	D	0.074	b	B	0.087	a	A

Prairie root mass accumulated fastest in the top five cm during 2009 when compared to prairie root accumulation at each other depth, but roots at 0-5 cm stopped accumulating by 2010. In 2010 and 2011, prairie roots had the highest rates of accumulation at 5-15 cm when compared to each other depth. In 2012 and 2013, prairie roots accumulated fastest at 15-30 cm in the fertilized prairie and both 15-30 cm and 60-100 cm in the unfertilized prairie when compared to each other depth (Fig. 3, Table 4).

Unfertilized prairie had greater rates of root accumulation than fertilized prairie from 0-60 cm in 2008 and 2009 and from 5-60 cm in 2010 and 2011. Root accumulation was not different between prairie treatments at 60-100 cm until unfertilized prairie root accumulation rates exceeded fertilized prairie root accumulation rates in 2012 and 2013. During these same years (2012 and 2013), fertilized prairie had greater root mass accumulation rates at 30-60 cm (Fig. 3, Table 4).

Row crops showed no differences in accumulation rates between depths during 2008-2010 except for a higher rate at CCW 5-15 cm than the other CCW depths in 2010. In 2011, accumulation rates at depths still were not different in row crops except for a higher rate in CCW 5-15 cm than all other depths and a lower rate at CCW 0-5 cm than all other depths. In 2012 and 2013, all row crop root accumulation was greater at 15-100 cm than 0-15 cm (Fig. 3, Table 4). In 2008 and 2009, row crops did not have different accumulation rates than each other and had smaller accumulation rates than both prairie treatments, except at 60-100 cm, where rates were not different from fertilized prairie. In 2010 and 2011, continuous corn with cover crop (CCW) had higher rates than the other row crops at 5-15 cm, but otherwise row crops did not have different accumulation rates and accumulated more slowly than both prairie treatments, except for at 0-5 cm where row crops did not have different accumulation rates than fertilized prairie in 2010 and had higher accumulation rates than both prairie treatments in 2011. In 2012, none of the systems were accumulating roots at 0-5 cm. Generally, in the rest of the depths, rates were highest in unfertilized prairie followed by fertilized prairie, then continuous corn with cover crop

(CCW), then the other row crops. In 2013, accumulation at 0-5 cm remained at 0 in all treatments and approached 0 in the 5-15 cm depth of the row crops. Below 15 cm, prairie treatments had the highest rates of accumulation, followed by continuous corn with cover crop, continuous corn, and the corn-soybean rotations (Fig. 3, Table 4).

3.4 Root Distribution

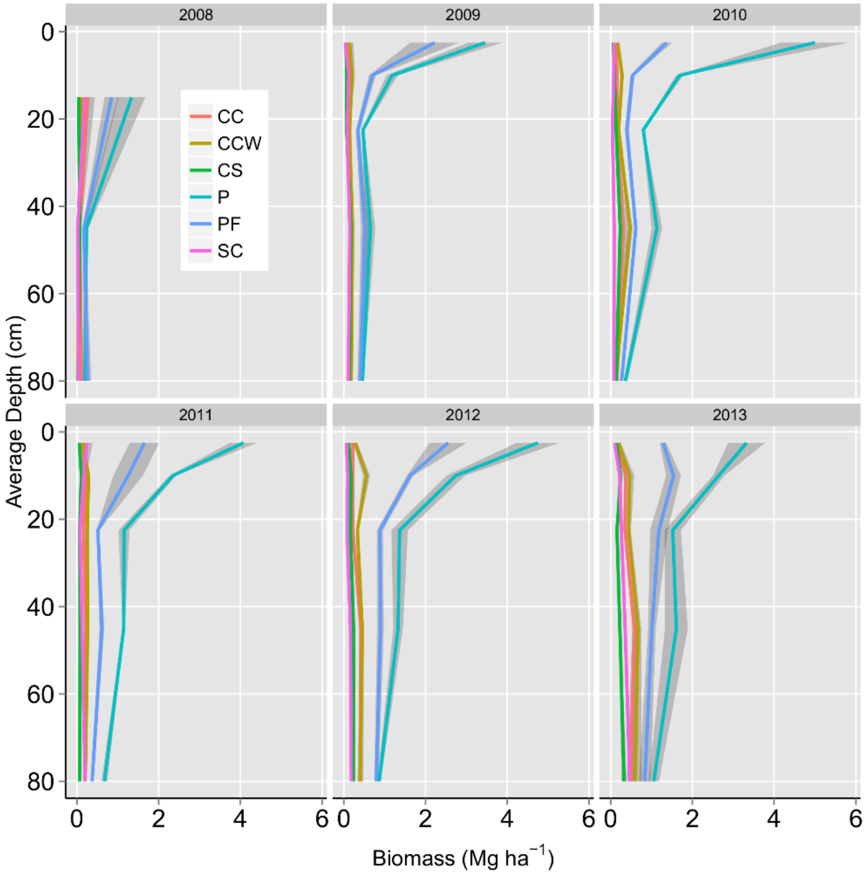


Figure 4. Root pool mass in each depth increment of each year. Data is plotted at the midpoint of each depth increment 0-5 cm is 2.5 cm, 5-15 cm is 10 cm, 15-30 cm is 22.5 cm, 30-60 cm is 45 cm and 60-100 cm is 80 cm. Treatments are continuous corn (CC), continuous corn with winter cover crop (CCW), corn-soybean rotation (CS), soybean-corn rotation (SC), fertilized prairie (PF), and unfertilized prairie (P). Shading represents one standard error of the mean.

In addition to having more total root pool mass in the prairie treatments, both treatments often had more root pool mass throughout the entire soil profile. In 2009 unfertilized prairie had more root mass than all other treatments at 0-5 cm and fertilized prairie had more than all of the row crops at 0-5 cm, but there were no differences between any of the treatments at the 5-100 cm depths. In 2011prairie had the most root mass at 0-5 cm and 5-15 cm, followed by fertilized prairie then the row crops. At 15-30 cm, unfertilized prairie had the most biomass when compared to all other treatments, which were not different from each other. Unfertilized prairie had more root mass than all row crops, but not fertilized prairie at 30-60 cm. Fertilized prairie root mass was not different from row crops at 30-60 cm. The only difference at 60-100 cm was between unfertilized prairie and corn-soybean rotation (soybean year). By 2013, relationships between treatments were still similar to 2011, but with more differences between treatments at lower depths. At 30-60 cm, unfertilized prairie had the most root mass, followed by fertillized prairie, continuous corn, and continuous corn with cover crop. The corn-soybean rotations had less root mass than fertilized prairie, but not significanly less than the continuous corn treatments. At 60-100 cm, the unfertilized prairie treatment had more root mass than the corn-soybean rotations and the continuous corn, but these treatments were not different from fertilized prairie or each other (Fig. 4).

In 2013, unfertilized prairie root mass at 60-100 cm was greater than any of the row crops root mass at 0-5 cm. Both prairie treatments had more root mass at each depth increment from 0-60 cm than the row crops had at 0-5 cm (Fig. 4).

Most of the roots in the prairie treatments were located in the top 0-15 cm of the soil, whereas roots in the row crop systems were more evenly distributed through the soil profile. Root distribution changed signficantly from 2009 to 2013 in both prairie treatments as a smaller proportion of roots was found in the top 0-5 cm and a slightly larger proportion was found in each of the lower depths. Root distribution also changed from year to year in the row crops, but there was no clear pattern of proportional increase or decrease over time for any of the depths (Fig. 5).

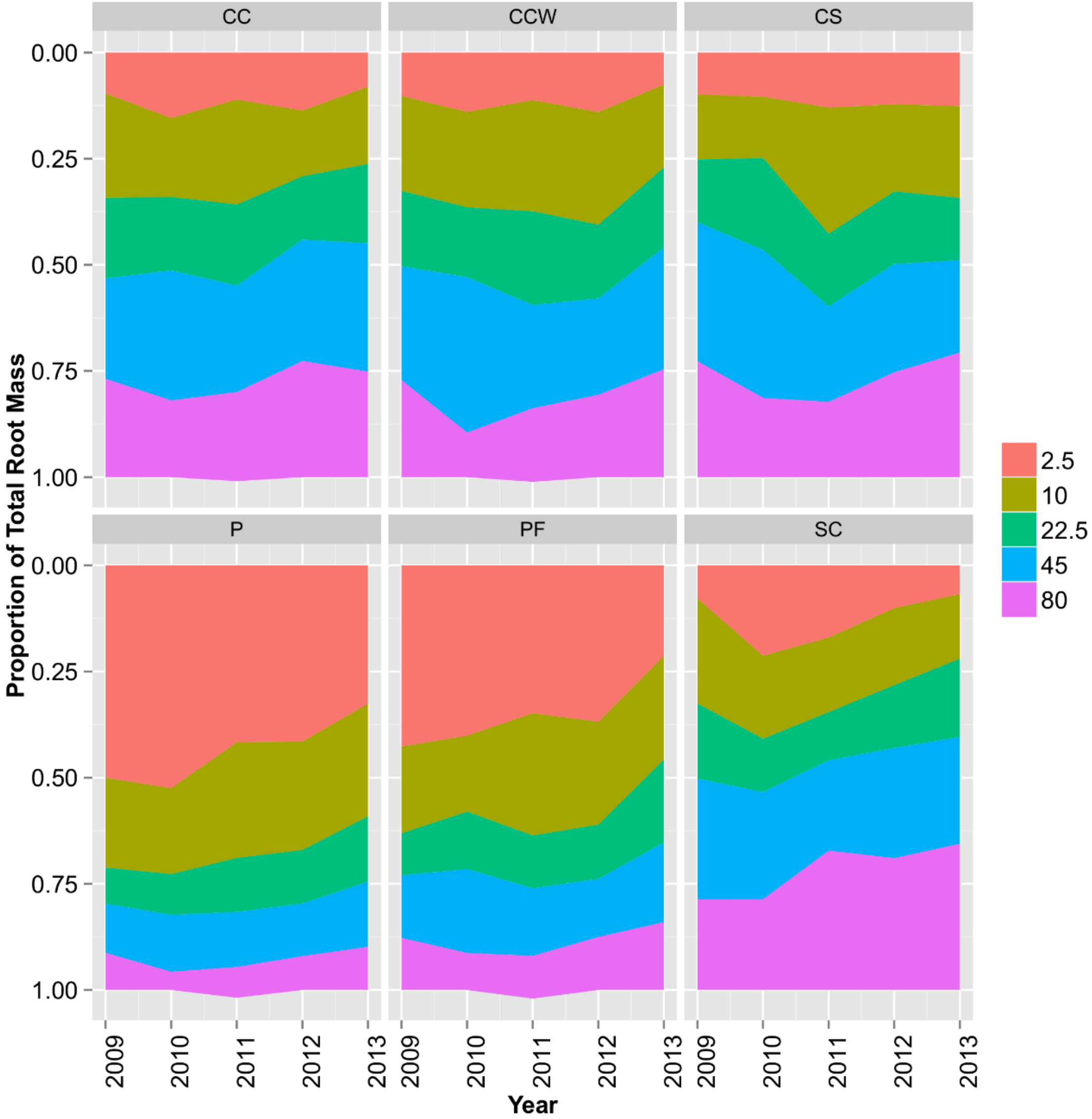


Figure 5. Proportion of total root mass found at each depth increment from 2009-2013. Depths are represented by the midpoint of the increment (different depth increments were measured in 2008 and are not shown). Treatments are continuous corn (CC), continuous corn with winter cover crop (CCW), corn-soybean rotation (CS), soybean-corn rotation (SC), fertilized prairie (PF), and unfertilized prairie (P).

3.5 C:N Ratios of Root Tissue

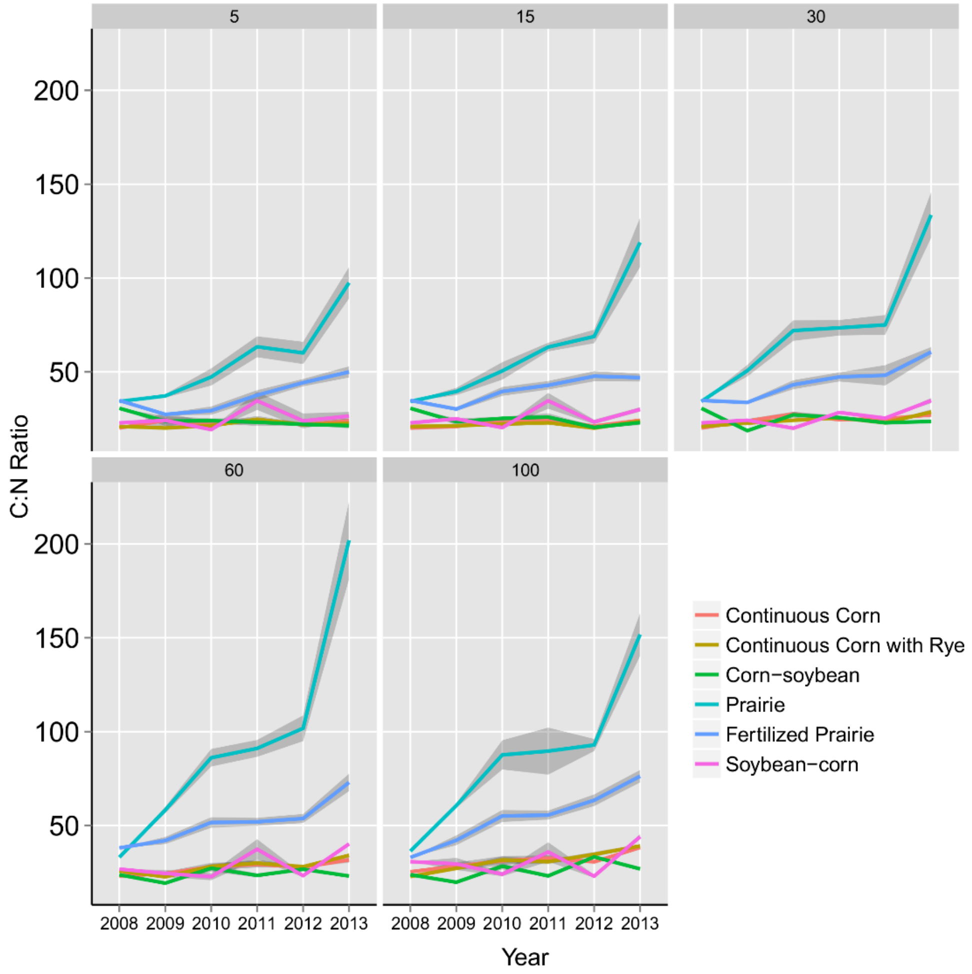
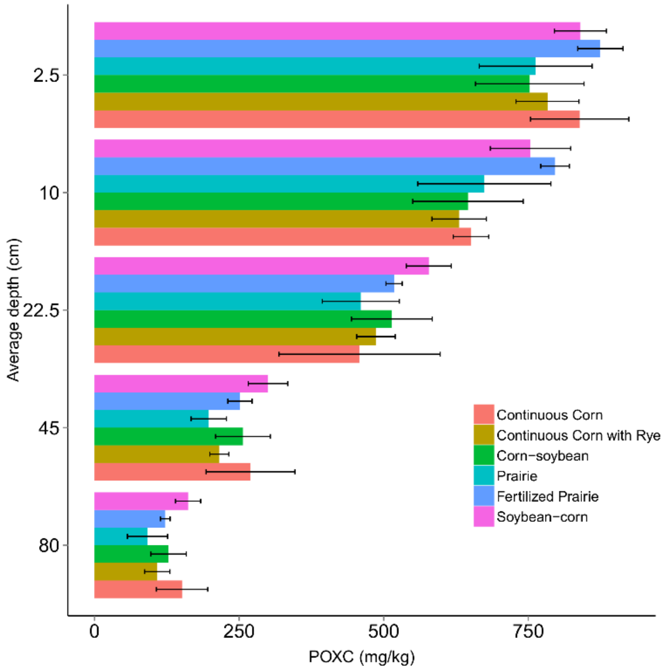


Figure 6. C:N ratios of root tissue at each depth increment from 2008-2013. 5 is 0-5 cm, 15 is 5-15 cm, 30 is 15-30 cm, 60 is 30-60 cm, and 100 is 60-100 cm. Shading represents one standard error of the mean.

