Catena 160 (2018) 282–297

Contents lists available at ScienceDirect

Catena

journal homepage: www.elsevier.com/locate/catena

Landscape dependent changes in soil properties due to long-term cultivation and subsequent conversion to native grass agriculture

Cody J. Zilverberg[a,*], Kyle Heimerl[b], Thomas E. Schumacher[c], Douglas D. Malo[c], Joseph A. Schumacher[c], W. Carter Johnson[a]

[a] Department of Natural Resource Management, South Dakota State University, Brookings, SD 57007, United States
[b] Department of Environment and Natural Resources, State of South Dakota, Pierre, SD 57501, United States
[c] Department of Agronomy, Horticulture, and Plant Science, South Dakota State University, Brookings, SD 57007, United States

ARTICLE INFO

Keywords:
Soil organic carbon
Erosion
Prairie
Restoration
Wetlands
Kastanozem

ABSTRACT

On farmland in undulating landscapes, soil organic carbon (SOC) stocks depend on landscape position. In the North American Prairie Pothole region, we compared a native prairie reference site with a nearby farm undergoing transition to perennial agriculture ("restoration") after a century of producing annual crops. We quantified legacy effects of farming at four upland landscape positions (to 0.9-m soil depth) and three wetland positions (to 1.0-m soil depth). We also quantified short-term (4 years) changes in SOC stocks (to 0.15-m soil depth) during restoration, and how these changes were impacted by historic erosion.

Surface (to 0.05-m soil depth) measurements indicated degradation of the cropland soil relative to the prairie at all landscape positions due to less soil organic matter (SOM) and altered soil properties (e.g., water aggregate stability and microbial activity). All upland and wetland positions of the farm lost SOC stocks (Mg ha^{-1}) relative to the prairie in the top 1.5 Gg ha^{-1} of soil (~14-cm depth). However, when considering a larger mass of soil, 4.5 Gg ha^{-1} (~39-cm depth), loss of SOC stocks was significant ($p < 0.001$) only at the summit (46 Mg ha^{-1}) and shoulder (63 Mg ha^{-1}) landscape positions. Differences in SOC stocks between farm and prairie were smaller and not significant at the backslope, footslope, and in wetlands.

Contrary to expectations, sites of soil deposition did not accumulate soil carbon after restoration. Accretion of soil C during restoration differed according to the severity of historic erosion ($p < 0.001$), with severely eroded soils gaining soil C at the fastest rate. Historic loss of clay at the shoulder and backslope and subsoil compaction in the wetlands may prevent these landscape positions from full restoration of soil C stocks, net primary productivity, and historic vegetation.

1. Introduction

Globally, 70% of naturally occurring grasslands have been cleared or converted for more intensive agricultural use (Ramankutty et al., 2008). In the western corn belt of North America, the situation is especially extreme with 99% of native tallgrass ecosystems converted to cropland or to other land uses (Samson and Knopf, 1994; Wright and Wimberly, 2013). The loss of grasslands is especially significant where the western corn belt overlaps with the Prairie Pothole Region of North America (Fig. 1).

The Prairie Pothole Region is a 750,000 km^2 area in the heart of North America, two-thirds of which is located in Canada and one-third in the north-central United States (Fig. 1). The region contains approximately 5–8 million wetland basins of glacial origin embedded in irregular topography and heterogeneous soils (Van der Valk, 1989). The combination of highly productive grassland and diverse complexes of wetlands produces 50–80% of the wild ducks in all of North America each year (Johnson et al., 2010). The most numerous wetlands are classified as temporary with small shallow basins that hold water for one or two months in spring and early summer (Johnson et al., 2004). The region also includes many larger seasonal and semi-permanent wetlands with longer hydroperiods.

Much of the conversion of the region's native prairie to farmland occurred in the late 19th and early 20th centuries. Prairie Pothole Region wetlands were some of the last parts of the landscape to be converted (DeLuca and Zabinski, 2011) but conversion is still ongoing,

Abbreviations: cPOM, Coarse POM; FDA, Fluorescein diacetate hydrolysis; fPOM, Fine POM; InC, Inorganic C; MAOM, Mineral-associated organic matter; POM, Particulate organic matter; SOC, Soil organic C; SOM, Soil organic matter; TEP, Tillage Erosion Prediction model; TSN, Total soil nitrogen; WAS, Water aggregate stability

* Corresponding author at: Dakota Lakes Research Farm, South Dakota State University, P.O. Box 2, Pierre, SD 57501, United States.
E-mail address: cjzilverberg@gmail.com (C.J. Zilverberg).

http://dx.doi.org/10.1016/j.catena.2017.09.020
Received 24 August 2016; Received in revised form 24 August 2017; Accepted 25 September 2017

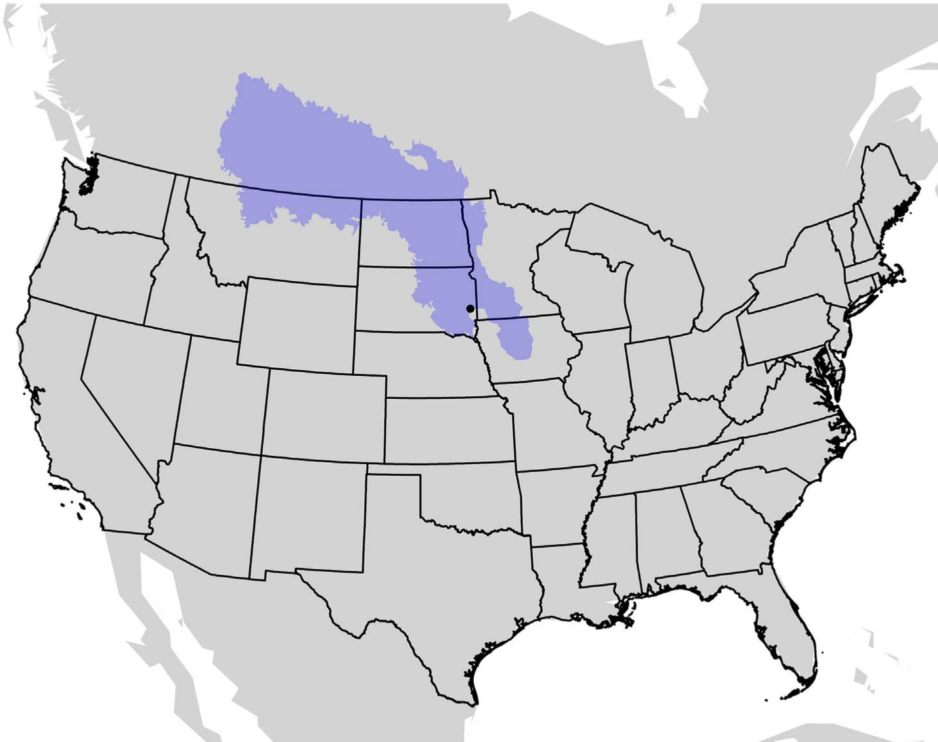

Fig. 1. The study location (44°02′ N, 96° 49′ W) is indicated by a dot in the state of South Dakota, United States of America. The Prairie Pothole Region is the shaded area extending across the border between the United States and Canada. Adapted from Johnson et al. (2010).

partly in response to high commodity crop prices from 2006 to 2011 (Wright and Wimberly, 2013). Converting the region's landscapes to cropland has included farming through intact temporary wetlands during dry years as well as wetland drainage via surface ditches, underground pipes, and underground tile drains. Nearly half of the original wetlands in eastern South Dakota have been drained (Johnson and Higgins, 1997).

Until the latter part of the 20th century, the preferred method of cultivation utilized the moldboard plough and secondary tillage. This resulted in high oxidation rates of soil organic carbon (SOC) within the first 5–30 years after cultivation (DeLuca and Zabinski, 2011). Additionally, intensive tillage combined with the hummocky nature of the landscape has resulted in a high degree of lateral soil transfer within the landscape. The processes of tillage erosion and water erosion interact with one another and occur frequently in this semi-humid region (Schumacher et al., 1999; Lobb, 2011). Depositional sites include footslope positions and wetland depressions within fields. In many cases these are closed basin systems with minimal opportunity for deposition into streams (Richardson et al., 1994) unless artificial surface drainage systems (shallow ditches) were created to connect basins to streams.

Cultivation can cause large changes to physical, chemical, and biological properties within the surface horizon. Significant modifications can also occur in subsoils, affecting hydrology, biogeochemical cycles, greenhouse gas emissions, carbon dynamics, and biological productivity (Chirinda et al., 2014; Smith et al., 2016). Cultivation and changes to soil properties impact ecosystem services associated with the region's wetland complex, including flood abatement, water quality, biodiversity, aquifer recharge, wildlife habitat, waterfowl sustainability, and soil carbon management (Johnson et al., 2010).

Management of SOC has both global and local implications. Increases in SOC provide a positive feedback mechanism for net primary productivity, agricultural yield, and C fixation in soil. Conversely, loss of SOC is a major factor in the degradation of soil (Lal, 2015). Globally, flux of C between soils and the atmosphere has implications for climate change (Amundson et al., 2015). In an actively eroding landscape, soil carbon dynamics are fundamentally changed; controlling processes have been comprehensively described in recent reviews (Kirkels et al., 2014; Doetterl et al., 2016). During dynamic replacement, eroding landscape positions that are depleted of soil organic carbon have increased rates of SOC accumulation while soil transport to areas of deposition during erosion events continues (Stallard, 1998; Harden et al., 1999; Li et al., 2015).