C:N ratios increased in both prairie treatments in every depth over time, although the increase in fertilized prairie was not always different between consecutive years. Row crops seldom showed any difference in C:N ratios among years. By 2013, unfertilized prairie had higher C:N ratios than fertilized prairie which had higher C:N ratios than all the row crops. The row crops did not have C:N ratios different from each other (Fig. 6).

3.6 Soil Carbon



Treatment	Depth	POXC (mg kg^{-1})		
CS	0-5	752.5	(93.8)	a
	5-15	645.7	(95.6)	a
	15-30	514.1	(69.8)	b
	30-60	256.6	(47.4)	c
	60-100	127.9	(30.7)	d
CC	0-5	838.8	(85.0)	a
	5-15	650.9	(30.7)	a
	15-30	458.3	(139.3)	b
	30-60	269.7	(76.8)	c
	60-100	151.4	(44.4)	d
CCW	0-5	783.2	(54.4)	a
	5-15	630.5	(47.1)	a
	15-30	486.7	(33.4)	b
	30-60	215.9	(16.4)	c
	60-100	108.5	(21.8)	c
P	0-5	762.7	(97.6)	a
	5-15	674.0	(115.2)	a
	15-30	460.3	(66.6)	b
	30-60	197.5	(30.5)	c
	60-100	91.6	(34.8)	c
PF	0-5	874.6	(39.1)	a
	5-15	796.3	(24.8)	a
	15-30	517.8	(14.1)	b
	30-60	251.4	(21.0)	c
	60-100	122.3	(8.4)	d
SC	0-5	840.1	(44.9)	a
	5-15	753.8	(69.5)	a
	15-30	577.9	(38.9)	b
	30-60	300.0	(34.2)	c
	60-100	161.8	(21.8)	d

Figure 7 and Table 5. POXC measurements for each depth increment in 2012 displayed by midpoint of the increment, 2.5 is 0-5 cm, 10 is 5-15 cm, 22.5 is 15-30 cm, 45 is 30-60 cm, 80 is 60-100 cm. Error bars and parentheses are one standard error of the mean. Different letter in the table denote differences between depths within treatments. Treatments are continuous corn (CC), continuous corn with winter cover crop (CCW), corn-soybean rotation (CS), soybean-corn rotation (SC), fertilized prairie (PF), and unfertilized prairie (P).

There were no differences in POXC between treatments when compared within depths. There were differences between depths within treatments. POXC was greatest at 0-5 cm and 5-15 cm, followed by 15-30 cm then 30-60 cm then 60-100 cm, except in CCW and P, where 30-60 cm and 60-100 cm were not different (Fig. 7, Table 5).

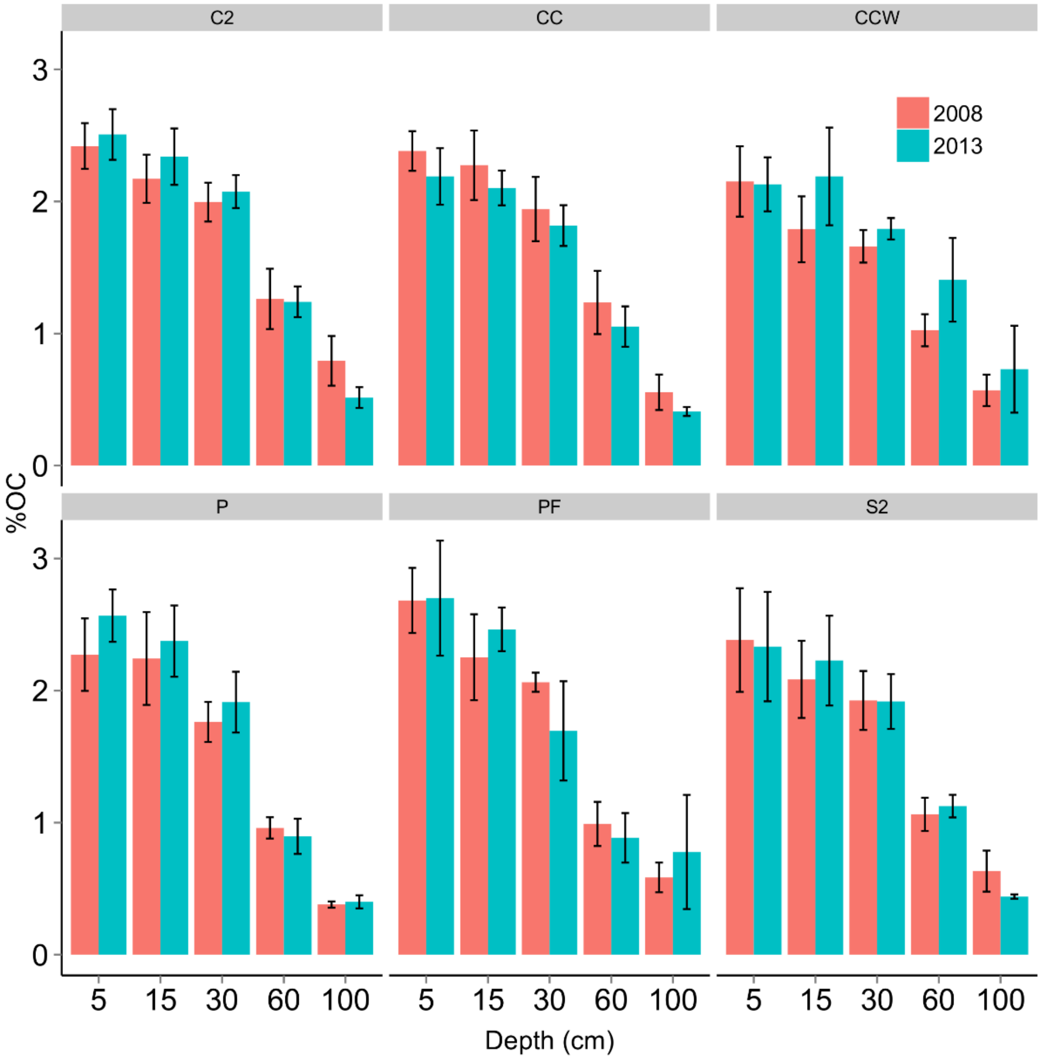


Figure 8. Total organic carbon (TOC) in each depth increment in 2008 and 2013. 5 is 0-5 cm, 15 is 5-15 cm, 30 is 15-30 cm, 60 is 30-60 cm, and 100 is 60-100 cm. Treatments are continuous corn (CC), continuous corn with winter cover crop (CCW), corn-soybean rotation (CS), soybean-corn rotation (SC), fertilized prairie (PF), and unfertilized prairie (P).

No differences were found between 2008 and 2013 for total organic carbon (TOC) in any depth of any treatment. Combining the depth increments together to compare TOC across treatments at 1 m also did not result in any differences between treatments or years (Fig. 8).

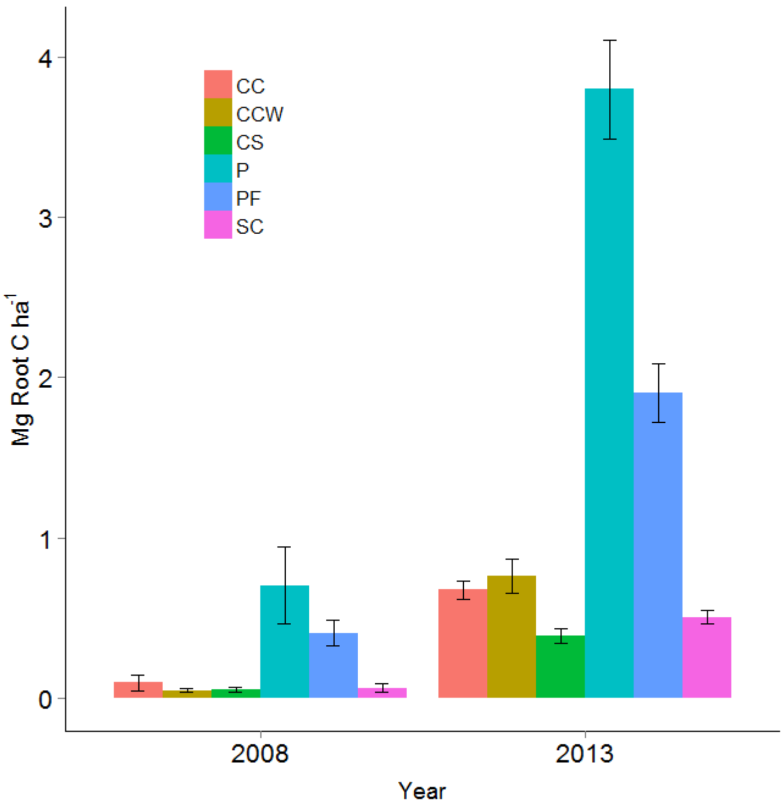


Figure 9. Amount of C found in the root C pool in 2008 and 2013. Error bars represent one standard error of the mean. Treatments are continuous corn (CC), continuous corn with winter cover crop (CCW), corn-soybean rotation (CS), soybean-corn rotation (SC), fertilized prairie (PF), and unfertilized prairie (P).

By 2013, 3.8 Mg ha^{-1} of C was found in the unfertilized prairie root C pool, 1.9 Mg ha^{-1} of C was found in the fertilized prairie root pool, 0.71 Mg C ha^{-1} was found in the continuous corn root pools, and 0.45 Mg ha^{-1} of C was found in the root C pools of the corn-soybean rotations (Fig 9).

4 Discussion

Prairie treatments placed more C belowground as root C than corn-based treatments, and there is strong evidence that the prairie root C pool will function as a C storage pool as long as prairies remain in place. However, it was not evident that belowground root C additions would contribute to SOC or SOC functions such as increased cation exchange capacity or water holding capacity.

4.1 Prairies placed more roots belowground

As hypothesized, prairie treatments had higher annual root inputs and more accumulated root biomass than corn-based systems (Fig. 2, Table 3). This came as no surprise because the prairie treatments were made up of perennial species that invest resources belowground for survivorship, whereas the annual plants corn and soybean invest resources for fecundity through seed production (Hunt 1986). Greater amounts of roots found in the prairie treatments were also consistent with other studies that examined differences in amounts of roots in corn and prairies or native grasses (Tufekcioglu et al. 2003, Guzman et al. 2009, Jarchow and Liebman 2013).

4.2 All treatments are accumulating root mass below 5 cm, prairies at the fastest rate

Root accumulation is a function of both new root production and older root senescence and decomposition. A stable level of root biomass and accumulation rates below zero at 0-5 cm in all of the treatments suggests that root additions are equal to root decomposition (after 2010 in the prairie treatments). Following the maximum rate of prairie root accumulation down the soil profile and through years, it appears that accumulation rates represent the expansion of perennial roots into available soil space (more roots into deeper depths each year). Unfertilized prairie growth rates peaked first in 2008 (298 days) for 0-5 cm, 2009 (695 days) for 5-15 cm, 2012 (1631 days) for 15-30 cm, 2012 (1774 days) for 30-60 cm, and have not yet peaked for 60-100 cm (Fig. 3). Evidence of prairie roots filling available soil space over time was also seen in a shift of root mass proportions by depth over the six years of growth (Fig. 5). As the proportion of roots found at 0-5 cm decreased, the proportion of roots found in the other depth increments increased. This showed that as long as soil space remains available for prairie roots, these systems will continue to expand and add biomass belowground, whereas corn-based systems will not. Other studies on the annual expansion of prairie roots were not found.

As prairie root accumulation rates at 5-15 cm approached zero in 2013, it appears that root production at this depth began reaching an equilibrium with root decomposition (Fig 3), but it is not known how much root mass remained from the previous year, how much was new growth, and how much was lost through decomposition. Similarly, while root biomass increased below 30 cm over time, this increase occurred at the same time as root sloughing and decomposition.

4.3 Prairie root C is less likely to decompose than row-crop root C

By 2013 unfertilized prairie had more root mass at 60-100 cm than row-crop treatments had at any depth (Fig. 4). This is important because less oxygen and lower temperatures at deeper depths make conditions less favorable for decomposition. This means that prairie treatments had more root mass placed at depths less favorable for decomposition. Gill et al. (1999) found that particulate organic matter (POM) in a shortgrass prairie at 75-100 cm equaled that at 0-5 cm and was greater than POM at any other depth increment. POM at 75-100 cm also had the lowest decomposition rate, which was attributed to the poor decomposition conditions found at depth (Gill et al. 2009).

Differences in root tissue composition also indicated that prairie roots were more resistant to decomposition (Fig. 6). C:N ratios are one indicator of the recalcitrance of organic material. C:N ratios around 20-30:1 are desirable for mineralization by microorganisms and ratios above 30:1 indicate N limitation that may restrict microbial use or force N use from another source, such as the surrounding soil. In 2013, row-crop roots had a C:N ratio of 29.4 when averaged across depths and row-crop treatments while fertilized prairie roots had an average C:N ratio of

61.4 across depths and unfertilized prairie had an average C:N ratio of 140.8 across depths. These ratios indicate that while row-crop root mass was still in the acceptable range for microbial mineralization, roots from the prairie treatments would most likely restrict mineralization due to N limitations.

These differences in C:N ratios among treatments were reflective of the amount of N supplied to the systems through fertilization (or N-fixation for soybeans). Row-crops received the most N fertilizer and were least likely to experience plant N limitation, whereas fertilized prairie received less N fertilizer. Unfertilized prairie had no N fertilization and probably experienced plant N limitation. These C:N ratio differences were also due to the growth behaviors of the different systems. While row-crops put out completely new roots every year, prairie plants maintain root systems perennially, investing C in the structure every year. As a perennial root grows and matures, more of the tissue becomes structural and less of the tissue is involved in active processes that require N (Kramer and Boyer 1995). Indeed, in the prairie we observed both an increase in %C and a decrease in %N in the root of both prairie treatments (data not shown).

4.4 Belowground C increases were only observed in the root mass pool

Despite large differences in root mass between the prairie treatments and row-crop treatments, there was no evidence of treatment differences in POXC or TOC pools six years after initiation of the experiment (Fig.7,8). Measured changes in the TOC pool were not expected because changes in TOC pools are difficult to detect in soils that are already high in C. But changes in POXC were expected because POXC represents a pool of C that has been found to be responsive to management changes on short-term time scales (Culman et al. 2012). While this lack of treatment differences could be a shortcoming of the POXC analysis (e.g. it is unknown if the KMnO4 was reduced by other compounds in the soil), there are other reasonable explanations.

The rhizosphere priming effect is the stimulation or suppression of soil organic matter (SOM) decomposition by live roots and associated rhizosphere organisms when compared to SOM decomposition from rootless soils under the same environmental conditions (Chen et al. 2014). Prairies are likely to lead to high positive priming effects because they have massive root systems that support large microbial communities. As root C becomes available through senescence, these microbial communities may quickly metabolize the newly available substrate, especially if most of the senescing roots are fine roots. We may have found no differences in POXC because very little C ever made it to the POXC pool.

As C moves out of the microbial biomass pool, it is theorized that it can be protected from further decomposition (and loss through microbial respiration) through associations with clay and other minerals. But if these C association sites are already filled, the soil can be considered C saturated (Six et al. 2002). The high levels of C found in the soils of this experiment suggest they may be C saturated, leaving new C exposed to further decomposition and loss, thus no changes in labile C pools such as POXC. This incapacity for high C soils to store C had also been recently supported by work by Tan and colleagues (2014), who suggest that as soil C content increases, the humification of organic C decreases and the decomposition rate increases.