SOC decomposition and stabilization rates during transport and deposition depend on a variety of circumstances, including duration of transport phase, degree of local mixing with C-depleted subsoil, depth and stratification of sediment burial, rate of chemical weathering of parent materials, intensity of the erosion process, moisture content of eroding aggregates, spatial variation in plant growth, differences in field management, the age of eroded aggregates, the degree of aggregation of eroded materials, and soil type (Quinton et al., 2010; Van Hemelryck et al., 2011; Fiener et al., 2015; Doetterl et al., 2015; Hu and Kuhn, 2016). Eroded SOC, though not indefinitely stable, may persist for periods of decades to centuries after burial (Doetterl et al., 2015). Although there have been disagreements about the net global effect of erosion on soil carbon stores (Van Oost et al., 2007, 2008; Lal, 2008), there is broad agreement on the detrimental effect of cultivation-induced erosion on crop productivity and the functioning of global ecosystems (Kirkels et al., 2014).

Despite continued conversion from grassland to cropland in the Prairie Pothole Region, declines in commodity crop prices have recently increased interest in returning some farmed soils to grassland cover (P. Bauman, personal communication, July 2016). A successful conversion of cropland to grassland minimizes erosion and thus may impact both local soil quality and global C stores. Because nearly all land in this region is privately owned, large-scale conversion of cropland to grassland is only viable when the process includes agriculturally based solutions that are profitable to the landowner. These may include the sale of carbon credits (DeLuca and Zabinski, 2011).

A review by Doetterl et al. (2016) recognized the need to link terrestrial and aquatic cycles of C, N, and P but most research has focused on terrestrial C dynamics alone. In the Prairie Pothole Region, few studies have evaluated the C dynamics of cultivated and native landscapes, and fewer yet have included both uplands and wetlands. Several studies in southern Saskatchewan, Canada, which is part of the Prairie Pothole Region, evaluated wetlands (Bedard-Haughn et al., 2006) or uplands (Slobodian et al., 2002; Pennock, 2003). However, their research took place in a different natural ecosystem, a shorter mixed-grass prairie type, and was more than 1000 km from our research site. A few studies have examined soil and SOC distribution within the mesic, tallgrass portion of the Prairie Pothole Region (Papiernik et al., 2007; Olson et al., 2014) but these studies did not include detailed measurements within wetlands. Other studies in adjacent regions have evaluated SOC dynamics in hillslopes or in wetlands fundamentally different than those in the Prairie Pothole Region (Guzman and Al-Kaisi, 2010; O'Connell et al., 2016).

Critical to the rehabilitation of Prairie Pothole ecosystems is an understanding of the impact of past agricultural practices on soil carbon dynamics (Lal, 2015). The use of a simple model to identify regions within fields that are the most degraded and/or that have the greatest potential for improvement could be useful for targeting management practices and resources in the rehabilitation/restoration process. Re-establishing permanent vegetation in cultivated wetlands has been suggested to have greater potential for SOC accumulation than upland positions because of the high degree of SOC storage in ephemeral wetlands in hummocky landscapes (Bedard-Haughn et al., 2006). However, upland landscape positions with a history of dynamic SOC replacement and relatively low SOC concentrations (Li et al., 2015) may continue to have high rates of SOC accumulation during rehabilitation/restoration of cultivated uplands.

Our objectives were: 1) to evaluate differences in soil properties, especially C, between cultivated fields and virgin prairie within a closed depression landscape, and thereby establish realistic goals for rehabilitation and restoration of cropland; and 2) determine the effects of native grass establishment on spatial distribution of soil carbon and nitrogen on former cropland. Our study differs from previous studies by concurrently examining both cultivated and native tallgrass prairie uplands and wetlands within the Prairie Pothole Region, and incorporating past effects of tillage with short-term effects of returning cropland to grassland.

We hypothesized that:

1) Surface (0–15 cm) soil properties of cultivated fields at each landscape position indicate degradation relative to virgin prairie of similar topography and soils;
2) SOC and total soil nitrogen (TSN) stocks of cultivated fields are depleted relative to virgin prairie soils at all landscape positions, with greater depletion occurring on eroded positions; and.
3) The highest rates of SOC accumulation after native perennial establishment occur in sites of soil deposition.

2. Material and methods

2.1. Study sites

The study included two nearby sites with similar soil mapping units and landforms in the historic tallgrass prairie region and Prairie Pothole Region of eastern South Dakota, near the town of Colman (Fig. 1). The sites were a crop farm (hereafter "cropland"; 44°01′34.31″ N, 96°51′00.36″ W; Zilverberg et al., 2014c, 2015) designated for vegetation restoration and the "Sioux Prairie" (hereafter "prairie"; 44°01′50.79″ N, 96°47′05.24″W), a virgin prairie owned by The Nature Conservancy (Fig. 2). The undulating topography of this area was formed on Early Wisconsin glacial sediments (South Dakota Geological Survey, 2009) and has silty clay loam and loam textures. Soils studied at both sites were dominated by a Wentworth-Egan silty clay loam soil association with 2–6% slope (Soil Survey Staff, 1985; Table 1). Slopes at both sites were 0–9%, having relief predominated by ridges leading down to footslopes. Mean annual precipitation was 601 mm and mean annual maximum and minimum temperatures were 13° and 0 °C, respectively, from 1893 to 2014 at the Flandreau, SD weather station (High Plains Regional Climate Center, 2016).

The cropland site was 262 ha and was cultivated for approximately 100–130 years with conventional tillage techniques (Novotny, 2008). Many of the wetlands were drained around 1900 and drainage ditches were cleaned out and modified in the 1960′s to maintain dry basins for farming (Novotny, 2008). Recent cropping has been a corn (*Zea mays*) and soybean (*Glycine max*) rotation using conventional chisel-plough tillage. Conversion of this property to mixed grasslands began in 2008 (Zilverberg et al., 2014a, 2014c, 2015), shortly before soil samples were collected for the present study. The relief of the cropland is indicative of the Prairie Pothole Region with many small wetlands present among the gently rolling hills. Drainage of many of these wetlands by the construction of ditches corresponded to an intensification of agriculture on the property. Restoration of several wetlands was initiated using ditch plugs, and in some cases, water control structures used to regulate water levels. Native species were established using plugs and direct broadcasting of seed. The most common planted species were prairie cordgrass (*Spartina pectinata*), prairie wedgegrass (*Sphenopholis obtusata*), American sloughgrass (*Beckmannia syzigachne*), slough sedge (*Carex atherodes*), woolly sedge (*Carex pellita*), and smooth cone sedge (*Carex laeviconica*).

The prairie site (81 ha) was located approximately 4.8 km east of the cropland. An 8-ha portion on the northwest corner of this property was tilled from 1945 to 1970 (Ode, 1978). The remainder was used for grazing (Ode, 1978). Since acquisition of the prairie in 1971 by The Nature Conservancy, the property has been managed by selective use of herbicide, mowing, and controlled burns to maintain the more than 200 native plant species present. The relief of the prairie is similar to that of the cropland with a mixture of gently rolling hills and wetlands. The prairie wetlands have no history of drainage but have become dominated by hybrid cattail (*Typha x glauca*).

2.2. Collection of soil samples

2.2.1. Baseline study

Sampling was conducted during the summer of 2009, one year after the cropland had been seeded to a mixture of native prairie plants. We created digital elevation maps of the two sites by using point samples that were collected every 25 m in a grid with a survey-grade GPS (Leica Geosystems GPS System 500, SR530 receivers - RTK). The spatial information was input to the Tillage Erosion Prediction model (TEP; Lindstrom et al., 2000). This model used landscape configuration to identify locations at the two sites (cropland and prairie) where quantities of soil loss or deposition due to tillage would have been the same if the two sites had experienced the same historic tillage. The WATEM model (Van Oost et al., 2000), which also incorporates effects of water erosion, was used to verify the TEP results. Results from TEP were combined with soil maps and on-site inspection so that comparisons between the cropland and prairie would occur between positions that were similar in soil type and erosion potential. This process resulted in categorizing upland sampling positions into one of four landscape position categories: Summit, shoulder, backslope, and footslope within four or five transects in both the cropland and prairie (Fig. 3; Heimerl, 2011). Transects were laterally separated by a minimum of 15 m and maximum of 425 m

Loose organic residue was cleared from the soil surface before a hydraulic-style probe (Giddings Rear Mounted Soil Probe Model GPSI S) with a 6.2- or 7.6-cm diameter was used to collect soil cores to 90 cm. The cores were then divided in the field at intervals of 0 to 5 cm, 5 to 15 cm, 15 to 30 cm, 30 to 60 cm, and 60 to 90 cm. At each sampling point, two subsamples were taken within 0.5 m of one another, and subsamples were combined in the field. Each composite sample was bagged and transported indoors to air-dry. The total number of upland samples taken to the laboratory, after subsamples were composited, was 186 (2 sites × 4 landscape positions × 4–5 replicates × 5 depths).

Fig. 2. A satellite image (USDA-NRCS Geospatial Data Gateway, https://datagateway.nrcs.usda.gov/) shows the two study locations, located 4 km from one another. The matrix of agricultural fields and wetlands is apparent. A distance of 1.6 km typically separates parallel roads, which appear as light grey lines.

In addition to upland sampling, wetlands from each location were classified based on the Stewart and Kantrud (1971) system. To compare sites, two temporary and one semi-permanent wetland from each site were selected. In most years, temporary wetlands are flooded in spring but dry by early summer, whereas semi-permanent wetlands typically hold water throughout the growing season. Each wetland was surveyed using a laser level (CST/Berger ALH, 225 W Fleming ST, Watseka, IL 60970) and divided into three zones based on elevation (wetland edge, the highest elevation; intermediate depth; and wetland center, the lowest elevation). Three randomly selected points were sampled within each zone of the semi-permanent wetland and two randomly selected points within each temporary wetland.

Loose organic residue was cleared from the soil surface before a push probe (diameter 6.2 cm) was used to collect the soil sample to a depth of 1 m. A modified piston corer with a 5-cm diameter (Cushing and Wright, 1965) was used where site conditions prohibited a push probe. Samples were divided by 10-cm increments (0–10, 10–20, …, 90–100 cm). At each sampling point, two subsamples were taken within 0.5 m of one another, and subsamples were combined in the field. Each composite sample was bagged and transported indoors to air-dry. The total number of wetland samples taken to the laboratory, after subsamples were composited, was 419 of a possible 420 (2 sites × 3 wetlands/site × 3 wetland elevation positions × 2–3 replicates × 10 depths).

Table 1
Textural class and taxonomic name of soils found at the research site.

Soil map units	Textural class
Ethan-Egan complex	Loam/silty clay loam
Wentworth-Egan silty clay loam	Silty clay loam
Worthing silty clay loam	Silty clay loam

Primary soil series	Textural class	USDA soil taxonomy classification (Soil Survey Staff, 2017)	World reference base for soil resources classification (IUSS Working Group, 2015)	Landscape position
Egan	Silty clay loam	Fine-silty, mixed, superactive, mesic Udic Haplustolls	Haplic Kastanozem (Cambic, Calcaric, Loamic)	Summit, nearly level to slightly convex
Ethan	Loam	Fine-loamy, mixed, superactive, mesic Typic Calciustolls	Calcic Kastanozem (Loamic)	Shoulder, convex
Wentworth	Silty clay loam	Fine-silty, mixed, superactive, mesic Udic Haplustolls	Haplic Kastanozem (Cambic, Calcaric, Loamic)	Backslope, linear
Trent	Silty clay loam	Fine-silty, mixed, superactive, mesic Pachic Haplustolls	Haplic Chernozem (Cambic, Loamic, Pachic)	Footslope, concave
Worthing	Silty clay loam	Fine, smectitic, mesic Vertic Argiaquolls	Chernic Gleysols (Luvic, Provertic)	Wetlands, concave

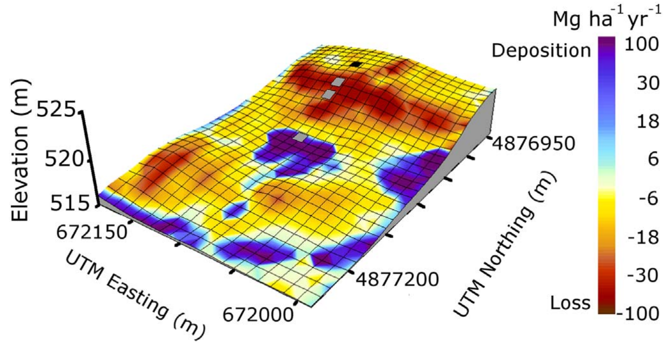

Fig. 3. A 3-dimensional terrain map of the cropland study site shows the location of four upland sampling points (summit, shoulder, backslope, footslope) from one transect in the cropland site. Sampling points are represented by filled black or grey boxes overlaid on modeled loss and deposition of soil. For this figure, deposition or loss of soil was modeled using WATEM, a combination tillage erosion and water erosion model (Van Oost et al., 2000).

2.2.2. Restoration study

Using a 10-m × 10-m grid, the TEP model was used to simulate historic erosion and deposition on 111 ha of the cropland. The results from the model were used to group each grid point into 1 of 5 sampling zones. The zones were as follows, with positive numbers representing deposition and negative numbers representing erosion: zone 1 (> 24 Mg ha^{-1} yr^{-1}, high rate of deposition, 4 sampling points); zone 2 (6 to 24 Mg ha^{-1} yr^{-1}, moderate deposition, 10 sampling points); zone 3 (6 to − 8 Mg ha^{-1} yr^{-1}, mild levels of erosion or deposition, 10 sampling points); zone 4 (− 8 to − 20 Mg ha^{-1} yr^{-1}, moderate erosion, 9 sampling points); zone 5 (< − 20 Mg ha^{-1} yr^{-1} severe erosion, 8 sampling points). Zones could typically be associated with a landscape position. For instance, zone 5 was associated with the upper shoulder, a highly convex position with a very high likelihood of severe annual erosion. Zone 4 represented areas of moderate convexity associated with the upper backslope. Zone 3 represented level to nearly level areas within the landscape. Zone 2 included areas of moderate concavity and deposition often associated with the footslope. Zone 1 represented areas of a high degree of concavity, such as wetland edges. Within each zone, geographic coordinates were randomly selected at initiation of the experiment. Soil cores to a depth of 15 cm were collected within 1 m of the coordinates in summer of 2010. The same coordinates were resampled in summer 2014. Each sample was composed of 4 cores that were composited, mixed, and subsampled for laboratory analysis.

2.3. Laboratory analysis and calculations

2.3.1. Baseline study

Surface samples (0–5 cm for uplands and 0–10 cm for wetlands) were analyzed for particulate organic matter (POM), soil organic matter (SOM), fluorescein diacetate hydrolysis (FDA), and water aggregate stability (WAS) to evaluate the effect of farming on soil quality. Particulate organic matter was further divided into coarse POM (cPOM) and fine POM (fPOM). Soil particle size was determined to a depth of 15 cm for uplands and 20 cm for wetlands. Samples from all depths were measured for bulk density (Mg m^{-3}), pH, C (g ∗ (100 g)$^{-1}$), N (g ∗ (100 g)$^{-1}$), and inorganic C (InC, g ∗ (100 g)$^{-1}$).

Cylindrical cores of known volume segmented by depth increment were oven-dried at 105 °C, weighed, and divided by core volume to determine bulk density (Grossman and Reinsch, 2002). After determining bulk density, samples were prepared for physical and chemical analysis by dry sieving the fraction less than 2-mm in size. Samples were also randomized prior to analysis. Total microbial activity was measured by the FDA method of Adam and Duncan (2001) as modified by Schumacher et al. (2015). Fluorescein diacetate hydrolysis measures the enzymatic activity of soil as fluorescein diacetate is cleaved by enzymes during hydrolysis, resulting in an end product of fluorescein measured with a spectrophotometer (Genesys 10 Series, Thermo Electron Corporation, Madison, WI). Particulate organic matter was measured by physical separation in a procedure simplified from Cambardella et al. (2001). The modifications made to this method were a smaller sample size (10 g instead of 30 g) and a shorter shaking time (≥ 2 h substituted for 18 h). Soil organic matter was measured by weight loss-on-ignition at 450 °C (Cambardella et al., 2001). Wet aggregate stability was measured by separating 1–2-mm aggregates by dry sieving soil and then stressing in water by wet sieving using a sieving machine (Kemper and Rosenau, 1986).

Soil particle size analysis was conducted using the sieve and pipette method (Gee and Bauder, 1986) for two transects at all upland landscape positions and the intermediate depth of the wetland. Subsamples of sieved soil were fine-ground with a mortar and pestle in preparation for chemical analysis. pH was measured using a 1:1 soil to water mixture (Thomas, 1996). Total C and TSN were determined by combustion on 2 g of soil using an Elementar Vario MAX CNS analyzer (Elementar, Germany). A standard soil was interspersed with experimental samples to determine coefficients of variation (CV) for C (2.3%) and N (1.0%; n = 74). Inorganic C was determined by the modified pressure-calcimeter method (Sherrod et al., 2002). The standard curve for the calcimeter prepared from $CaCO_3$ standards and a reference soil was highly linear with an r^2 = 0.999. The calcimeter had a CV of 4% at values of 1% InC (n = 19). Soil organic C was calculated by subtracting InC from total soil C. Coarse POM (0.5 to 2.0 mm) and fPOM (0.053 to 0.5 mm) were determined by the method described by Cambardella et al. (2001) and Gajda et al. (2001). We first dispersed approximately 30 g soil in sodium hexametaphosphate for 24 h. Dispersed soil was then agitated for 1 h before it was poured and rinsed through nested sieves with mesh sizes of 0.5 (cPOM) and 0.053 (fPOM) mm. Sieved material was placed in aluminum pans and subjected to the loss on ignition method at 450 °C for 4 h. Total POM was calculated as the sum of fPOM and cPOM. The mineral-associated organic matter fraction (MAOM) was calculated by subtracting POM from SOM. We also calculated the ratios POM:SOM and SOM:SOC.

We calculated SOC and TSN concentrations based on a soil mass (kg 100 kg^{-1}) and on a soil volume (kg m^{-3}) basis. Because bulk density differed between the sites, we also followed the procedure of Ellert et al. (2001) to calculate stocks of SOC and TSN (Mg ha^{-1}) on an equivalent mass basis. This procedure corrects for differences in bulk density across treatments by selecting a mass of soil (we used three different soil masses: 1.5, 3.0, and 4.5 Gg ha^{-1}) and determining the mass of SOC contained within it for each treatment.

Olson et al. (2014) measured SOC and TSN at different upland sites on the same cropland and prairie as our experiment (Fig. S1). To allow comparison of Olson et al.'s (2014) work and ours, we calculated mean loss of SOC (Mg ha^{-1}) from the prairie to cropland across summit, shoulder, backslope, and footslope positions to a depth of 30 cm from Olson et al.'s (2014) published data. Below 30 cm, differences in sampling intervals between our work and Olson et al. (2014) prevented direct comparison.