4.5 N fertilization in prairies led to less root mass that accumulated slower and was more susceptible to decomposition

Nitrogen fertilization of prairies relieved plants of N stress, leading to less need for N-scavenging roots and more need for radiation-capturing leaves. Thus, more biomass was allocated aboveground in fertilized prairies and belowground in unfertilized prairies. This allocation effect from N fertilization was also found by Jarchow and Liebman (2012). Less root mass meant less mass over time and lower rates of accumulation. Lower rates of accumulation may also have been due to higher rates of decomposition as fertilized roots had higher C:N ratios than unfertilized roots and the soil environment was less N-limited in general.

4.6 Six years after establishment, prairies placed more C belowground than row-crops with indications that this belowground C would slowly continue to increase if not disturbed.

Unfertilized prairies placed ~6.5 x more C belowground than row-crop systems and fertilized prairies placed ~3.5 x more C belowground than row-crop systems six years after establishing the experiment (Fig. 9). All of this C was measured in the form of roots. At deeper depths (below 15 cm), prairie roots were continuing to accrue mass and show increases in C content. The combination of high recalcitrance and location at deeper depths in the soil makes root C in the prairie treatments likely to remain belowground for a long time. If cropping systems are to be valued for removing C from the atmosphere and storing it belowground, we have provided evidence that prairies would be very valuable, especially if left unfertilized. However, if soil C is desired for other purposes such as cation exchange capacity, water retention, better aggregation, microbial substrate, or a source of plant growth-inducing compounds, prairie root C will not serve these functions until it moves out of the root C pool.

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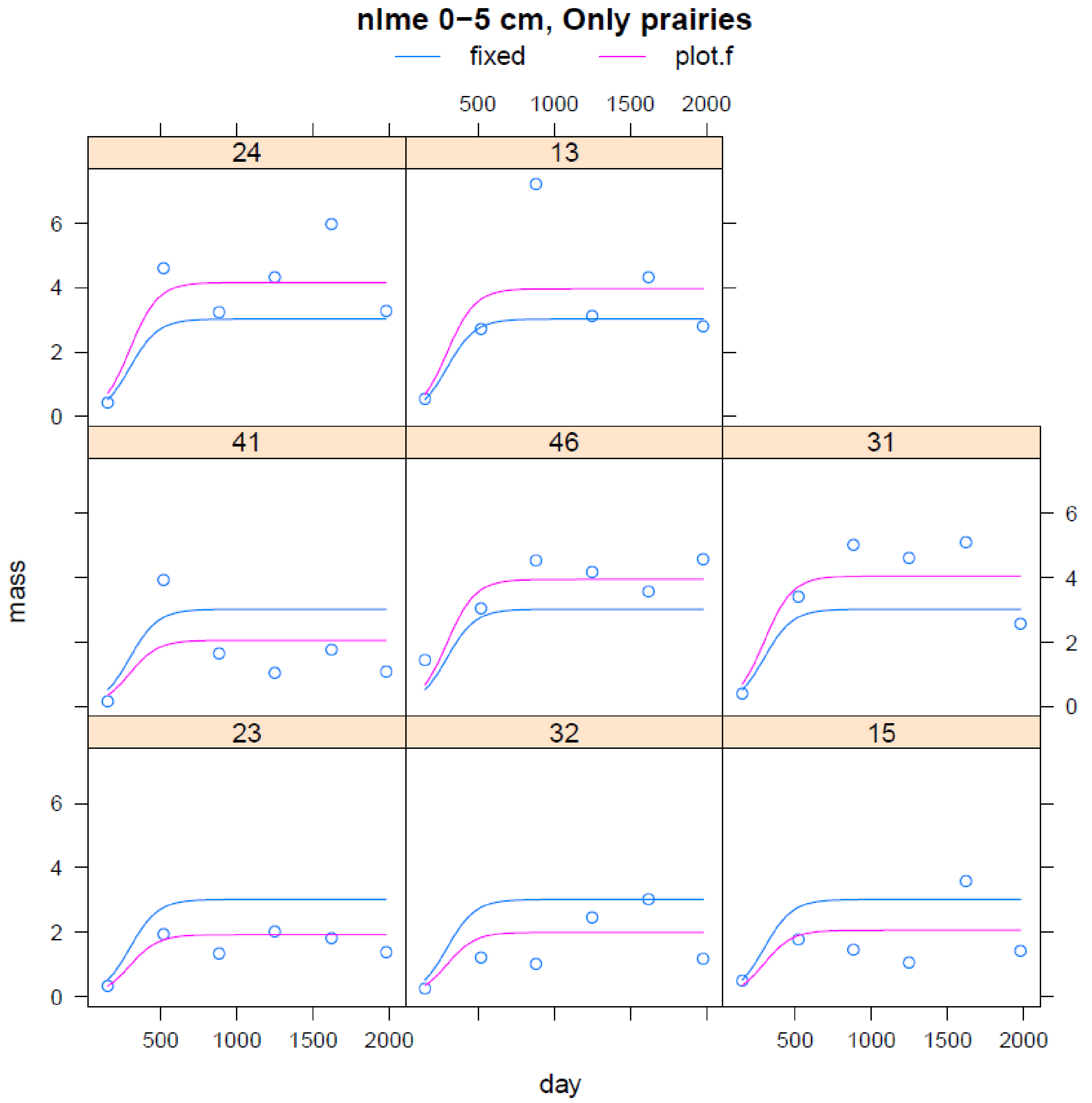
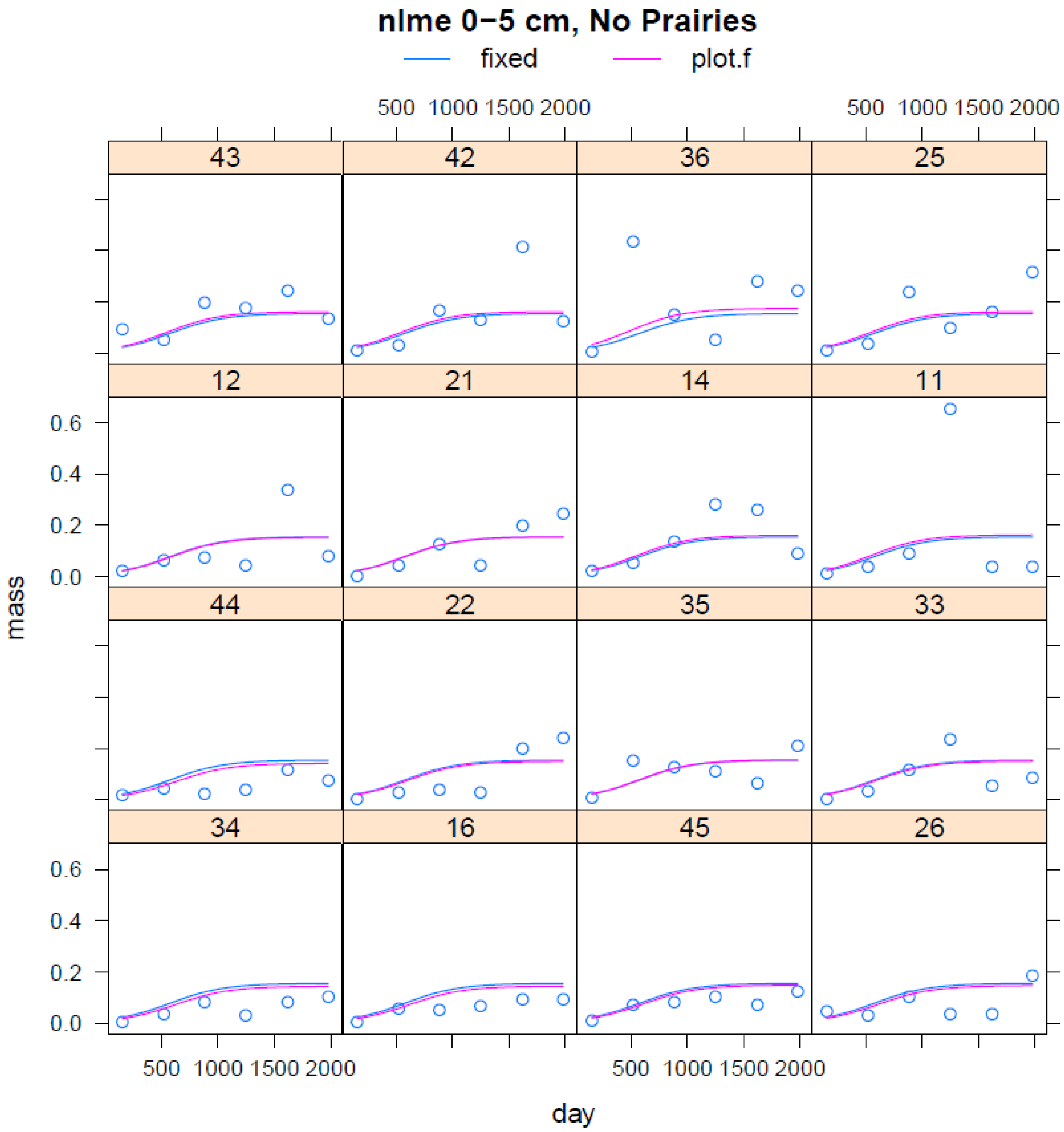
6 APPENDIX B

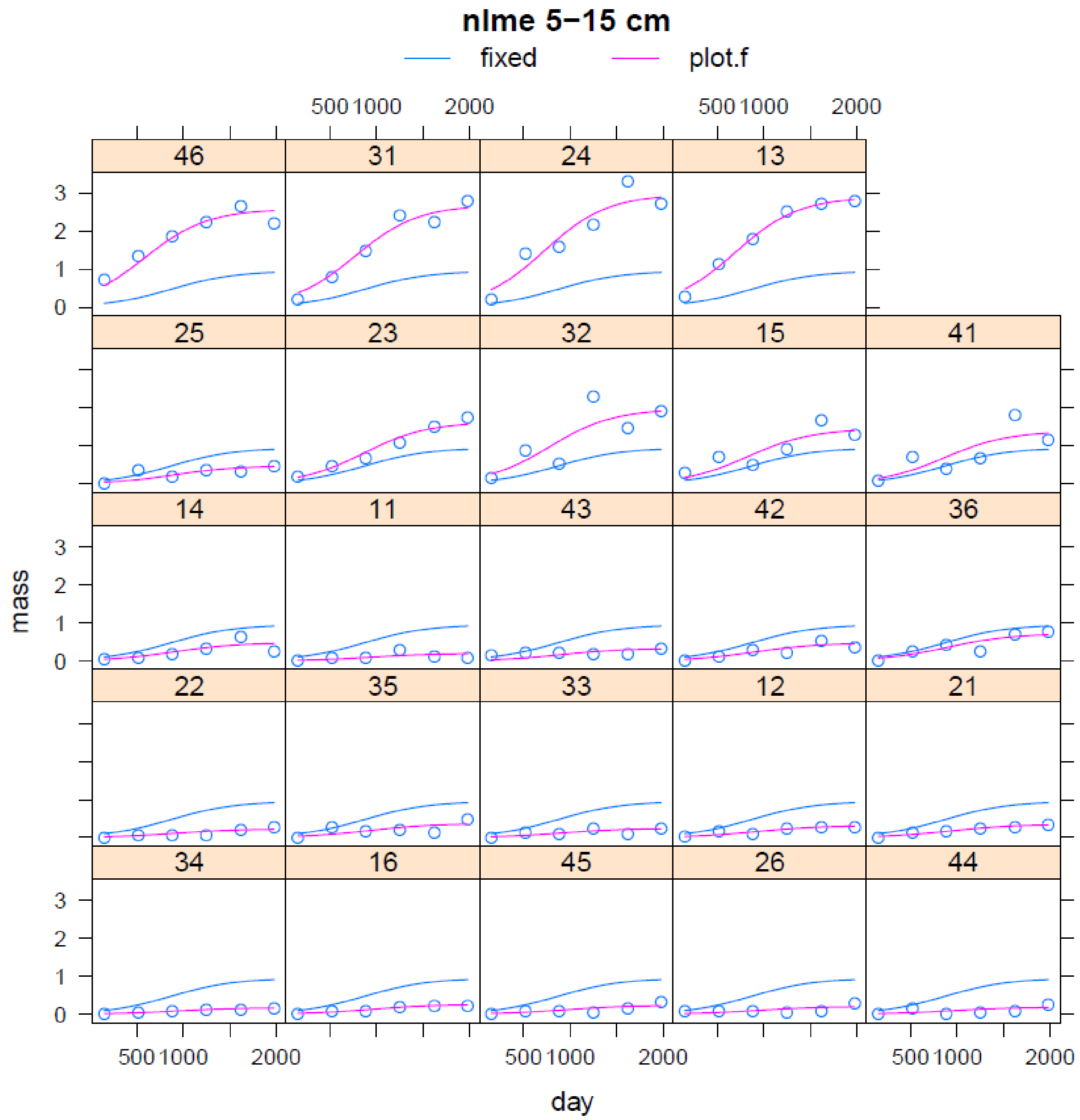
Logistic curve fits used to generate predicted root accumulation for each depth. Each panel represents one experimental plot (number is plot number).



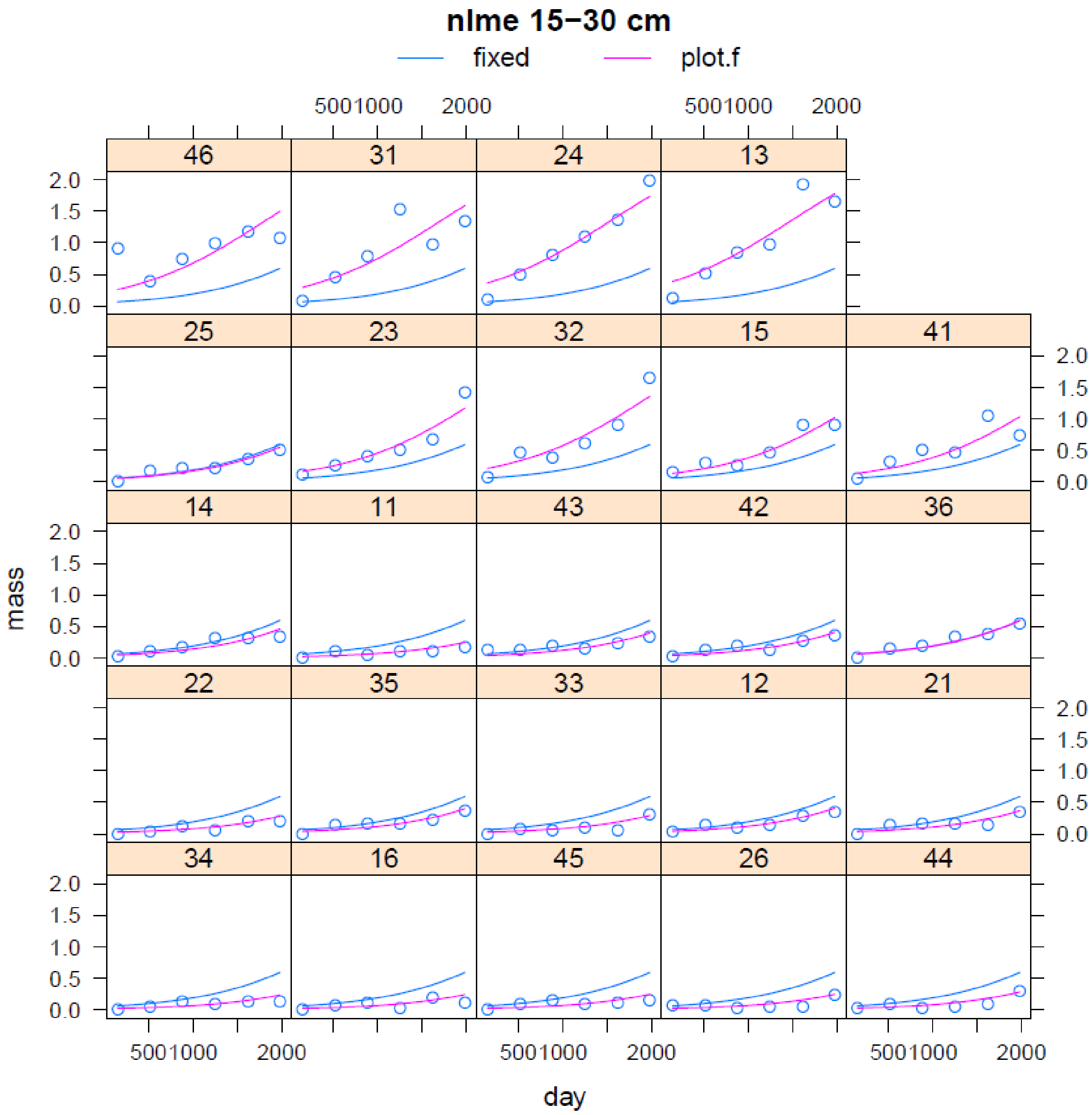
Appendix Fig 1. Fits of logistic curves to 0-5 cm prairie and unfertilized prairie root mass over six years (represented in days after establishment). Pink lines are the fit for each experimental plot and were used to make predictions.