2.3.2. Restoration study

Archived samples from both sampling years (2010 and 2014) were analyzed in the laboratory at the same time. Total C and total N were determined as in the baseline study. Measurements of InC indicated no difference in 2010 and 2014 samples, therefore the change in C between 2010 and 2014 reflects a change in SOC. The change in C from 2010 to 2014 was calculated as

$$\Delta C\ (g\ g^{-1}) = C_{2014} - C_{2010}$$

Thus, positive values of ΔC indicate an increase in SOC over the 4-year period. The ΔN was calculated similarly.

2.4. Statistical analysis and plotting

2.4.1. Baseline study

To compare the two sites (cropland and prairie), all laboratory results and calculated values were analyzed using one-way analysis of variance. A separate comparison was made for each of the four upland landscape positions and three wetland elevations at each soil depth. We used the Kolmogorov-Smirnov test to test the residuals for normality. Of the 455 tests conducted, only 3 (< 1%) failed at $p < 0.05$. Thus, we concluded that the one-way analysis of variance was appropriate

In addition, key measurements and calculated values (SOC, TSN, WAS, bulk density, pH, POM, FDA, and SOM) were analyzed to determine whether there were differences among the four upland landscape positions within each site. Similar analyses were conducted for the three wetland elevations. These analyses were carried out using a one-way analysis of variance, with separate comparisons made for each depth. The Kolmogorov-Smirnov test indicated less than 1% of the residual distributions (1 of 136 tests) failed a test for normality, so we proceeded with the one-way analysis of variance. When a soil profile is missing a bulk density value at a particular depth, calculating soil mass for that depth is impossible and the profile cannot be used to evaluate soil C on an equivalent mass basis. Therefore, for the purpose of calculating soil mass of a profile, we filled in missing bulk density values. Ten wetland and 8 upland profiles were filled. Ruehlmann and Körschens (2009) and Johnston (2014) demonstrated the exponential relationship between SOC and bulk density in a range of soils, including wetlands. Likewise, we found that the relationship between SOC and bulk density for an individual wetland was described by a logistic relationship (r^2 of 0.50 to 0.61, depending upon the wetland) and we used these regressions to fill missing bulk density values. In uplands, the relationship between SOC and bulk density was better described by a linear function ($r^2 = 0.75$). We tested the sensitivity of profile equivalent mass SOC to the filled values by increasing or decreasing the filled values by 50%. This resulted in an average change of − 5 to + 4% in equivalent mass SOC and − 6 to + 5% in equivalent mass N for 4.5 Gg soil ha^{-1}, so we concluded that inaccuracies in estimating bulk density would have very little impact on results. After filling values, there were 32 valid upland and 39 valid wetland profiles for statistical analysis. The number of valid samples for other statistical analysis are presented in Table 2. In the discussion of our results, we assume that cropland soils were similar to prairie soils when they were first farmed, and that differences between cropland and prairie are a result of the 100 + years of differences in management.

Results were considered significant at a p-value of 0.05 but other p-levels (i.e., 0.01 and 0.001) are also reported. Statistical analyses were conducted using R version 3.2.2 (R Core Team, 2015). Plotting was done with the ggplot2 package (Wickham, 2009) version 1.0.1 in R. When plotted as point values, values were plotted at the mean of the depth range (e.g., the range 0 to 10 cm was plotted with a point at 5 cm).

2.4.2. Restoration study

We transformed the data by adding 1 to the SOC values and taking the natural log of the result to obtain homogeneous variances. Then, we conducted a one-way analysis of variance followed by F-protected mean separation ($\alpha = 0.05$). In addition, we ran a multiple linear regression with ΔC as the dependent variable to determine if differences in ΔC were associated with sampling zones (related to the TEP model), per se, or better defined by initial C level (C_{2010}). Independent variables were sampling zone, C_{2010}, and their interaction. Sampling zone was a categorical variable. Multiple linear regression was conducted with the lm function of base R. To estimate Mg C ha^{-1} gained after restoration began, we assumed a bulk density of 1.25 g cm^{-3}, which was the weighted average mean of the upland bulk densities in the cropland from 0 to 15 cm.

3. Results

3.1. Uplands

3.1.1. Measurements at the surface (0 to 5 cm)

Measures of POM, fPOM, cPOM, SOM, WAS, and POM:SOM (Figs. 4–6) at the surface (0 to 5 cm) were greater on the prairie than on the cropland at all four upland landscape positions (summit, shoulder, backslope, and footslope). Microbial activity (FDA) was greater on the prairie than the cropland at all landscape positions except the footslope (Fig. 4); MAOM was greater on the prairie than the cropland at the shoulder and backslope but not the summit or footslope (Fig. 5). The SOM:SOC ratio was greater on the cropland than the prairie at the summit and shoulder but not at other upland landscape positions (Fig. 5).

At the surface, the greatest difference between the two sites was in the concentration of POM, of which the cropland contained just 17–26% of the prairie, mostly due to reductions in fPOM. For WAS, POM, and FDA, neither the cropland nor the prairie differed across landscape positions (Figs. 4, 6). SOM differed across landscape positions at the cropland but not the prairie (Fig. 4) due to less loss of SOM at the cropland's footslope relative to its other landscape positions. Clay content was less on cropland than prairie at the shoulder and backslope but did not differ at other landscape positions (Table 3).

3.1.2. Measurements from 0 to 90 cm

The prairie contained greater concentrations of SOC and TSN than the cropland at one or more depths at all landscape positions (g ∗ [100 g soil]$^{-1}$), but differences were attenuated by depth (Fig. 7). Soil pH was greater on the cropland than on the prairie at three of five

Table 2
The number of valid samples used for statistical analysis. Abbreviations are: Water Aggregate Stability (WAS), Soil Organic Matter (SOM), Fluorescein Diacetate Hydrolysis (FDA), Particulate Organic Matter (POM), coarse POM (cPOM), fine POM (fPOM), Mineral Associated Organic Matter (MAOM), Total Soil Nitrogen (TSN), Carbon (C), Inorganic C (InC), and Soil Organic Carbon (SOC).

	Values measure or calculated at the surface only								
	WAS	SOM	FDA	POM	cPOM	fPOM	POM:SOM	MAOM	SOM:SOC
Upland	33	33	33	33	33	33	33	33	32
Wetland	42	34	34	31	31	31	30	30	34

	Values measured or calculated at multiple depths							
	pH	TSN	C	InC	C:N	Bulk density	SOC	Clay
Upland	162	162	162	162	162	173	162	16
Wetland	415	415	415	412	415	400	412	4