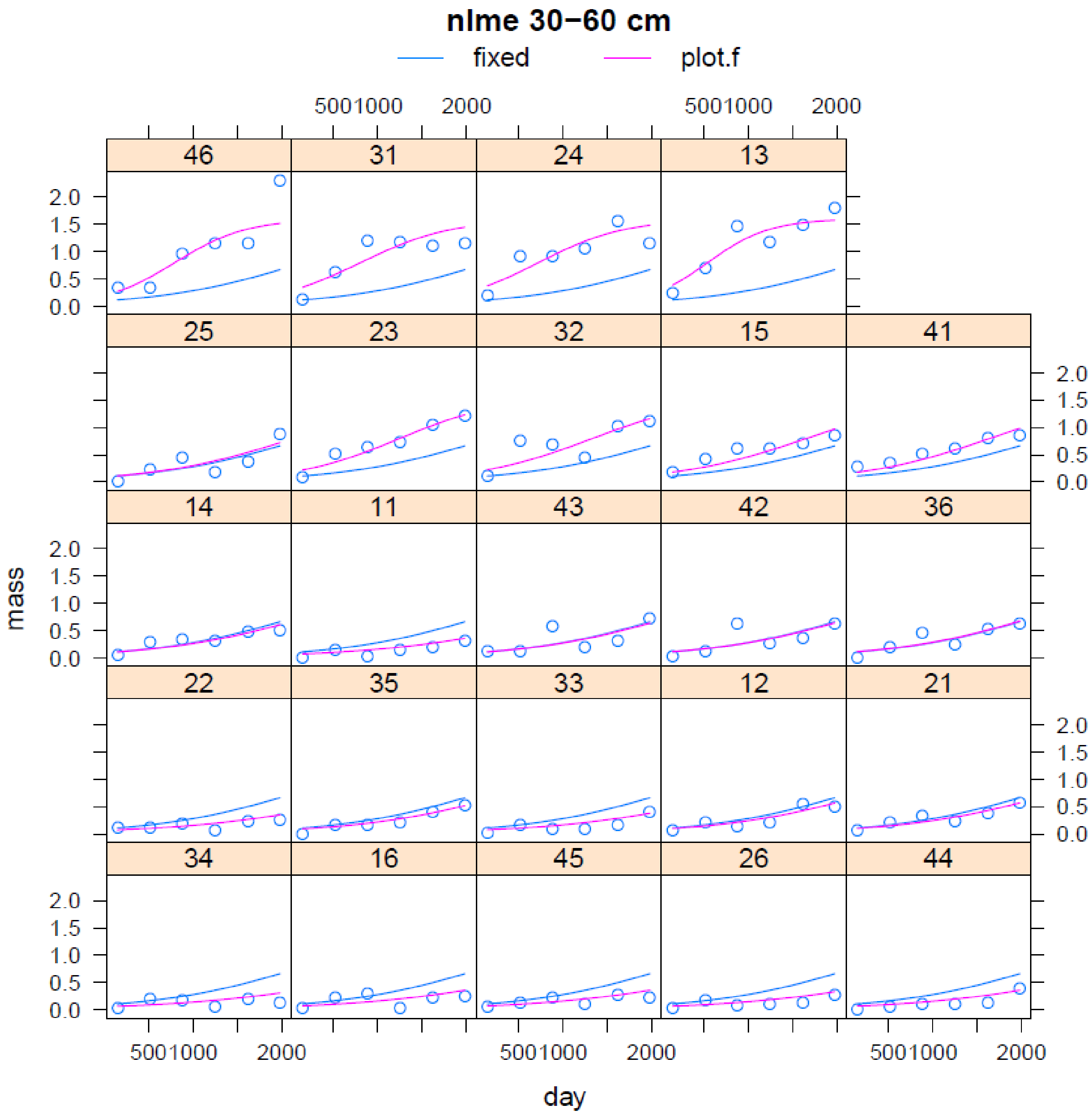
Appendix Fig 2. Fits of logistic curves to 0-5 cm row-crop root mass over six years (represented in days after establishment). Pink lines are the fit for each experimental plot and were used to make predictions.



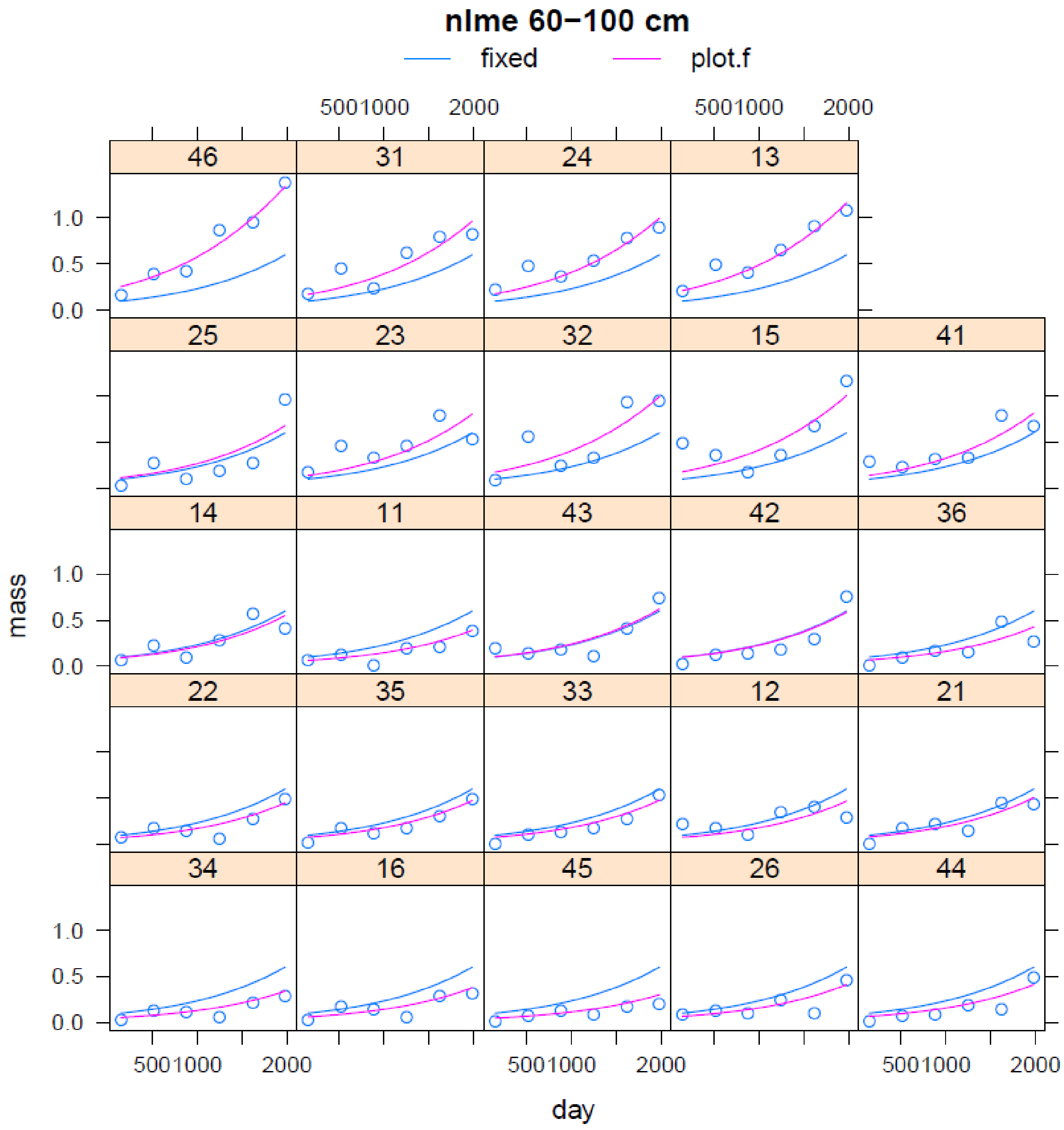
Appendix Fig 3. Fits of logistic curves to 5-15 cm root mass over six years (represented in days after establishment). Pink lines are the fit for each experimental plot and were used to make predictions.



Appendix Fig 4. Fits of logistic curves to 15-30 cm root mass over six years (represented in days after establishment). Pink lines are the fit for each experimental plot and were used to make predictions.



Appendix Fig 5. Fits of logistic curves to 30-60 cm root mass over six years (represented in days after establishment). Pink lines are the fit for each experimental plot and were used to make predictions.



Appendix Fig 6. Fits of logistic curves to 60-100 cm root mass over six years (represented in days after establishment). Pink lines are the fit for each experimental plot and were used to make predictions.

CHAPTER 3. PREDICTED CHANGES IN SOIL ORGANIC CARBON OVER FIFTY YEARS IN CORN- AND PRAIRIE-BASED CROPPING SYSTEMS

1 Introduction

One of the major goals of replacing fossil fuels with biofuels is moving to a system that is less environmentally harmful. An ideal biofuel feedstock production system will be one that balances economic feasibility and ecological value. Jarchow et al. (2014) recently compared corn- and prairie- based biofuel cropping systems using the economic and environmental performance indicators harvestable yield, net energy balance, root production, and nutrient fluxes. They found corn-based treatments produced more biomass and had higher net energy balances than prairie-based treatments, but prairie-based treatments required and lost fewer nutrients and produced more root biomass than corn-based treatments. Carbon storage is another environmental indicator to be considered when economic advantages are weighed against environmental benefits.

Storing C in the soil decreases harmful CO_2 in the atmosphere and increases beneficial organic C in the soil. Soils are the biggest reservoir of C next to the ocean, and at a 1 m depth, contain 7 times the content of C in the atmosphere. If agricultural soils were returned to their native soil organic matter (SOM) levels, this would offset 9-12% of annual anthropogenic emissions (Magdoff and Weil 2004). Carbon in the soil is mostly present as a part of SOM and enters the soil as such. SOM serves many purposes that enable soil to function as a substrate for plant growth and an ecosystem base. SOM is the primary source of the nutrients nitrogen (N), phosphorus (P), and sulfur (S) and its decomposition and capacity for cation exchange regulate nutrient availability. Soil water retention and availability are also regulated by the ability of

SOM to absorb and hold H_2O. Association of organic matter with soil minerals promotes the formation of aggregates, providing soil structure for air and water exchange (Horwath 2008).

Restoration of prairie systems is a possible way to bring SOM levels back toward original levels. In the Midwestern United States, conversion of 99% of native prairie ecosystems to row-crop agriculture has resulted in the loss of 30-50% of SOM in these soils due to erosion and tillage induced increases of microbial metabolism of SOC (David 2009). This has contributed to an estimated loss of 55 Pg of C worldwide over the last 200 years (Amundson 2001) and a loss of 5 Gt of C in croplands of the United States (Lal 1998). A study of restored prairie chronosequences from ages 2 to 24 years showed that 50% of lost C could be restored in 100 years (Matamala 2008), while a similar study resulted in a model that predicted original SOC levels would be met 55-75 years after prairie restoration (McLauchlan et al. 2006).

Changes in SOC are difficult to measure because they happen slowly and in the Midwestern United States, changes happen against high levels of existing SOC. Carbon budgeting approaches are static and also unreliable due to uncertainties in above- and belowground plant production and root-derived vs. microbially derived respiration (Cahill et al. 2009). Prairie soil C gains found under budgeting approaches ranged from -3.9 Mg C ha^{-1} y^{-1} (Brye et al. 2002) to 5.3 Mg C ha^{-1} y^{-1} (Guzman 2009) and are often found to be both negative and positive in a given system, depending upon the year of measurement (Brye et al. 2002, Kucharik et al. 2006, Guzman et al. 2009). One way to overcome the abovementioned difficulties is the use of process-based simulation models that account for year-to-year variability in plant growth and biomass production and evaluate SOC changes on a relevant timescale.

Previous efforts to model historical changes in SOC under reconstructed Midwestern United States prairies have been pursued through the use of chronosequences (McLaughlan et al. 2006, Matamala et al. 2008), but only one mechanistic model has been used to make predictions about future SOC levels after prairie reconstruction in the Midwestern United States. Kucharik and colleagues (2001) used the Integrated Biosphere Simulator (IBIS) to model increases in SOC in no-till corn and reconstructed prairies, but the modeled results were vastly different from the measured results and no confident conclusion was reached.

We set out to predict and compare changes in SOC over 50 years in no-till corn grown for biofuel, prairie grown for biofuel, and a no-till cash crop corn-soybean rotation. Within these treatments we also tested the effect of a winter rye cover crop in continuous corn and the effect of N fertilization on prairie. We hypothesized that SOC would increase in all treatments over time, but would accumulate at a higher rate in treatments with more belowground C inputs.

2 Materials and Methods

2.1 Site Conditions and Experimental Design

We conducted the experiment in Boone County, IA, USA on the Iowa State University Agronomy and Agricultural Engineering Research Farm (41°55′N, 93°45′W). Soils at the site were primarily Webster silty clay loam (fine-loamy, mixed, superactive, mesic Typic Endoaquoll) and Nicollet loam (fine-loamy, mixed, superactive, mesic Aquic Hapludoll). The 60-year mean growing season precipitation 11 km from the site was 720 mm. Prior to initiation of the field experiment in 2008, the site was used for maize and soybean production and was planted with soybean in 2007. Soil sampling to 15 cm depth in November 2007 indicated mean soil pH was 6.7, mean organic matter concentration (via dry combustion analysis with a conversion factor of 1.724 from total C to organic matter [Schumacher 2002]) was 51 g kg^{-1}, mean extractable phosphorus concentration (via Bray-1 procedure) was 11 mg kg^{-1}, and mean extractable potassium (via Mehlich-3 procedure) was 141 mg kg^{-1}.

Experimental plots were 27 m x 61 m and were arranged as a spatially balanced complete block design (van Es et al. 2007). Five cropping systems were studied: a corn-soybean rotation with annual grain removal (hereafter corn-soybean rotation; CS), continuous corn with annual grain and 50% stover removal (hereafter continuous corn; CC), continuous corn with grain and 50% stover removal and rye used as a winter cover crop (hereafter continuous corn with rye; CCW), reconstructed multispecies prairie with annual aboveground biomass removal (hereafter unfertilized prairie; P), and N-fertilized reconstructed multispecies prairie with annual aboveground biomass removal (hereafter fertilized prairie; PF). All of the treatments were managed without tillage. Conventional farm machinery was used for planting, fertilization, crop protection, and harvest operations. Herbicides were not used in the prairie systems except for a small number of spot treatments for Canada thistle (*Circium canadense*) control, and the timing and frequency of herbicide use in the annual cropping systems varied among treatments. Nutrient management also varied among all treatments (Table 1).