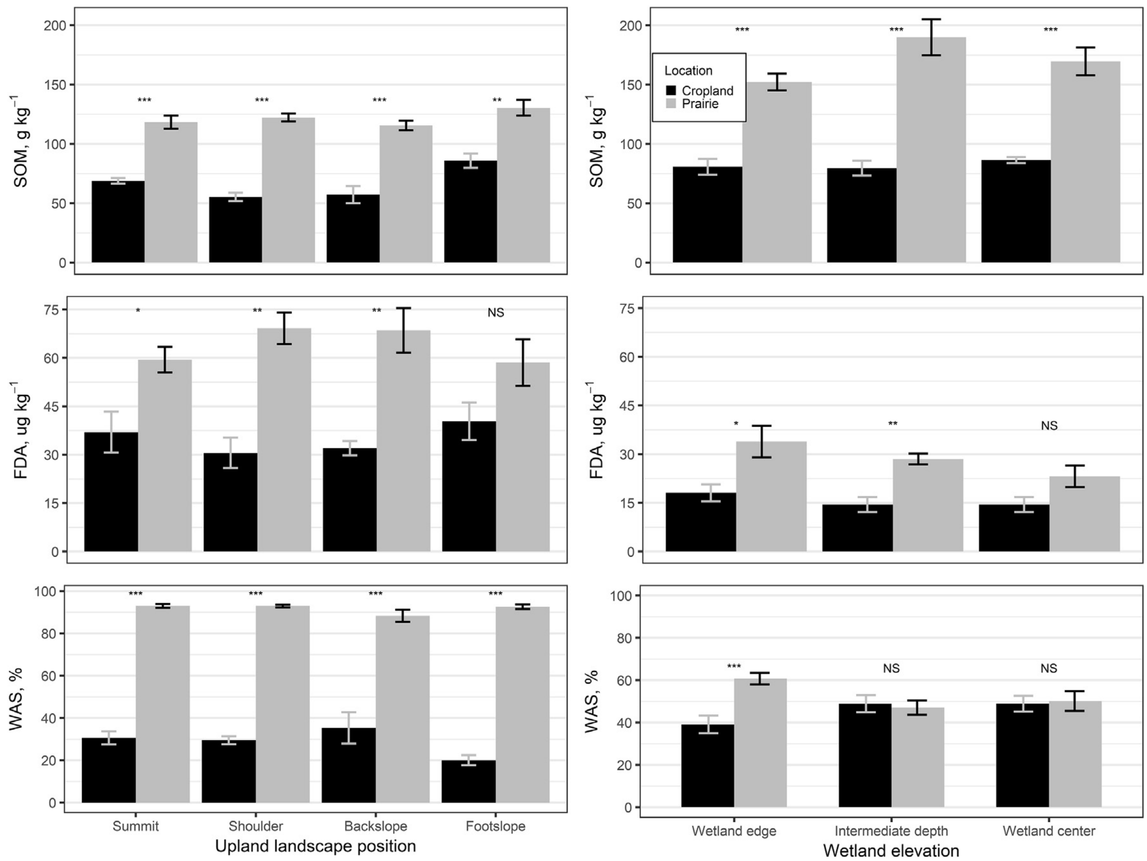

Fig. 4. Comparison of surface soils (0–5 cm) on cropland designated for restoration (black bars) and reference prairie (grey bars) at different landscape positions and elevations (44°02′ N, 96° 49′ W). Y-values are soil organic matter (SOM), microbial activity (FDA), and water aggregate stability (WAS) for the uplands (left) and wetlands (right). SOM differed between upland positions on the cropland ($p < 0.01$) but not on the prairie uplands ($p = 0.23$), prairie wetlands ($p = 0.07$), or cropland wetlands ($p = 0.64$). FDA did not differ among upland landscape positions on the cropland ($p = 0.57$) or prairie ($p = 0.45$), or in the wetlands of the cropland ($p = 0.49$) or prairie ($p = 0.28$). WAS did not differ among upland positions on the cropland ($p = 0.13$) or prairie ($p = 0.18$), nor did it differ among positions of the cropland wetlands ($p = 0.16$). WAS differed among prairie wetland elevations ($p = 0.05$). Error bars show the standard error of the mean. Asterisks indicate statistical difference between cropland and prairie at a given landscape position or wetland elevation. Levels of significance are $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***), or NS for $p > 0.05$. Soil classifications were: summit, Egan (Udic Haplustolls); shoulder, Ethan (Typic Calciustolls); backslope, Wentworth (Udic Haplustolls); footslope, Trent (Pachic Haplustolls); wetlands, Worthing (Vertic Argiaquolls).

depths (5–15 cm, 30–60 cm, and 60–90 cm) at the footslope position, but little difference was found at other landscape positions (Fig. S2). Bulk density was greater at the cropland than the prairie to a depth of 15 or 30 cm, depending upon landscape position (Table 4). Mean InC values were 0.5 g $*$ (100 g soil)$^{-1}$ and 23 g $*$ (100 g C)$^{-1}$ in uplands (Table S1).

When comparing one landscape position to another, SOC concentrations based on a SOC mass to soil volume ratio (kg m^{-3}) varied more across landscape positions on the cropland than on the prairie, with the range of maximum to minimum values on the cropland up to 5 times greater than on the prairie (Fig. 8). Statistical tests confirmed the difference among landscape positions at all depths in the cropland and from 30 to 60 and 60–90 cm on the prairie (Fig. 8).

Like SOC, the range of TSN concentrations based on soil volume across landscape positions was larger on the cropland than on the prairie, except at the greatest depth (Fig. S3). For both cropland and prairie, 2 of the 5 depths had TSN values that differed across landscape position.

For equivalent soil volumes, SOC (kg m^{-3}) differed between cropland and prairie at the higher elevations (summit and shoulder), but there were fewer differences at the backslope and no differences at the footslope (Fig. 8). When SOC stocks were measured on an equivalent soil mass basis (Mg ha^{-1} for a constant soil mass) to account for differences in bulk density, the greatest differences in SOC stocks were found in the summit and shoulder positions (Fig. 9). Fewer differences in SOC stocks were found in the backslope and footslope positions, with no differences at these positions for the highest equivalent soil mass (4.5 Gg ha^{-1}), which corresponded to an average soil depth of 36 cm in the cropland and 41 cm in the prairie. For an equivalent mass of 4.5 Gg ha^{-1}, losses by landscape position were as follows, with p-values comparing cropland and prairie stocks: summit (46 Mg ha^{-1}; $p < 0.001$), shoulder (63 Mg ha^{-1}; $p < 0.001$), backslope (34 Mg ha^{-1}; $p = 0.10$), and footslope (22 Mg ha^{-1}; $p = 0.22$; Fig. 9). For TSN stocks, cropland and prairie differed at the summit and shoulder for all equivalent masses, but differed only for 1.5 Gg ha^{-1} soil at the footslope and never differed at the backslope (Fig. 9).

3.2. Wetlands

3.2.1. Measurements at the surface (0–10 cm)

Measures of SOM, POM, and MAOM were greater in the surface soils (0–10 cm) of the prairie than the cropland at all wetland elevations (Figs. 4–6). Wetland soils in cropland had lost about half of their SOM, but 65–84% of their POM, mostly due to losses of fPOM (Fig. 6). Both FDA and WAS were greater for the prairie than the cropland at the wetland edge, but only FDA was different at the intermediate depth, and neither measure differed at the wetland center (Fig. 4). The SOM:SOC ratio was greater in the cropland than the prairie at all wetland elevations. Clay content did not differ between the cropland and prairie (Table 3). In both the cropland and prairie, POM differed among wetland elevations (Fig. 6). Water aggregate stability differed among wetland elevations on the prairie but not on the cropland

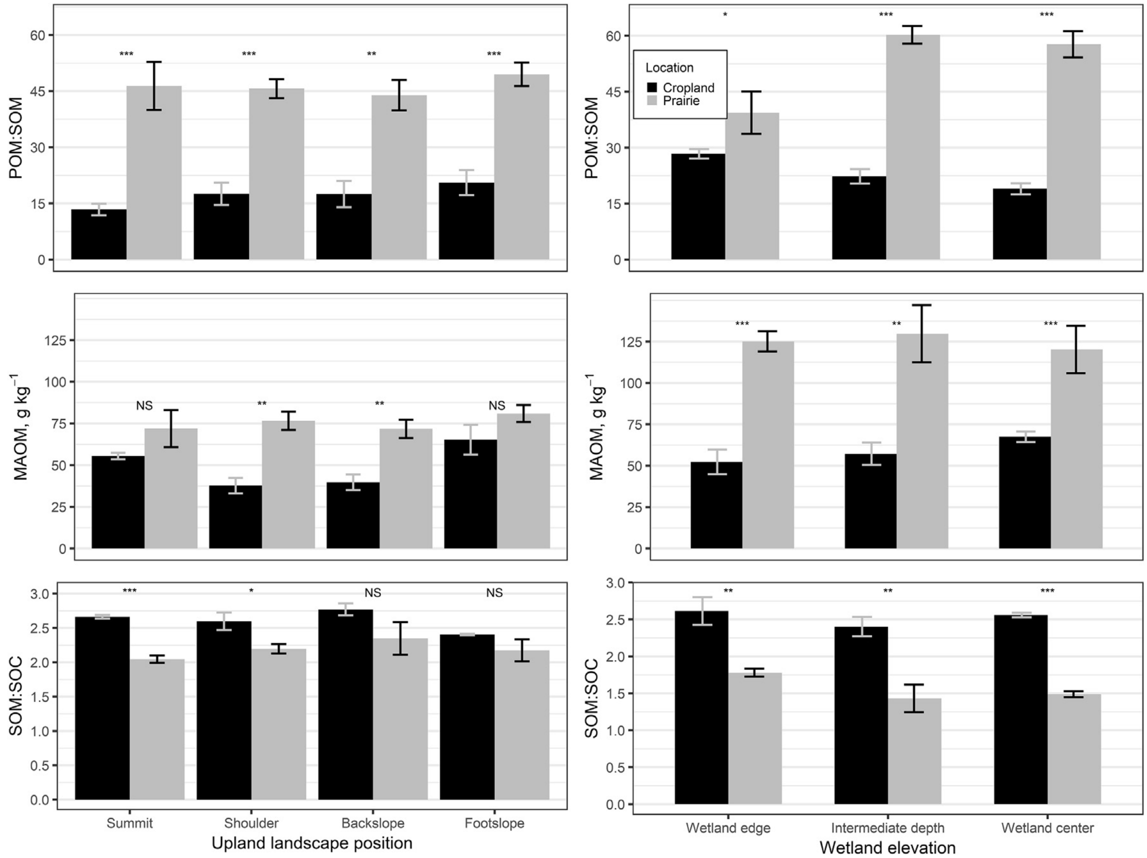

Fig. 5. Comparison of surface soils (0–5 cm) on cropland designated for restoration (black bars) and reference prairie (grey bars; 44°02′ N, 96° 49′ W) at different landscape positions and elevations (44°02′ N, 96° 49′ W). Y-values are the ratio of particulate organic matter to soil organic matter (POM:SOM), mineral associated organic matter (MAOM), and the ratio of SOM to soil organic C (SOM:SOC) for the uplands (left) and wetlands (right). Error bars show the standard error of the mean. Asterisks indicate statistical difference between cropland and prairie at a given landscape position or wetland elevation. Levels of significance are $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***), or NS for $p > 0.05$. Soil classifications were: summit, Egan (Udic Haplustolls); shoulder, Ethan (Typic Calciustolls); backslope, Wentworth (Udic Haplustolls); footslope, Trent (Pachic Haplustolls); wetlands, Worthing (Vertic Argiaquolls).

(Fig. 4). Neither FDA nor SOM differed among wetland elevations within a site (Fig. 4).