Both prairie treatments were sown on 19 May 2008 with the same custom seed mix obtained from Prairie Moon Nursery (Winona, MN, USA) that contained 31 species, including C_3 and C_4 grasses and leguminous and non-leguminous forbs (Table S1). All species were perennial and sourced from within 240 km of the experiment site. The composition of the seed mix by weight was 12% C_3 grasses, 56% C_4 grasses, 8% legumes, and 24% non-leguminous forbs. A detailed description of the prairie plant community compositions can be found in Jarchow and Liebman (2013). The fertilized prairie treatment received no fertilizer in 2008 (the establishment year), and was fertilized at a rate of 84 kg N ha^{-1} year^{-1} in all subsequent years. This fertilizer rate was chosen because it was similar to the maximum rate of pre-planting N fertilization recommended for maize (Blackmer et al. 1997) and the expected N removal in the harvested biomass of perennial grasses grown in the area (Heggenstaller et al. 2009). Fertilization timing can be found in Chapter 2, Table 1.

The maize hybrid used was a 104-day relative maturity hybrid with transgenes for glyphosate resistance, corn borer (*Ostrinia nubilalis*) resistance, and corn rootworm (*Diabrotica* spp.) protection (Agrigold 6325 VT3). Maize was planted following standard Midwestern United States production practices in rows spaced 76 cm apart at 79,500 seeds ha^{-1} on 6 May 2010 and 82,500 seeds ha^{-1} on 11 May 2011 (Abendroth et al. 2011). Fertilizer rates and types can be found in Table 1. Rates of N added after planting were based on results of late-spring tests of soil nitrate-N concentration (Blackmer et al. 1997). All N was applied as urea-ammonium nitrate (32% N). An unfertilized maize treatment was not included in the experiment because the effects of N fertilizer on maize have been extensively studied and modeled, with N fertilization leading to greater biomass and higher grain yields (Cerrato and Blackmer 1990; Sawyer et al. 2006).

2.2 Data Collection

2.2a Aboveground Biomass

Aboveground biomass was measured by clipping 0.56 m^2 (two 0.28-m^2 quadrats) in each plot approximately every two weeks beginning at shoot emergence in April for the prairie treatments and in May for the maize, similar to methods used by Loecke et al. (2004). Dead litter was discarded and biomass was then dried at 60° C for at least 48 hours and weighed. Species identities were not assessed within the quadrats used for biomass collection, rather the species composition of both prairie treatments was determined by Jarchow and Liebman (2013) using a point intercept method (Jonasson 1988). In mid-August, eight 1-m^2 quadrats per plot were sampled by dropping a long pin into each quadrat 12 times and recording identity and number of contacts that each species had with the pin. More details can be found in Jarchow and Liebman (2013). Aboveground biomass and grain yields were also recorded when harvested.

2.2b Soil Collection

Soil cores were taken to 1 m depth in all plots each year using a hydraulic soil probe (Giddings Machine Co., Windsor, CO, USA) after all crops were harvested. Sampling occurred by replicate block from 31 October-25 November 2008, 9-11 November 2009, 25-28 October 2010, and 28-31 October 2011, 16-17 October 2012 and 7-11 October 2013.

In 2008, two cores were taken per plot. A 0-30 cm fraction was taken with a 10.2 cm internal diameter soil probe; a 30-100 cm fractions of the cores was taken within the same hole as the 0-30 cm fraction, but with a smaller soil probe. In Blocks 1 and 4, the internal diameter of the core was 6.0 cm. In Blocks 2 and 3, the internal diameter of the core was 5.2 cm.

In 2009 and 2010, four cores were taken per plot. The 0-30 cm fraction of the cores was taken with a 10.2 cm internal diameter soil probe; the 30-100 cm fraction of the cores were taken directly below the 0-30 cm fraction with a 5.1 cm internal diameter probe. In 2011-2013, four cores were taken per plot, and the entire core was taken with a 5.1 cm internal diameter probe. Soil cores were ultimately divided into three or five depth increments. In 2008, depth increments were 0-30 cm, 30-60 cm, and 60-100 cm. In 2009-2013 depth increments were 0-5 cm, 5-15 cm, 15-30, cm, 30-60 cm, and 60-100 cm. Following division and extraction from the field, soil cores were stored at 5°C until processing was initiated.

2.2c Roots

Root extraction from the soil began by washing the soil samples in wire mesh tubes (0.28 mm mesh) for 3 h in an elutriator (Wiles et al., 1996). Roots were removed from the remaining soil by suspending the air-dried sample in water and collecting the roots, which floated, with sieves followed by manually removing any remaining non-root material that was present in the samples. Any plant crowns that were present in the samples were removed and were not considered to be root biomass. Roots were then dried at 70°C for at least 4 h before being weighed. All above- and belowground biomass samples were ground to 2 mm with a centrifugal mill and concentrations of C and N were determined by combustion analysis at the Soil and Plant Analysis Laboratory at Iowa State University (Ames, IA, USA).

Each year before roots were washed, 60-100 g of root-free soil was removed from each depth increment, air-dried, and archived in airtight containers at room temperature. In 2008 and 2013, this soil was ground on a roller-mill and organic C content was determined by catalytic oxidation and CO_2 measurement with NDIR in an Elementar TOC Cube at Brookside Laboratories, Inc. (New Bremen, Ohio).

2.2c Soil temperature and moisture sensors

Volumetric soil water contents and temperatures were measured using Decagon 5TE ECH2O sensors and Em50 data loggers at 5, 10, 17.5, 35, and 50 cm depths. Sensors were installed midway between center and border of each plot for all 24 plots in 2008. Sensors were assumed to represent soil water contents and temperatures at 0-7.5, 7.5-13.75, 13.75-26.25, 26.25-42.5 and 42.5-57.5 cm depths intervals.

2.2d CO_2 Measurements

Soil-surface CO_2 efflux measurements were taken at weekly intervals between the annual planting of corn seed and harvest. Soil-surface CO_2 efflux survey measurements were made between 800 and 1200 h in 2008 – 2009 and between 800 and 1030 h in 2010 – 2011. Weekly survey measurements were made with Licor 8100-103 series infrared gas analyzer(IRGA; Licor Bioscience, Lincoln, NE) systems during 1.5 minute sampling duration on PVC collars (20 cm diameter x 12 cm height) installed to approximately 9 cm depth.

2.3 Modeling with APSIM

The Agricultural Production Systems Simulator (APSIM; Keating et al., 2003) is a farming systems modeling platform that includes approximately 60 crop and soil models. APSIM simulates various production situations, including potential plant growth, water, N, and/or phosphorus limited plant growth, and actual plant growth. APSIM includes more than 30 crop species and can simulate crop rotations, weed competition, and inter-cropping systems (Robertson et al., 2002; Wang et al., 2002; Keating et al., 2003, Snow et al., 2013). The crop models contain numerous cultivars to allow model application in different environments. For the soil aspect, APSIM simulates various processes such as C, N, and phosphorus dynamics, greenhouse gas emissions (CO_2 and N_2O), water balance using either simple (cascading approach) or comprehensive (Richards' equation) modules, and soil erosion (Probert et al., 1998, 2005; Thorburn et al., 2010, Huth et al., 2012). APSIM uses a multi-layer soil profile.

2.3a APSIM configuration

To replicate the observed data and to fulfill the objective of this study, the following APSIM modules were used: MAIZE to simulate corn growth, modified WHEAT to simulate rye cover crop, modified AgPasture to simulate inter-cropping (prairie) systems, SOIL N to simulate soil C and N dynamics, SWIM for soil water balance simulation using Richards' equation, SURFACEOM to simulate residue dynamics, MicroMet for calculation of potential evapotranspiration in the inter-cropping system, and the following management rules: sowing, harvesting, fertilizer, residue removal, and rotations. The APSIM version 7.5 was used on a daily time step.

2.3b APSIM description

A full description of all APSIM's modules can be found at www.apsim.info (including references and source code). A brief overview of the important modules used in this study is provided below.

The APSIM-maize crop model

The most important processes included in the maize crop model are phenology, leaf development, biomass production and partitioning. Briefly this model is an updated version of the well-known CERES-maize model (Jones and Kiniry, 1986). Biomass production is estimated using a combined resource capture approach, in which the daily crop growth rate is calculated as the minimum of two daily estimates, one limited by light (radiation use efficiency; RUE) and one limited by water (TE; transpiration efficiency adjusted for vapor pressure deficit). This estimate is adjusted further to account for temperature, N, and soil moisture effects on canopy photosynthesis. Partitioning of dry matter to different plant organs is stage dependent. The maize model captures the variation among maize hybrids. The APSIM-maize model has been tested in Iowa and proved to be reliable (Malone et al., 2007; Hammer et al., 2009; Archontoulis et al., 2014a).

The APSIM-soybean crop model

In general, the soybean model attempts to chart a middle course between simple (Sinclair, 1986) and very detailed (CROPGRO-soybean; Boote et al., 1998) soybean crop models so that crop growth and development can be simulated with satisfactory comprehensiveness, without the necessity of defining a large number of parameters. The model simulates the same crop processes as the maize model with few modifications. For a detailed description of the soybean model structure see Robertson et al. (2002). Recently Archontoulis et al. (2014b) used the model to simulate soybean development and their analyses resulted in the incorporation of 40 soybean cultivars of varying maturity group into the model. Simulations of grain yield in Iowa were close to measured yields.

The APSIM-wheat crop model

We used the wheat model as a basis to simulate growth and development of cereal winter rye (cover crop). This is a common approach taken by modelers (e.g. Malone et al., 2007; Archontoulis et al., 2014a) to simulate cover crops. The reason for the lack of specific cover crops models is the perceived low economic importance of the species. Any error introduced by this approximation is assumed to be small as the rye crop is terminated months before it reaches physiological maturity. Also, the growth of different winter cereals is very similar during the initial crop stages. Like the soybean model, the wheat simulates all the processes mentioned in the maize model, but with different algorithms. Archontoulis et al. (2014a) simulated the growth of triticale cover crop in Iowa very well (see their Figure 9).

The APSIM-AgPasture model

The AgPasture model was designed for the simulation of mixed perennial pastures of C3 and C4 species, making it a good candidate to simulate mixed-species prairies. Alternative options were the use of a single perennial species (e.g. bambatsi (*Panicum coloratum* var. makarikariense) or alfalfa (*Medicago sativa*)). The default AgPasture model has been parameterized for perennial ryegrass, white clover, and paspalum. The structure of the AgPasture model is very different compared to maize, soybean, and wheat models. For example, biomass production is simulated using the leaf photosynthesis and not the resource capture approach. The water, N, temperature, and CO_2 modifiers on daily crop growth rate are very different in AgPasture too. Crop transpiration is simulated using the Penman-Monteith physical approach instead of the physiological approach (transpiration efficiency) that is used in other APSIM models. Most importantly, the model has functions to cope with competing species (competition for light interception and water/nutrients from the root zone). The inclusion of competition was the main reason for choosing the AgPasture model to simulate prairie growth and biomass production. Given that the growth pattern of prairies is much different compared to traditional pasture systems, careful parameterization was implemented in this study (see results).

The APSIM SWIM soil water model

The APSIM SWIM model, one of the two soil water models available in APSIM, was used. The SWIM model uses the Richards' equations (Huth et al., 2012). APSIM runs a water balance on a daily basis in which the following processes are included: soil evaporation, crop transpiration (calculated via the transpiration efficiency and Penman-Monteith approaches, depending on the crop model), runoff (calculated via the USDA curve number method), and tile drainage (calculated similar to DRAINMOD model). Run-on is optional and was not used in this study. For a comprehensive description of the SWIM model see Huth et al. (2012) and www.apsim.info.

The APSIM soil N and surface organic matter models

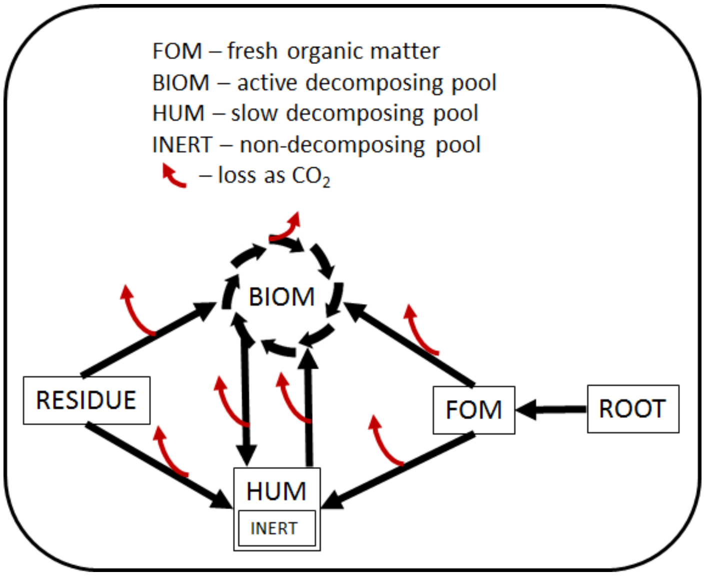


Figure 1. Organic matter pools in APSIM and C transfers among pools in no-till systems.

The SoilN model simulates mineralization, immobilization, nitrification, denitrification, and urea hydrolysis. The soil organic matter is divided into three conceptual pools, fresh organic matter (FOM), which contains the roots from the previous crop and the crop residues if these have been incorporated into the soil by tillage, a more active C pool (BIOM, as in microbial biomass), and a slower decomposing pool (HUM, as in humic), which includes within it a non-decomposing pool (INERT) (Figure 1). The FOM pool is divided into three sub-pools known as carbohydrate-like (FPOOL1), cellulose-like (FPOOL2), and lignin-like (FPOOL3) pools at default fractions 0.2, 0.7 and 0.1, respectively (Keating et al., 2003). In the absence of tillage, residue does not enter the FOM pool, but goes directly to BIOM and HUM. Each pool has its own decomposition rate constant (note that decomposition follows first order kinetics), which is mediated by soil temperature, moisture, and C:N for the FOM pools. During decomposition, part of the C is lost as CO_2 respiration and the remaining is synthesized into soil organic matter. Nitrogen mineralization or immobilization (of mineral N) is determined as the balance between release of N during decomposition and immobilization during microbial formation and humification. APSIM provides CO2 output from the soil, but not for a combination of the roots and soil, as was measured in our experiment. To calculate the root+soil CO2 for calibration, we applied the following equation from Texieria et al. (2009) at a daily timestep:

$$Rm_{root} = \left[0.015Q_{10}\left(\frac{T_{soil} - 20}{10}\right)\right] DM_{root}$$

Where Rm_{root} is root respiration, Q_{10} is the rate of change if the temperature increases by 10 °C, T_{soil} is the soil temperature, and DM_{root} is the amount of dry matter gained that day.

2.3c Calibration protocol

We followed the calibration protocol used by Archontoulis et al. (2014a): a) provided data on climate, soil, and management to the model; b) incorporated the measured data (Table 1) into the software platform to make use of APSIM's graphical and statistical tools; c) developed cultivar phenological parameters for maize and d) then we followed an iterative approach in which several aspects of the systems were evaluated in the order of: crop phenology, soil water, soil N, biomass production, biomass partitioning, and economic yield. We also performed numerous sensitivity analyses prior to and during the calibration to identify pathways towards improving model predictions and ensuring acceptable model behavior. Model calibration was completed when a good balance was achieved between measured and predicted values for the variables evaluated.

For model calibration, we utilized the first three years (2008, 2009, and 2010) of the experimental data from every cropping system and for model testing, the remaining data (2011, 2012, and 2013). It should be mentioned that the data used for model testing are not entirely independent as they were derived from the same experimental field and the model analysis was sequential. In the majority of crop model applications, the analysis is seasonal (starts at sowing and ends at harvesting). In such cases, it is relatively easy to have an independent dataset for model testing. On the other hand, a sequential analysis better reflects reality, and it is appropriate when soil parameters are of interest. In general, a sequential analysis is much more complex than a seasonal analysis and the benefits outweigh the disadvantages caused by lacking an independent dataset.

2.3d Model initial conditions

We initialized the model approximately 10 years before the starting date (May 2008). A corn/soybean system was simulated following standard Midwestern United States production management practices. This technique provided enough time for the labile soil organic matter pool (microbial biomass) and the soil water balance model to reach equilibrium. Model initial conditions have a great impact on simulation outputs when a seasonal analysis is used. In our case (sequential analysis) we bypassed this sensitivity.