3.2.2. Measurements from 0 to 100 cm

For samples taken throughout the soil profile, only one of 30 position × depth combinations differed for pH between cropland and prairie (Fig. S2). Bulk density of cropland soils was greater than prairie soils at most depths within the wetland, regardless of elevation within the wetland (Table 4). As in the uplands, wetland surface soils in the cropland had lower concentrations (g ∗ [100 g]$^{-1}$) of SOC and TSN than prairie soils, but the effect disappeared with depth (Fig. 7). In both wetlands and uplands, the cropland's lesser concentration of SOC and TSN near the soil surface (to ~40 cm, depending on landscape position) but not at greater depths resulted in a vertical homogenization of SOC and TSN (Fig. 7). However, unlike the uplands, SOC across wetland elevations was not made more heterogeneous by farming (Fig. 8). That is to say, the range of wetland SOC values across elevations were generally similar in the cropland and prairie, and p-values comparing elevations within a site were mostly not significant. On a soil volume (kg m^{-3}) basis, the statistical differences in SOC and TSN concentrations between cropland and prairie nearly disappeared (Fig. 8; S3). When using the equivalent mass basis (1.5 Gg soil ha^{-1}) to correct for differences in bulk density, wetland soils in cropland lost SOC and TSN relative to the prairie (Fig. 9), but cropland and prairie did not differ when larger masses (3.0 or 4.5 Gg soil ha^{-1}) of soil were used for comparison. Although not statistically significant at 4.5 Gg ha^{-1}, SOC stocks in wetlands were numerically greater in the prairie than on the cropland at all positions, with differences between cropland and prairie being: wetland edge (31 Mg ha^{-1}; $p = 0.35$), intermediate wetland depth (27 Mg ha^{-1}; $p = 0.33$), and wetland center (30 Mg ha^{-1}; $p = 0.30$; Fig. 9). Mean InC values were 0.2 g ∗ (100 g soil)$^{-1}$ and 13 g ∗ (100 g C)$^{-1}$ in wetlands (Table S1).

3.3. Restoration study

In the restoration study, we found that ΔC to 15-cm depth during restoration and rehabilitation (2010–2014) differed by sampling zone ($p < 0.001$; Table 5). Multiple regression ($r^2 = 0.48$) indicated a highly significant effect of initial C (C_{2010}) on ΔC ($p < 0.001$; Table 5) and a trend on the effect of zone ($p = 0.07$), but no interactive effect of zone by initial C ($p = 0.79$). Sampling zones 1–5 represented different portions of the cropland (5%, 22%, 49%, 17%, and 7%, respectively). Taking these proportions into account, the net gain in C across the cropland from 2010 to 2014 was 0.08 Mg C ha^{-1} (Fig. 10).

4. Discussion

4.1. Loss and movement of SOC due to a century of farming uplands and wetlands

There is strong evidence of a decrease in SOC concentration (g ∗ [100 g]$^{-1}$) to at least 15 cm of the cropland relative to the prairie (Fig. 7). The loss of SOC occurred in both uplands and wetlands. However, because of differences in bulk densities between cropland and prairie (Table 4), equivalent volumes of soil contained more soil mass in the cropland than the prairie and the differences in SOC on this basis

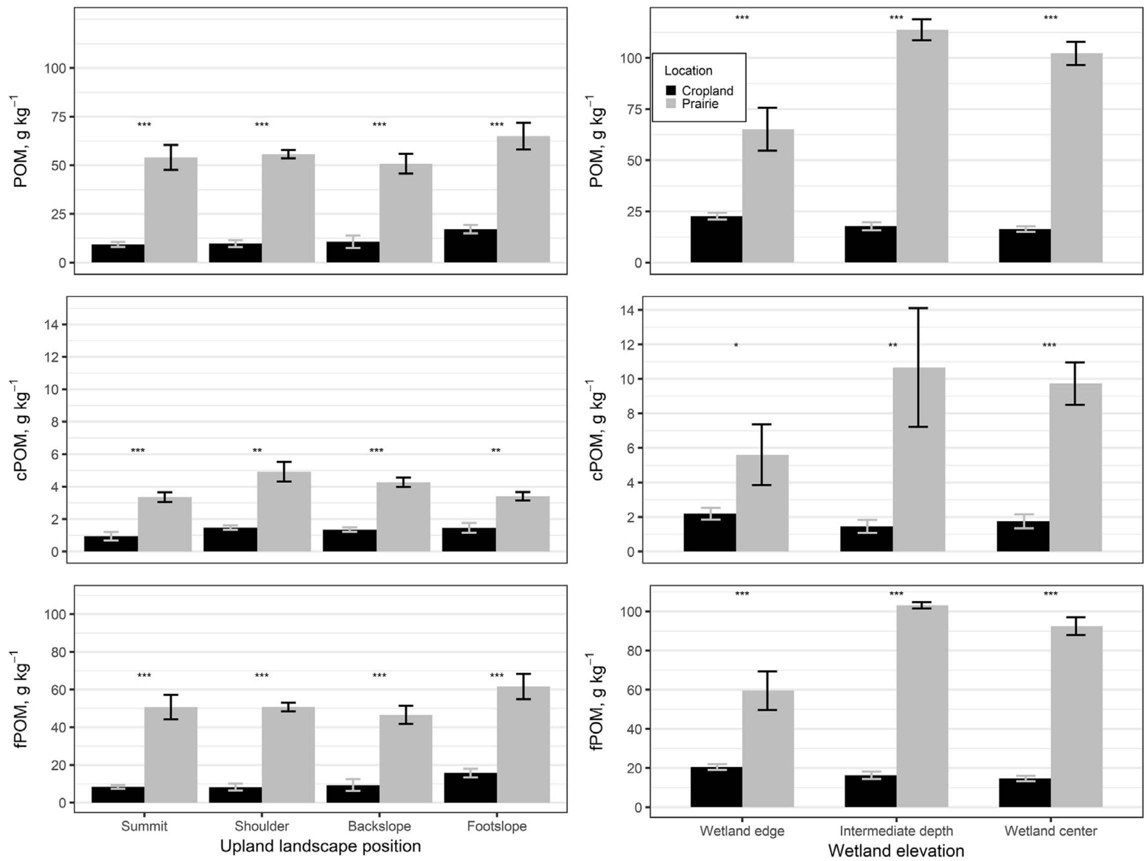

Fig. 6. Comparison of surface soils (0–5 cm) on cropland designated for restoration (black bars) and reference prairie (grey bars; 44°02′ N, 96° 49′ W) at different landscape positions or wetland elevations. Y-values are total particulate organic matter (POM), coarse POM (cPOM), and fine POM (fPOM) for the uplands (left) and wetlands (right). POM did not differ among upland positions on the cropland ($p = 0.07$) or the prairie uplands ($p = 0.33$), but differed among elevations in prairie wetlands ($p = 0.01$) and cropland wetlands ($p = 0.03$). Error bars show the standard error of the mean. Asterisks indicate statistical difference between cropland and prairie at a given landscape position or wetland elevation. Levels of significance are $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***). Soil classifications were: summit, Egan (Udic Haplustolls); shoulder, Ethan (Typic Calciustolls); backslope, Wentworth (Udic Haplustolls); footslope, Trent (Pachic Haplustolls); wetlands, Worthing (Vertic Argiaquolls).

(kg m^{-3}) are less apparent and less likely to be statistically significant (Fig. 8). Even so, a dramatic change in SOC (kg m^{-3}) to a depth of 30 cm is apparent in the cropped uplands, where sites of soil loss (summit, shoulder, and backslope) have less SOC than the footslope, a site of soil deposition. Others have found similar farming-induced losses of SOC and lateral transfers of SOC in upland positions (Slobodian et al., 2002; Pennock, 2003; Bedard-Haughn et al., 2006; Papiernik et al., 2007; Berhe et al., 2008; Guzman and Al-Kaisi, 2010; Olson et al., 2014; Chirinda et al., 2014; Rejman et al., 2014; Wiaux et al., 2014; Zhang et al., 2015; Szalai et al., 2016).

Whereas farming increased the heterogeneity of lateral SOC distribution, farming homogenized the vertical distribution of SOC in the uplands (Fig. 7). That is to say, farming lessened the concentration of SOC near the soil surface, giving surface soils and deeper soils similar SOC concentrations. In contrast, surface soils in the prairie were stratified and enriched with SOC relative to the subsoil.

Olson et al. (2014) measured SOC and TSN at different upland sites on the same cropland and prairie as our experiment. Mean loss of SOC mass (Mg ha^{-1}) for an equivalent volume of soil from the prairie to cropland across upland landscape positions to a depth of 30 cm was 22% in their study and 28% in ours (Fig. 8). However, because farming significantly compacted the soil (Table 4), there is more soil mass in the 0–30 cm depth interval in the cropland than in the prairie. Thus, using an equivalent soil volume basis underestimated the loss of SOC relative to equivalent soil mass comparisons, which we found to average 34% (range: 15 to 53%) across upland landscape positions for 4.5 Gg ha^{-1} soil (Fig. 9). The significant differences in SOC and TSN between cropland and prairie that were apparent with a small equivalent mass (1.5 Gg ha^{-1}) disappeared from the wetlands and upland landscape positions, except for the summit and shoulder, when using a larger equivalent mass (4.5 Gg ha^{-1}). This happened for two reasons: 1) as deeper soils were added to increase the equivalent mass, the difference

Table 3
Mean clay content (g * [100 g^{-1}]) of the cropland and reference prairie sites (44°02′ N, 96° 49′ W) for upland landscape positions (to 15 cm depth) and the intermediate depth of wetlands (to 20 cm depth). Means are given with the standard error of the mean in parentheses. *p*-values indicate probability of a difference between cropland and prairie for a given landscape position.

	Landscape positions and soil classification				
Site	Summit, Egan (Udic Haplustolls)	Shoulder, Ethan (Typic Calciustolls)	Backslope, Wentworth (Udic Haplustolls)	Footslope, Trent (Pachic Haplustolls)	Wetland intermediate depth, Worthing (Vertic Argiaquolls)
Cropland	29.6 ± 0.5	26.6 ± 0.0	21.8 ± 0.4	32.0 ± 1.5	34.5 ± 0.8
Prairie	30.4 ± 0.8	34.4 ± 0.3	33.2 ± 0.8	32.4 ± 0.2	34.4 ± 2.3
p-value	0.49	0.001	0.006	0.80	0.98

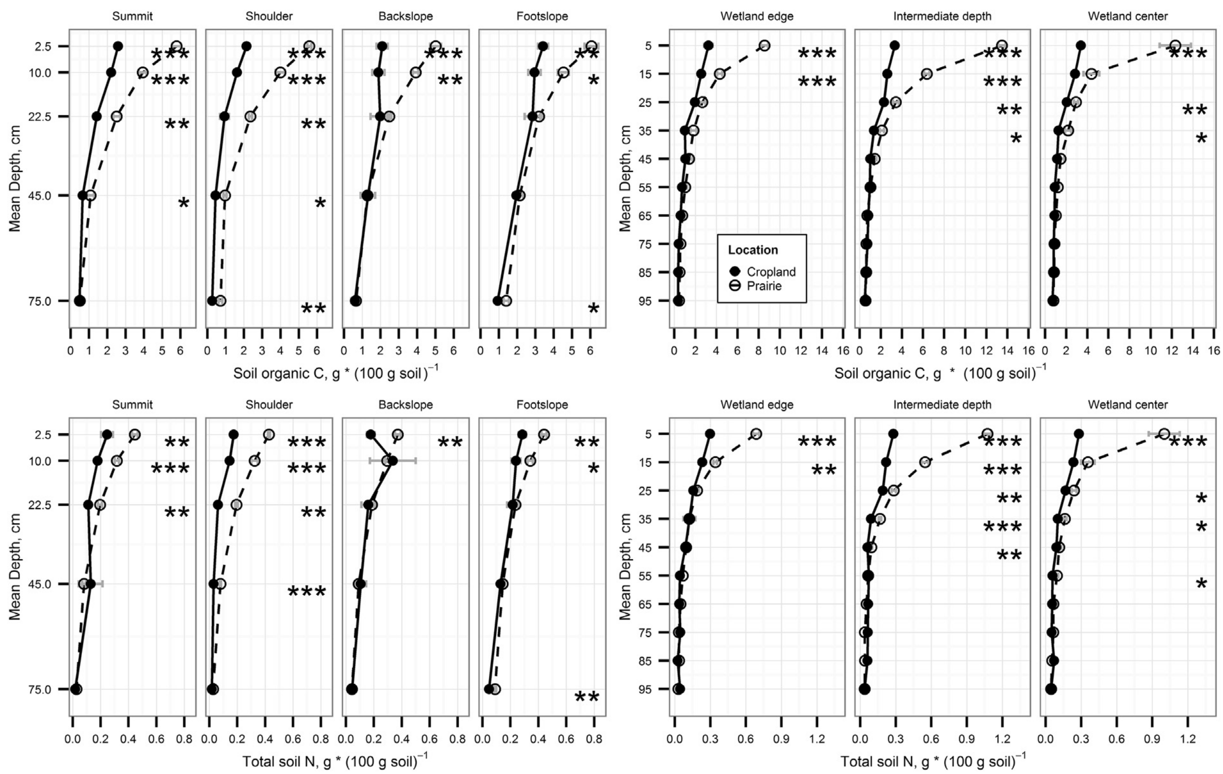

Fig. 7. Soil organic C and total soil N of soils on cropland designated for restoration (solid lines) and reference prairie (dashed lines; 44°02′ N, 96° 49′ W) at different landscape positions in uplands (left) and wetlands (right). Y-axes differ for each graph. Error bars show the standard error of the mean but are typically so small that they are obscured by the plotting points. Asterisks indicate statistical difference between cropland and prairie at a given landscape position or wetland elevation and depth. Levels of significance are $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***). Soil classifications were: summit, Egan (Udic Haplustolls); shoulder, Ethan (Typic Calciustolls); backslope, Wentworth (Udic Haplustolls); footslope, Trent (Pachic Haplustolls); wetlands, Worthing (Vertic Argiaquolls).

Table 4

Bulk density (Mg m^{-3}) of soils on cropland designated for restoration and a reference prairie (44°02′ N, 96° 49′ W) at different upland landscape positions wetland elevations. Means are given with standard error of the mean in parentheses. Asterisks indicate statistical difference between cropland and prairie at a given landscape position and depth. Levels of significance are $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***).

	Upland							
	Summit, Egan (Udic Haplustolls)		Shoulder, Ethan (Typic Calciustolls)		Backslope, Wentworth (Udic Haplustolls)		Footslope, Trent (Pachic Haplustolls)	
Depth, cm	Prairie	Cropland	Prairie	Cropland	Prairie	Cropland	Prairie	Cropland
0–5	0.71*** (0.01)	1.04*** (0.03)	0.83*** (0.02)	1.15*** (0.04)	0.81*** (0.01)	1.15*** (0.06)	0.73*** (0.02)	1.24*** (0.04)
5–15	1.00*** (0.01)	1.23*** (0.02)	1.02*** (0.02)	1.30*** (0.05)	0.94*** (0.02)	1.37*** (0.04)	0.89*** (0.03)	1.31*** (0.01)
15–30	1.18 (0.04)	1.21 (0.04)	1.22* (0.02)	1.32* (0.04)	1.21 (0.05)	1.35 (0.06)	1.04** (0.02)	1.25** (0.04)
30–60	1.29 (0.06)	1.25 (0.03)	1.38 (0.02)	1.34 (0.04)	1.28 (0.06)	1.27 (0.06)	1.21 (0.02)	1.22 (0.04)
60–90	1.41 (0.12)	1.39 (0.04)	1.54 (0.04)	1.62 (0.05)	1.46 (0.06)	1.34 (0.05)	1.32* (0.01)	1.57* (0.05)

	Wetland					
	Wetland edge, Worthing (Vertic Argiaquolls)		Intermediate depth, Worthing (Vertic Argiaquolls)		Wetland center, Worthing (Vertic Argiaquolls)	
Depth, cm	Prairie	Cropland	Prairie	Cropland	Prairie	Cropland
0–10	0.51** (0.11)	0.97** (0.10)	0.30*** (0.06)	1.02*** (0.04)	0.32*** (0.10)	1.04*** (0.02)
10–20	0.73* (0.18)	1.22* (0.04)	0.60*** (0.12)	1.22*** (0.05)	0.69** (0.13)	1.21** (0.04)
20–30	0.84* (0.18)	1.34* (0.03)	0.80** (0.14)	1.26** (0.06)	0.80** (0.18)	1.33** (0.04)
30–40	0.95* (0.21)	1.44* (0.07)	1.04 (0.17)	1.38 (0.06)	0.86** (0.16)	1.37** (0.05)
40–50	0.88** (0.17)	1.46** (0.04)	1.05 (0.17)	1.36 (0.04)	0.95* (0.21)	1.47* (0.08)
50–60	1.06* (0.19)	1.49* (0.04)	1.02 (0.21)	1.46 (0.08)	1.00* (0.20)	1.46* (0.07)
60–70	0.89* (0.23)	1.51* (0.04)	1.19 (0.21)	1.55 (0.11)	1.04* (0.19)	1.50* (0.06)
70–80	1.07 (0.17)	1.32 (0.17)	1.10 (0.21)	1.48 (0.06)	0.85** (0.13)	1.47** (0.11)
80–90	1.10** (0.14)	1.59** (0.05)	0.76** (0.18)	1.53** (0.08)	1.05 (0.22)	1.47 (0.08)
90–100	1.32 (0.25)	1.65 (0.06)	1.09 (0.21)	1.36 (0.13)	1.30 (0.22)	1.57 (0.11)