2.3e Meteorological files and future weather predictions

Daily maximum and minimum temperature, precipitation and radiation values were obtained from a meteorological station that was installed in the experimental site in May 2008. Before that period, we utilized data from Daymet (http://daymet.ornl.gov/) using site coordinates to run the model for the period 1998 to 2008.

Future weather predictions were generated using the AgMIP Guide for Running AgMIP Climate Scenario Generation Tools with R, found at www.agmip.org. AgMIP (the Agricultural Model Intercomparison and Improvement Project) defines itself as “a major international effort linking the climate, crop, and economic modeling communities with cutting-edge information technology to produce improved crop and economic models and the next generation of climate impact projections for the agricultural sector.” APSIM is included in the model intercomparison, so AgMIP produces files that are appropriate for its use. While creating the climate files, we selected predictions from all 20 different global climate models, the descriptions of which can be found in the Climate Scenario Generation guide. Results from these models were downscaled for our experimental site (1 km x 1 km area). All model predictions were based upon the Representative Concentration Pathway (RCP) 4.5. This pathway assumes increases in atmospheric CO_2 and radiative forcing until 2100, when levels become stable.

2.3f Soil profiles

APSIM requires several soil parameters (www.apsim.info). We developed soil profile parameters for APSIM following the approach described by Archontoulis et al., (2014a). Briefly as a starting point we used information from Web Soil Survey and measured data from the experimental site. During calibration some parameters were adjusted as needed.

2.3g Statistical indices for model performance

The goodness of fit was assessed by calculating the root mean square error (RMSE) and the relative root mean square error (RRMSE), or the RMSE divided by the mean of the observations. These indices provide a measure of the absolute and the relative error, respectively, between observed and simulated values (model fit improves as both indices approach zero). The corresponding equations can be viewed in Archontoulis and Miguez et al. (2013). Ma et al. (2011) stated that the performance of a “point” agricultural model like APSIM is very good if the RRMSE < 10%, good if RRMSE ≈ 15%, and satisfactory if RRMSE ≈ 20%. We utilized the above rating scale in this study.

3 Results

3.1 Calibration and model performance

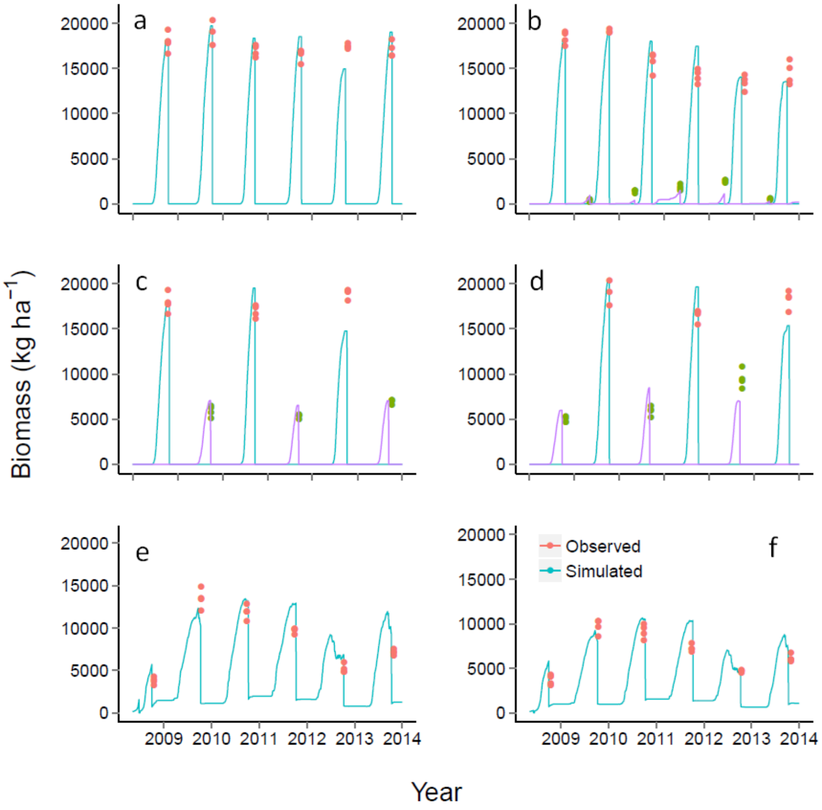


Figure 2. Aboveground biomass observed (circles) and simulated (lines) in a) continuous corn, b) continuous corn with winter rye cover crop, c) corn-soybean rotation, d) soybean-corn rotation, e) fertilized prairie, and d) unfertilized prairie. Calibration period was 2008-2010, testing period was 2011-2013.

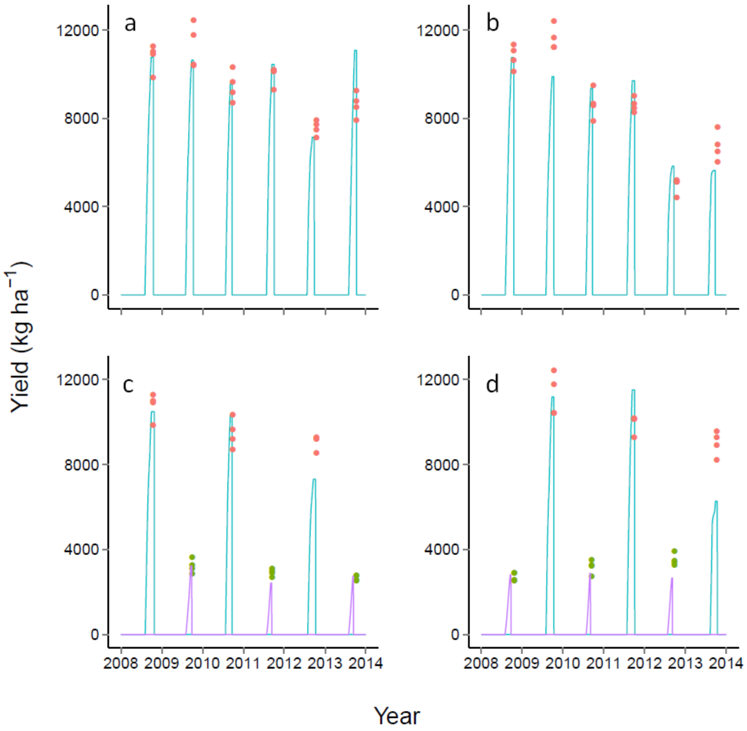


Figure 3. Grain yields observed (red circles) and simulated (blue and purple lines) in a) continuous corn, b) continuous corn with winter rye cover crop, and c) corn-soybean rotation, d) soybean-corn rotation. Calibration period was 2008-2010, testing period was 2011-2013.

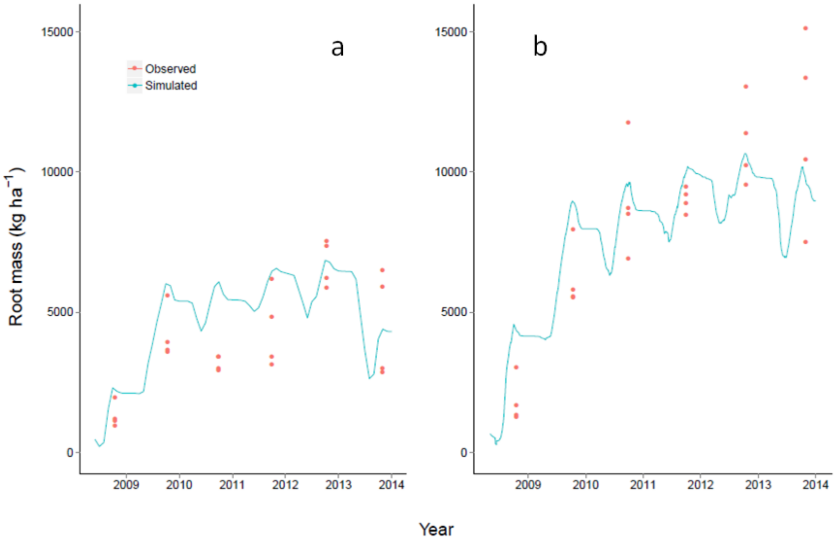


Figure 4. Root pool mass observed (red circles) and simulated (blue lines) in a) fertilized prairie and b) unfertilized prairie. Row-crop root measurements taken after harvest did not coincide with model output which only provided simulated root mass until the day of harvest. Calibration period was 2008-2010, testing period was 2011-2013.

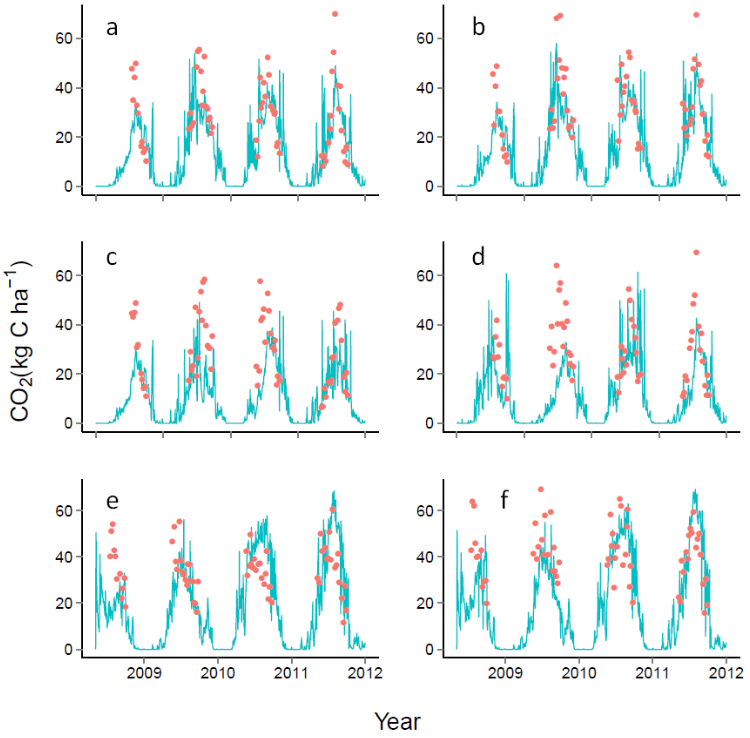


Figure 5. CO_2 (root + microbial) observed (red circles) and simulated (blue lines) in a) continuous corn, b) continuous corn with cover crop, c) corn-soybean rotation, d) soybean-corn rotation, e) fertilized prairie, and f) unfertilized prairie. Calibration period was 2008-2010, testing period was 2011-2013.

Table 1. Root mean square error (rmse, units kg ha^{-1} for biomass, yield and roots and kg C ha^{-1} for CO_2) and relative root mean square error (rrmse) of observed vs. simulated biomass, grain yield, root mass, and CO_2 efflux.

	Biomass		Yield		Roots		CO_2	
Trt	rmse	rrmse	rmse	rrmse	rmse	rrmse	rmse	rrmse
Continuous Corn	1644.40	0.09	1068.70	0.11	--	--	12.80	0.42
Corn with rye	1335.40	0.16	1058.70	0.12	--	--	12.78	0.39
Corn - Soybean	1224.20	0.02	832.50	0.13	--	--	18.18	0.60
Soybean - Corn	2322.01	0.19	1337.78	0.20	--	--	19.39	0.64
Fertilized Prairie	2356.45	0.28	----	----	1723.70	0.40	17.33	0.50
Unfertilized Prairie	1760.10	0.26	----	----	1666.40	0.21	9.29	0.30

APSIM performed well in simulating aboveground biomass of all crops when compared to tested years of measurement (Fig. 1, Table 1). The year of poorest simulation results was 2012, which was a drought. APSIM also performed well for grain yield (Fig. 2, Table 1) and root biomass (Fig. 3, Table 1) in the prairie treatments. Root mass in the row crops could not be compared because root measurements were made well after row-crops were harvested and APSIM stops outputting simulated root biomass after harvest. Archontoulis and colleagues (2014a) compared in-season APSIM maize root biomass predictions against experimental data and found a good agreement (see their fig 9 or 11). This minimizes concerns about belowground C production. APSIM performed well for CO_2 efflux when root respiration was also accounted for, although small differences in timing between the model and observed measurements resulted in relatively high RRMSE (Fig. 4, Table 1).

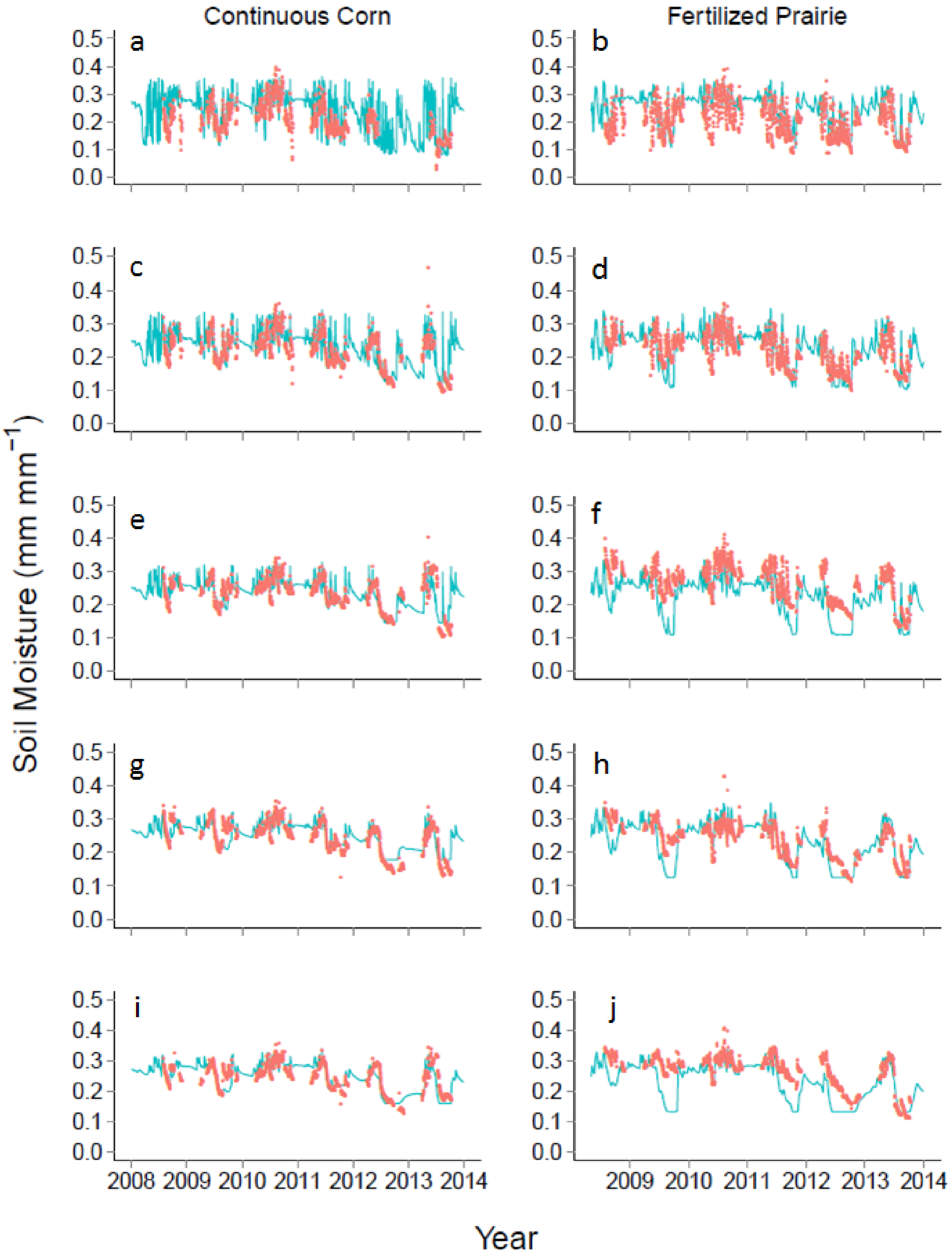


Figure 6. Soil water content observed (red circles) and simulated (blue lines) in continuous corn (left) and fertilized prairie (right) at depths a,b) 5 cm; c,d) 10 cm; e,f) 17.5 cm; g,h) 35 cm; i,j) 50 cm. Calibration period was 2008-2010, testing period was 2011-2013.

Table 2. Root mean square error (rmse) and relative root mean square error (rrmse) of observed vs. simulated water content and soil temperature for each treatment.

		Water content		Soil temperature	
Treatment	Depth (cm)	rmse	rrmse	rmse	rrmse
Continuous Corn	5	0.071	0.342	4.42	0.25
	10	0.055	0.253	4.02	0.23
	17.5	0.048	0.210	3.87	0.23
	35	0.042	0.173	3.51	0.21
	50	0.036	0.150	3.27	0.20
Corn with rye	5	0.06	0.30	4.54	0.26
	10	0.044	0.204	4.06	0.23
	17.5	0.038	0.163	3.86	0.23
	35	0.033	0.135	3.42	0.21
	50	0.035	0.143	3.31	0.20
Corn-Soybean	5	0.060	0.293	4.90	0.29
	10	0.046	0.208	4.41	0.26
	17.5	0.036	0.145	4.10	0.24
	35	0.040	0.179	3.87	0.24
	50	0.048	0.215	3.57	0.22
Soybean-Corn	5	0.054	0.252	4.82	0.30
	10	0.048	0.205	4.39	0.27
	17.5	0.044	0.171	4.03	0.25
	35	0.053	0.228	3.86	0.25
	50	0.040	0.162	3.52	0.02
Fertilized Prairie	5	0.060	0.297	5.54	0.35
	10	0.042	0.199	5.11	0.32
	17.5	0.063	0.248	5.13	0.33
	35	0.044	0.195	4.73	0.31
	50	0.060	0.235	4.29	0.29
Unfertilized Prairie	5	0.061	0.303	4.51	0.27
	10	0.051	0.238	4.19	0.24
	17.5	0.052	0.226	3.93	0.24
	35	0.059	0.248	3.41	0.21
	50	0.054	0.229	3.13	0.20

APSIM performed well in simulating both soil water content (Fig. 5) and soil temperature (Table 2), two aspects of the model upon which many processes, especially decomposition, are dependent. Five years after installation (in 2012), soil sensors began to wear out and this contributed to some missing values for testing as well as more variability in the measured numbers.

3.2 Soil organic C predictions

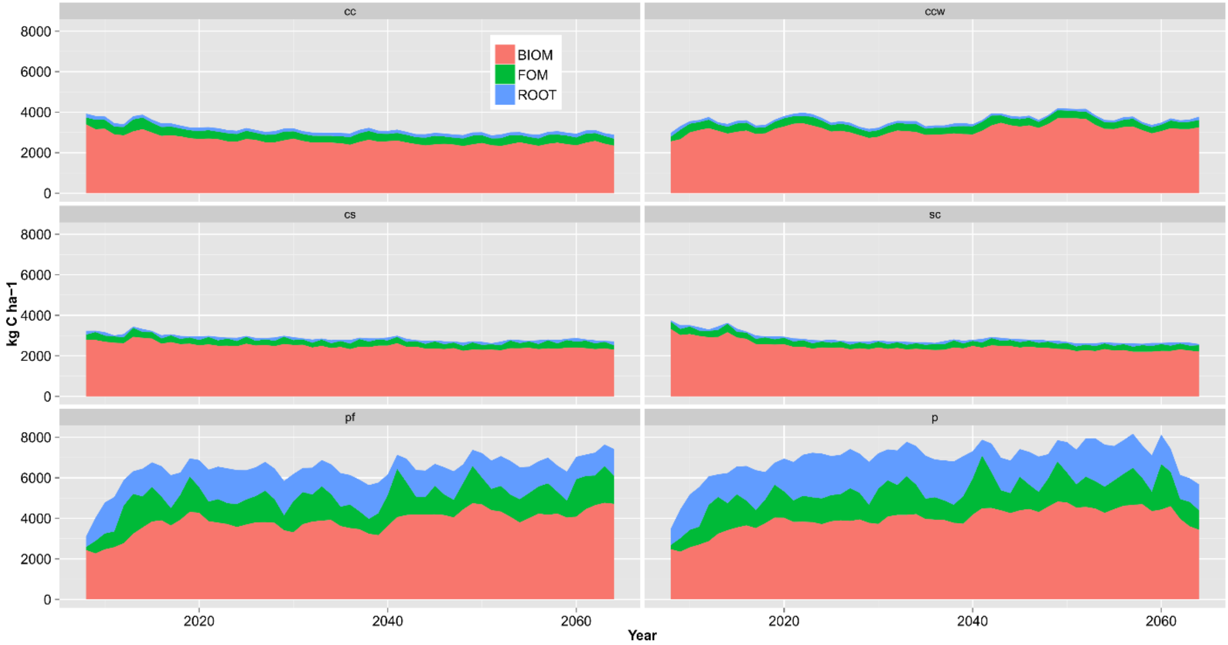


Figure 7. Predicted belowground C present in the root (blue), FOM (fresh organic matter) (green), and BIOM (microbial biomass and microbial products) (red) C pools from 2008 to 2064. The values shown are the averages of 20 different simulations from 20 different predicted weather files. Each panel is for one treatment – cc is continuous corn, ccw is continuous corn with cover crop, cs is corn-soybean, sc is soybean-corn, pf is fertilized prairie, p is unfertilized prairie.

All treatments began with the same amount of biom C, and prairies quickly accumulated biom C after establishment, then fluctuated, while continuous corn with cover crop slowly gained biom C, and the other row-crops slowly lost biom C. Carbon in the FOM pool of the prairie treatments followed the same pattern of a large increase just after prairies were established and then reaching a relatively stable point 10 years after establishment. Carbon in the FOM pool of row crops remained stable throughout the simulations and was smaller than the FOM pools of the prairie treatments. Prairie treatments also had bigger root C pools than the row crops and prairie root C pools remained at constant levels from 2018-2064. When these more labile pools were summed, prairies showed increases after establishment, whereas row-crops (except corn with cover crop) had small decreases. By 2064, prairie treatments had ~3-4 times more C in these pools than row-crops. However, these pools are relatively small when compared to the more stable pool, HUM (max 8,000 kg C ha^{-1} vs. max 220,000 kg C ha^{-1}).

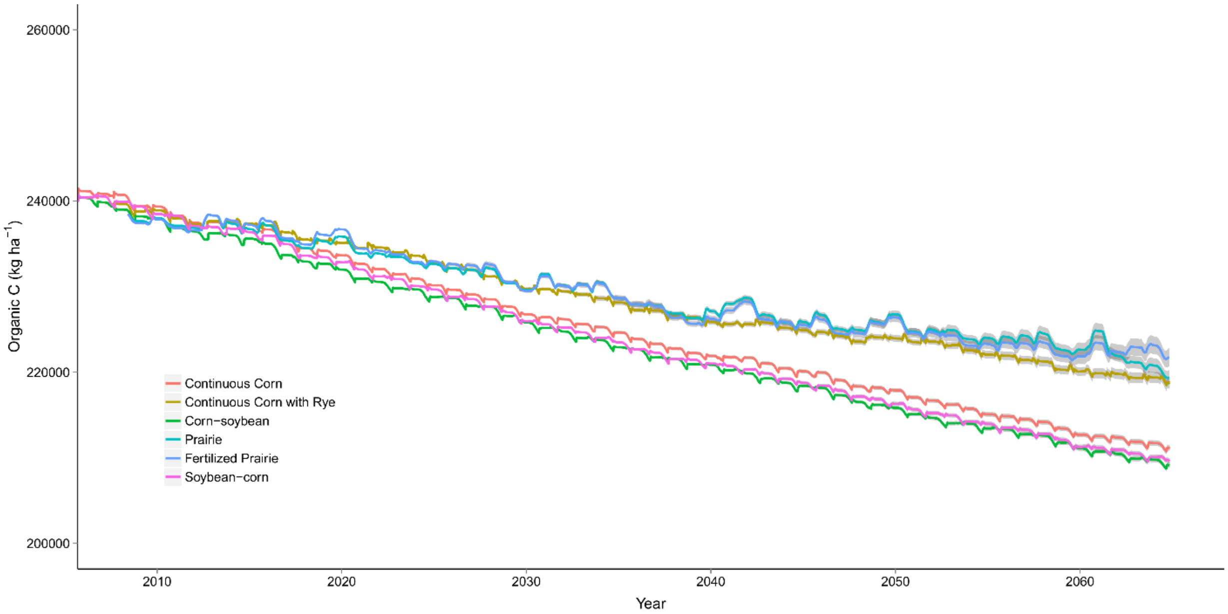


Figure 8. Predicted total organic C (fom + biom + hum pools) to 180 cm over 50 years. Grey shading represents standard error of the mean of 20 simulations run using predicted weather data from 20 different global climate models. Table 3 (inset). Mean and standard error (parentheses) of the linear slopes of each treatment. Treatments with different letters are significantly different.

When all organic C pools were summed, all treatments were found to lose C over time, all out of the HUM pool, which comprised most of the stable organic C. In terms of percent value (g/100g) this loss is in the order of 0.1–0.2%. Soil organic C decreased slowest in the prairie treatments (which were not different from each other), then in continuous corn with cover crop, then in continuous corn and the corn-soybean rotations. Prairies had the most variability between simulations and over time, followed by continuous corn with cover crop, and very little variability in the remaining row crops.

4 Discussion

4.1 We provided the first sequential cropping systems analysis for Iowa using APSIM

APSIM has previously been used in Iowa (Malone et al., 2007; Hammer et al., 2009; Archontoulis et al., 2014a), but not for simulations of consecutive years. Sequential analysis has been underexplored in model application history because of the complexity in concurrently simulating water, N, crop, and residue dynamics over fallow and cropping periods. The amount and detail of data available from the COBS site enabled a very good calibration of the different APSIM models as showed in all figures. We were concerned that the APSIM water balance would fail because of the lack of appropriate algorithms to explicitly model snow cover and melt, which are important in Iowa. However, we found that this limitation of the model did not affect the overall system performance as is shown in figure 6.

In general the uncertainty in modeling soil processes and properties is much higher than that of aboveground dynamics because comprehensive soil measurements that could verify hypotheses are costly and difficult to obtain, as well as because of the inherent complexity in soil processes and our limited understanding of them. This project advances scientific literature by providing comprehensive soil measurements and applies modeling concepts that account for soil water, N, plant growth, and soil organic C dynamics concurrently.

4.2 We modeled prairie growth and development by mechanistically accounting for functional group competition

Making modifications to the AgPasture model enabled us to use a model that simulated competition among prairie functional groups, plant-soil interactions, and belowground biogeochemical processes. To the best of our knowledge, this is the only such model with the capabilities to do so. We have used the model to focus on soil C dynamics, but many other possibilities exist for applications of the prairie model, such as examinations of N leaching or greenhouse gas emissions also measured at the COBS site, but not utilized in this study. Other models available (e.g. Agro-IBIS) overlook the high species competition that exists in prairie systems and treat prairie as a grass monoculture.

4.3 Prairies treatments and continuous corn with rye were predicted to gain C in active C pools, while continuous corn and corn-soybean rotations were predicted to lose C in these pools

The prairie treatments had more root biomass than row-crops and as this was transferred to the FOM pool, the prairie treatments also had more FOM C than row crops (Fig. 6). Root material that entered the FOM pool had very high C:N ratios (40-180) and as a result, fresh organic matter in this pool decomposed very slowly. However, even slow decomposition of such a large pool led to increases in the BIOM pool, which grew during the initial development of the prairie treatments. This is consistent with other studies that have found the more active or labile C pools to increase in response to prairies establishment (Baer et al. 2000, Guzman and al-Kaisi 2010). Ten years after prairie establishment, root, FOM, and BIOM pools were stable relative to initial increases, but still had a lot more variability than row-crop treatments. This was due to model sensitivity of root and FOM pools to dry conditions, during which decomposition was slowed or stopped and FOM pool sizes peaked.

Within the row-crops, continuous corn with cover crop was not predicted to lose C from the BIOM pool. A winter rye cover crop added relatively little C to the soil, but it affected the model in a number of ways that slowed decomposition and the loss of C. The cover cropped treatment experienced more N limitation and as this N was immobilized, decomposition was also limited. The cover cropped treatment also had drier soils at depth, both in APSIM and measured in the field (data not shown). The cover crop led to more surface cover and lower soil temperatures during part of the year. Corn following a cover crop had slightly less biomass aboveground than the other corn treatments. All of these factors contributed to slowing decomposition in the cover cropped treatment. Cover crops are often promoted as sources of C to be added to the soil, but in this simulation, the indirect effects of a cover crop were more important than the amount of C added for soil C dynamics.

4.4 No-till corn and soybeans were predicted to slowly lose total SOC over time

Carbon input into the soil through residue and roots was not enough to equal C lost from the soil through decomposition (Fig. 7). Decomposition is a function of temperature, moisture, and the properties of the material being decomposed. APSIM models decomposition with first-order kinetics, an accepted method common to other SOC models such as DAYCENT, DNDC, and RothC (Ranatunga 2001). Previous comparisons between APSIM, Century, and RothC have shown the models to produce similar results (Ranatunga 2001). Model validation showed that an accurate amount of C was being input to the model from biomass and roots, and the C:N ratios were consistent with empirical measurements. Soil moisture and temperature also tested well. Therefore, there are many reasons to find these results reliable.

The effect of adoption of no-till management on SOC in the Midwestern United States is still unclear. Johnson and colleagues (2005) found that no-till accumulated SOC in 44 paired comparisons in soils of the Midwestern United States at a rate of 400 kg C ha^{-1} $year^{-1}$, but with a standard error of 600 kg C ha^{-1} $year^{-1}$. The findings of many no-till studies have been recently questioned due to uncertainty in measurements affected by changes in bulk density, sampling depths, and lack of baseline measurements for comparison (Olson et al. 2014).

Long-term changes in SOC in Iowa cropland have been previously modeled, with conflicting results. This is due to assumptions used by different models (number of pools, decomposition rates, profile depth, etc.) and different crop and soil management. Through use of the EPIC model, Causarano and colleagues (2008) found Iowa croplands to have the potential to sequester 0 – 900 kg C ha^{-1} $year^{-1}$ to a depth of 20 cm after conversion to no-till. However, when the entire soil profile was included, all cropland was found to lose SOC over time (statewide 1835 Tg C in 1980 to 1771 Tg C in 2019). Liu and colleagues (2011) also found Iowa cropland to consistently lose SOC from 1972 – 2007 when this time period was modeled with GEMS (General Ensemble biogeochemical Modeling System). They found Iowa soils lost C at an average rate of 190 ± 380 kg C ha^{-1} $year^{-1}$. Farahbakhshazad and colleagues (2008) simulated SOC over 20 years of no-tillage or conventional tillage in Iowa and predicted no-till soils would gain SOC at an average rate of 415 kg C ha^{-1} $year^{-1}$, while conventionally tilled soils would lose SOC at a rate of 86 kg C ha^{-1} $year^{-1}$. The rate of SOC loss in row-crops predicted by APSIM (avg. 491 kg C ha^{-1} $year^{-1}$) was faster than those predicted by previous models.

In contrast to the aforementioned modeling studies which were basically "what-if" model scenario analyses that did not provide comprehensive evidence of model calibration, here we explicitly calibrated and tested the main drivers of organic matter dynamics: biomass (Fig. 2), amount of C leaving the system as economic yield (Fig. 3), root pool mass (Fig. 4), soil water content (Fig. 5), CO_2 efflux, and soil temperature at different depths (Table 1). We are not aware of any modeling studies that checked all these drivers before applying the models to predict future SOC trends. Our predictions are based on an extensive short term calibration and testing of the APSIM model (6 years total) and reflect our current understanding of SOC modeling.

4.5 Prairie treatments were also predicted to slowly lose SOC over time, but not as much as row-crop treatments

It was hypothesized that greater belowground inputs in the prairie treatments would lead to higher levels of SOC than in row-crops. It was not expected that the prairie treatments would be predicted to lose C over time. However, the predicted loss is small when compared to initial mass of organic matter. Guzman and Al-Kaisi (2010) found that reconstructed prairies and cropland in Jasper County, Iowa had ~44% less SOC than remnant prairie in the top 15 cm. Assuming a 44% loss of C down to a depth of 60 cm results in an estimated loss of 54,300 kg C ha^{-1} over the last 100 years. APSIM predicted a loss of ~15,000 kg C ha^{-1} in the prairie treatments by 2064, and this was to a depth of 180 cm. Therefore, predicted losses of SOC are well under historical losses of SOC.

In this study, most of the aboveground biomass was removed for biofuel production. Over 50 years, this has a large impact and therefore present predictions are not quite comparable with other studies where all of the prairie residue is incorporated. For example, assuming an average prairie aboveground production per year of 10 Mg ha^{-1} and an 80% residue removal rate, this means that 8 Mg ha^{-1} or 3.2 Mg C ha^{-1} leaves the system per year (or 160,000 kg C ha^{-1} over a 50 year period). Under different management practices, i.e. no residue removal, model future predictions would be different. For example, in the no residue removal scenario and assuming that 40% of the residue C ends up to the stable pool (Probert et al., 1998), this would have made a difference of 64,000 kg C ha^{-1}. In addition to the direct effects of less aboveground C inputs, less residue cover may have led to warmer soils and higher decomposition rates than in prairie soils that are protected by a thick mat of residue.

Although only one paper reports some loss of SOC after prairie reconstruction (Brye and Kucharik 2003), many more failed to find increases in SOC after the establishment of perennial grasses and forbs. Karlen and colleagues (1999) found no increases in SOC 2.5-6 years after establishment of Conservation Reserve Program (CRP) stands in Iowa and Minnesota. Baer and colleagues (2000) and Camill and colleagues (2004) found no increases in SOC 10 years after establishment of prairies in Illinois and Minnesota, respectively. Guzman and Al-Kaisi (2009) also found no differences in SOC among reconstructed prairies in Iowa that were 3, 8, and 13 years old. Kucharik (2007) did not find changes in SOC to 35 cm at 39 paired CRP-crop sites in Wisconsin. Another study by Kucharik and colleagues (2006) found that 65 years after prairie reconstruction, the examined soils still had 37% less SOC to 25 cm than an adjacent remnant.

Perhaps what makes the continued loss of C under reconstructed prairies most surprising is the fact that these C-rich soils formed under prairies, providing evidence that prairies do indeed lead to increases in soil C. However, historical prairies and reconstructed prairies have a key difference that greatly affects decomposition and C additions. Historical prairies developed over 8,000 – 10,000 years with no cultivation. Until European settlers introduced man-made drainage to the Midwestern United States, much of the prairie region experienced water-saturated soils frequently enough to make the land unsuitable for agriculture. Indeed, the first settlers to Central Iowa left accounts that much of the land was even unpassable by wagons and most of early commerce could occur only in the winter, over frozen soils and sloughs (Hamilton County 1986). Such wet, anaerobic conditions greatly encouraged C accumulation, but these conditions are absent from our experimental site due to tile drainage, a condition which is included in APSIM.

Changes in SOC in prairies, grasslands, or pastures have not been previously modeled in Iowa, but two studies in nearby states have addressed long-term SOC accumulation through the use of chronosequences. Matamala and colleagues (2008) used regression analysis of 8 prairie reconstructions and one remnant prairie site in Illinois to calculate an average annual increase of 180-210 kg C ha^{-1} year^{-1} in reconstructed prairies. McLauchlan and colleagues used linear regression of 31 CRP sites in western Minnesota that ranged in age from 20-40 years to calculate a rate of accumulation of 620 kg C ha^{-1}year^{-1}. These empirical results conflict with the predictions made in this study.

Most similar to our study, Kucharik and colleagues (2001) used the IBIS (Integrated Biosphere Simulator) model to predict changes in SOC in Wisconsin from 2000 to 2050 in no-till corn and reconstructed prairie systems (represented in the model by C3 or C4 grass systems). IBIS predicted annual increases of 863 kg C ha^{-1} in no-till corn and 745 kg C ha^{-1} in prairies. However, the reconstructed prairies upon which the experiment was based accumulated no C over 24 years. The authors concluded that because the field measurements did not agree with the model, something “unusual” must have been happening in the field.

4.6 Predicted mechanisms of SOC loss differ between row-crops and prairie

According to the model and under the given management scenarios, continuous corn and corn-soybean rotations lose SOC over time because C losses are greater than C additions – more C is being decomposed than is being added. Decomposition is slower in continuous corn with rye and that treatment has a slower C loss than the other treatments. The prairie treatments, on the other hand, are adding large amounts of C belowground, especially during the first ten years after establishment, but most of that C remains in the root or FOM pools. The high C:N ratios of the prairie root material result in N-limits to decomposition and the amount of C that is transferred to the BIOM pool (and then the HUM pool) is not enough to counteract the C decomposed from the HUM pool. It is unknown why the loss of C from the HUM pool is so large for all of the treatments.

The capacity of a soil to store C is dependent upon its texture and the amount of C already present in the soil. It has been widely observed that soils with low C content gain C more quickly than soils with high C content. It has been theorized that soils consisting of silt and clay provide more possible C-association sites that create physical protection for C, but if all of these sites are already occupied (as in C-rich soils), this physical protection is not available and C lost from the soil is equal to C gained in the soil – the soil C is at equilibrium. When working with soil C additions over a long period of time, the initial SOC is very important because it determines the equilibrium point. What-if APSIM model simulation analysis of corn-based systems in Iowa in soils with top soil OC of 1% (Zenor series), 2% (Clarion series), and 3% (Nicollet series), indicated that there was a SOC increase in the soil with SOC of 1%, the loss was little in the soil with 2% SOC, and OC loss (or HUM loss) over a 50 year period was highest in the soil with 3% SOC (Archontoulis et al. in prep.).

4.7 Further work is needed to improve SOC predictions

In the scientific community, there is an on-going discussion to improve SOC function in cropping systems models. Central to this discussion is the use of measureable pools instead of conceptual pools in models. Luo et al. (2014) developed an APSIM version with measurable pools and tested the new version again the default (version 7.4) using long term SOC and soil N data from Australia. They found that both versions predicted very similar SOC dynamics, but much different N dynamics, and that the new version (measurable pools) failed to replicate the observations accurately. They highlighted the need for more basic research on composition and underlying mechanisms of decomposition of measureable SOM pools.

4.8 Implications of soil C pool changes in reconstructed prairies and no-till corn in Iowa

Reconstructed prairie systems have the potential to greatly increase active C pools that consist of live roots, fresh organic matter, and microbial biomass, especially when compared to corn-based cropping systems. This C added to the soil represents an increase that is not present in corn-based systems, unless a winter cover crop is present. Increases in the active C pools were small relative to decreases in the more stable C pool, but still have functional meaning for the cropping systems. The active C pool represents a portion of the soil where nutrients are being cycled and soils with bigger active C pools and more microbial biomass are thought to be better able to support plant growth. However, it is these very activities that lead to more C loss from the system (Baer et al. 1999).

Predicted SOC losses in both no-till corn-based systems and prairie systems with residue removed has major implications for management aimed at increasing SOC. In general, the results of this study suggest that storing more C in high-C soils of Iowa will be difficult. Over a period of 50 years, it is even mechanistically possible that more SOC will be lost. Such a loss will mean continued decreases in soil health and increases in atmospheric CO_2. Reconstructing prairies without residue removal may help slow losses of SOC or stabilize SOC levels, but as long as soils maintain aerobic environments through tile drainage, remain at a C saturation point, and have available N, new C inputs will be decomposed and released to the atmosphere.

This study presented a comprehensive model analysis of soil water, temperature, soil C, and plant growth dynamics in six Midwestern production systems. The APSIM model replicated field observations fairly well for 2008-2013 and was used to predict SOC until 2064. Model predictions indicated a SOC decline in all cropping systems of about 0.1-0.2% by 2064, and that the prairie based systems are associated with less SOC loss, followed by continuous corn with cover crop. The continuous corn and corn-soybean systems had the greatest SOC loss. This study supports that managed prairies from bioenergy production offset soil C loss to a higher degree than managed corn systems for bioenergy production. However, caution should be exercised when the results from this study (predicted SOC status in 2064) are to be extrapolated across Iowa or different environments. Long term predictions are very sensitive to soil type, field management, weather, and initial SOC. The work presented here leads to further questions related to these sensitivities, such as how SOC will be affected by leaving residue on the field, weather predictions based on different CO2 scenarios, and no-till or prairie systems grown on low-C soils. This study provides a validated simulation platform to explore such questions and help design resilient Midwestern production systems.

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CHAPTER 5. SUMMARY, CONCLUSIONS, AND FUTURE RESEARCH

Increasing C in the soil is important both for removing harmful C from the atmosphere and improving the health of the soil In this dissertation, I set out to examine how planting and harvesting prairies on soils suitable for corn affected soil C storage when compared to corn-based systems. In the Midwestern United States, historical prairies created some of the world's most C-rich soils, so it would be expected that reconstructing such prairies would lead to high C storage. However, increasing C in the soil has not been found to be so straightforward. In several cases, the establishment of prairies has not led to any overall differences in SOC. In this dissertation, I addressed three questions designed to a) improve our understanding of the fundamental differences between how prairies and corn grow throughout the year, b) test how prairies and corn add C to the soil after establishment, and c) use our current understanding of prairie and corn growth and C and N dynamics to predict how SOC will change over the next 50 years.

First, I asked how prairies and corn assimilate and allocate C and use N over the course of the growing season. Above- and belowground growth was measured throughout the growing season and plant tissues were analyzed for C and N content. Measured data was fit with curves to determine and compare the growth parameters moment of maximum growth, maximum mass reached, and the moment maximum mass was reached (which was also the moment growth ended). Corn produced more aboveground and overall biomass with faster growth rates that peaked later in the season than prairie. Duration of growth was shorter in corn than prairie. Corn allocated a much smaller proportion of its biomass belowground than prairie and produced much less root biomass than prairie. Corn biomass had higher N concentrations, but less efficient growth relative to these concentrations. The relationship of timing between above and belowground growth was similar for corn and prairie, with belowground growth ending at the same time as aboveground growth in all treatments. Duration of belowground growth also did not differ much between treatments, nor did the moment when growth ended. These basic differences and similarities between perennial prairie and annual corn can help us understand how these cropping systems function differently with respect to C and assist in predictive modeling of the systems.

Next, I asked what evidence we have of differences in soil C storage between prairie- and corn-based systems six years after the experiment was established. The root pool was measured to a 1 m depth at the end of each growing season and root tissue was analyzed for C and N content. Five years after prairies and corn were established, a labile C pool that has been shown to be responsive to management differences (POXC) was measured. Total soil organic C was also measured at the establishment of the experiment and again six years later. Prairies had much greater root pool mass than corn-based treatments and this mass accumulated at a faster rate in prairies than in corn. In the prairies, root pool mass accumulation slowed and stopped first at 0-5 cm, then at 5-15 cm depth, then slowed at 15-60 cm, and continues to increase at 60-100 cm. This suggests that prairies roots meet a maximum density and then fill the next available soil space and shifts in the proportions of root depth distribution also support this. A continued increase in root pool mass at deeper depths shows that prairie roots have potential to continue adding root C after six years (albeit slowly), while no root accumulation at shallower depths suggests that any additions of root mass at these depths is equal to loss of root mass. Prairies also had more root mass at deeper depths than corn-based treatments, which is important because lower temperatures and less oxygen at deeper depths hinder decomposition. Prairie root pool mass had much higher C:N ratios than corn-based treatments, indicating higher recalcitrance for prairie roots. This difference in C:N ratios was especially strong at deeper depths and C:N ratios in prairie roots increased over time. Despite having more root mass that was more recalcitrant and located at depths unfavorable to decomposition, prairie did not have greater amounts of labile C (POXC) or total SOC than corn-based treatments, nor did it have greater amounts of total SOC than in the establishment year. Prairies placed ~5 times more C belowground as root C than corn-based treatments, which is significant in itself, but the lack of increase in soil C pools remains unexplained. It is possible that prairie roots create an environment that is rich in labile C (from root exudates and fine root turnover), which supports a large and active microbial population that readily metabolizes any decomposable C source. In addition, C moving out of the root pool may experience a lack of physical protection as all possible C-association sites may already be occupied in such a C-rich soil. If these possibilities are true, C entering the soil in prairie systems has three possible fates 1) remain in the root C pool (a good option for high C:N ratio material); 2) be mineralized by microbial populations and exit the system as CO_2; or 3) be incorporated into the microbial biomass C pool at an undetectable rate.

Finally, I asked what differences we will see in soil C storage in prairie- and corn-based cropping systems 50 years from now. A wealth of environmental and plant-related data available from the experimental site was used to calibrate a cropping systems simulation model (APSIM). Predicted weather files based upon simulations from 20 different global climates models were used to simulate the crop and soil environment until 2064. Simulations showed that prairies had much larger increases in root C, fresh organic matter, and microbial biomass pools, while a corn-based system with a winter cover crop maintained these pools, and continuous corn and corn-soybean rotations lost C in these pools. However, all treatments lost C from the more stable C pool, resulting in an overall loss of SOC after 50 years. This loss was greatest in the corn-based systems that did not have a cover crop, followed by continuous corn with a cover crop. Prairies had the smallest loss of SOC after 50 years when compared to the corn-based systems.

Chapter 1 showed that prairie-based systems assimilate as much C as corn-based systems and that much of this C is allocated belowground with relatively low amounts of associated N. Chapter 2 built upon these findings and showed that over 6 years, prairie-based systems are continuing to accumulate biomass belowground faster than corn-based systems and that belowground root C is less likely to be decomposed due to low C:N ratios and placement at depths that inhibit decomposition. Despite additions of belowground C in prairies and corn, there was no evidence for increases in soil C outside of the root C pool. Chapter 3 elaborated upon the lack of SOC gain shown in chapter 2 by simulating and examining SOC changes over 50 years. It was found that while prairies did have greater belowground inputs and bigger root C pools than corn (as in chapters 1 and 2), overall SOC decreased over time. Although data in chapters 1 and 2 were used to calibrate the simulation model, the simulations were dependent upon equations that have been derived from empirical data collected all over the world throughout several decades. Therefore, the fact that the model found increases in root and active C pools, but failed to find overall increases in the whole SOC pool was derived independently, but was also consistent with results shown in chapters 1 and 2.

Non-increasing SOC in chapter 2 and long-term SOC loss in chapter 3 were explained by mechanisms of soil C saturation combined with rhizosphere induced priming, but these possibilities need more investigation. Using a modeling approach allowed us to see some support for these mechanisms because SOC moved very inefficiently from the active C pools (also due to high C:N ratios) and most of the C lost from the soil came from the stable C pool (as would be expected with rhizosphere induced priming). However, more empirical data is needed to support these possible mechanisms of SOC loss and would be a promising avenue of future research.

Performing research on belowground soil processes is challenging because it is difficult to make measurements without disturbing the soil system and there is still so much that is not understood about things that we simply cannot witness firsthand, such as the fate of C entering an ecosystem. As a work focused on a belowground process and its interactions with aboveground processes, this dissertation has some inherent weaknesses. However, a combination of empirical and modeling approaches led to one strong conclusion. Increasing and maintaining an increase of C in soils already high in C will be difficult, if not impossible. This is not to say that management practices cannot improve the health of soils by affecting which pools C is in, or the physical structure of the soil, but if we desire to remove C from the atmosphere by placing it in the soil, soils high in silt and clay, but low in C content may provide a better option.