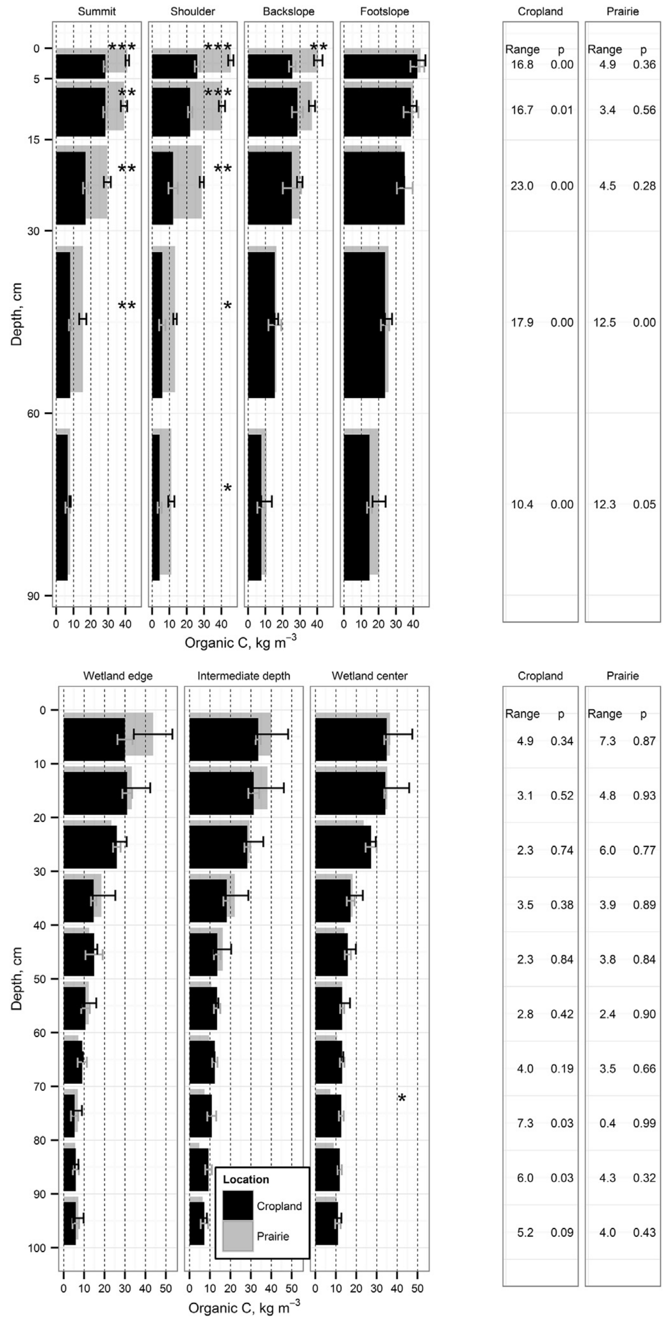

Fig. 8. Soil organic C (SOC; kg m^{-3}) on cropland designated for restoration (black) and reference prairie (grey; 44°02′ N, 96° 49′ W) at different landscape positions in uplands (top) and wetlands (bottom). In each figure, the y-axis is proportional to depth; thus, the area of each bar is proportional to the quantity of SOC found at that depth increment. The table at the right displays the range of values across landscape positions for cropland and prairie at each depth, and the *p*-value for comparing mean values of landscape positions on the cropland or prairie. Error bars show the standard error of the mean. Asterisks indicate statistical difference between cropland and prairie at a given landscape position or wetland elevation and depth. Levels of significance are $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***). Soil classifications were: summit, Egan (Udic Haplustolls); shoulder, Ethan (Typic Calciustolls); backslope, Wentworth (Udic Haplustolls); footslope, Trent (Pachic Haplustolls); wetlands, Worthing (Vertic Argiaquolls).

in SOC and TSN concentration of those soils was less than that of surface soils (Fig. 7) and; 2) the variability of the data increased. Variability was highest for bulk density of prairie wetlands. Thus, our second hypothesis was not well supported, as some landscape positions lost SOC stocks only when considering the lowest equivalent mass, 1.5 Gg ha^{-1}. Despite depositional landscape positions lacking statistical significance for 4.5 Gg ha^{-1} of soil, all contained numerically greater SOC stocks in the prairie than the cropland and a relatively narrow range of differences between cropland and prairie (loss of 22 to 35 Mg SOC ha^{-1}).

Several processes contributed to the loss of SOC in wetlands. When a dry year or series of years lower the water table, it is possible to farm through wetlands, especially the temporary wetlands which have a shorter hydroperiod. Once drained, tillage of wetlands becomes more frequent, resulting in increased biodegradation of SOM (Balesdent et al., 2000). Crops grown in wetlands often fail under conditions where the native vegetation thrives (Zilverberg et al., 2014b, 2015; von Haden and Dornbush, 2016) due to flooding after planting or because planting is prevented by wet soils, resulting in less organic matter input. Furthermore, drainage ditches installed in cultivated wetlands likely lowered the water table (Werner et al., 2016), shortened the hydroperiod (Werner et al., 2016), and increased the overland connectivity to adjacent wetlands and streams. Anaerobic conditions caused by a high water table can preserve SOC (Linn and Doran, 1984; Olson et al., 2013), while drainage increases the SOC oxidation rate (Everett, 1983). Because the Prairie Pothole Region has limited surface hydrologic connectivity (Richardson et al., 1994; Leibowitz and Liebowitz and Vining, 2003), export of C-enriched mineral from footslopes and wetlands would be quite minor within an intact wetland system. The increased connectivity of ditched wetlands in our cropland may have increased the export of C-enriched material from our sampling area into drainage ditches, other nearby wetlands, and a nearby stream. In addition, soil from upslope contained a lower concentration of SOC (g ∗ [100 g soil]$^{-1}$; Fig. 7) and may have diluted the SOC concentration at deposition sites, a process also described by De Alba et al. (2004).

The fate of SOC during transport after detachment is dependent on mechanisms of SOC stabilization and decomposition (Kirkels et al., 2014; Doetterl et al., 2016). The duration of exposure during transport from the eroding position to the deposition position has potential to affect decomposition and stabilization rates of SOC (Berhe et al., 2012; Doetterl et al., 2015; Hu and Kuhn, 2016). In our landscape, where both tillage and water erosion are significant processes, there is a mixture of long duration transport events associated with tillage erosion and short duration transport events associated with water erosion. Additionally, water erosion events are selective toward the finer clay and labile carbon fractions (Hu et al., 2016) which could increase the proportion of SOC loss relative to soil loss. In contrast, tillage erosion is nonselective (Kirkels et al., 2014). Due to mixed erosion processes the rate of decomposition during transport and subsequent deposition is likely to be variable and not easily predicted in a Prairie Pothole landscape.

The global implications of lateral SOC transfers on SOC storage in an eroding landscape are comprehensively reviewed in Doetterl et al. (2016) and Kirkels et al. (2014). Because we do not know the ultimate fate of SOC eroded on our farm, we cannot definitely determine a historic C balance within our landscape. Besides various historic decomposition processes that may have occurred, an undetermined amount of eroded SOC is likely to have been lost from deposition sites via artificially constructed drainage ditches. Rare occurrences of extremely wet conditions also provide aboveground connectivity of prairie wetlands and could have transported sediment out of our sampling area. Nevertheless, it is clear that a century of farming depleted upland SOC stocks.

4.2. Additional impacts of farming

Our results indicated that not only was there a loss of SOC and TSN mass, there was also a change in SOM composition. Organic C was a smaller portion of the SOM fraction on the cropland relative to the prairie, indicating the cropland's SOM had undergone more oxidation (Fig. 5). In addition, the prairie contained much more POM and a higher POM:SOM ratio. The proportion of “fresh” or “active” organic matter residue (e.g., POM) may be more important for soil quality than

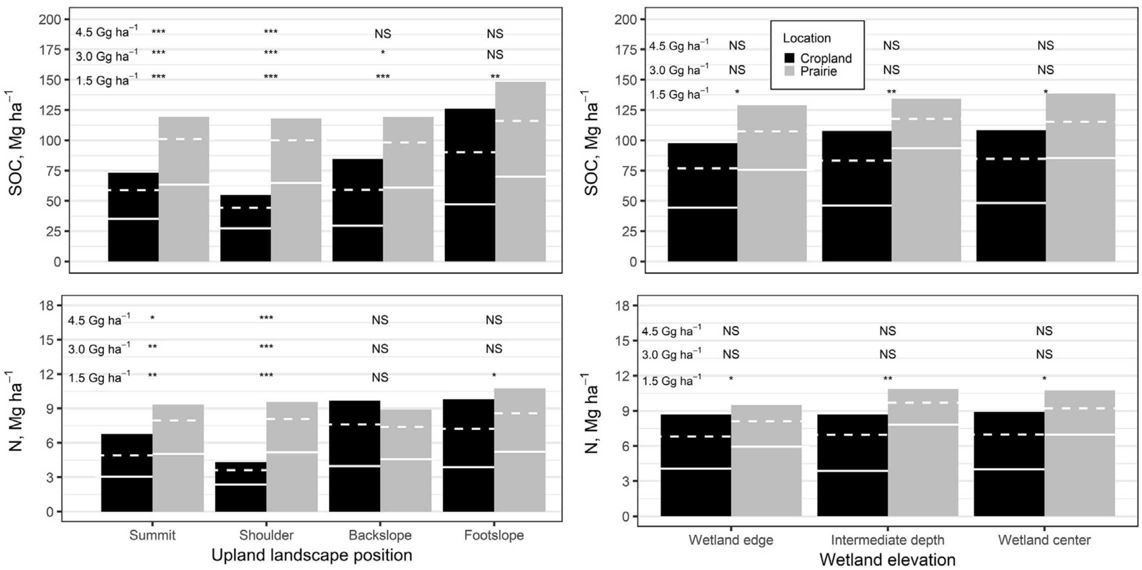

Fig. 9. Soil organic C and TSN from cropland and nearby reference prairie (44°02′ N, 96° 49′ W), calculated on an equivalent mass basis. Calculations were made using three equivalent soil masses: 1) 1.5 Gg soil ha^{-1} (solid horizontal lines; mean depth in cm: farmed uplands, 12; prairie uplands, 16; farmed wetlands, 14; prairie wetlands, 29), 2) 3.0 Gg soil ha^{-1} (dashed horizontal lines; mean depth in cm: farmed uplands, 24; prairie uplands, 29; farmed wetlands, 26; prairie wetlands, 47), 3) 4.5 Gg soil ha^{-1} (bars; mean depth in cm: farmed uplands, 36; prairie uplands, 41; farmed wetlands, 37; prairie wetlands, 63). Uplands are on the left and wetlands on the right. Statistical differences between cropland and prairie are indicated above the bars for each landscape position or wetland elevation and equivalent soil mass used. Levels of significance are $p < 0.05$ (*), $p < 0.01$ (**), and $p < 0.001$ (***). Soil classifications were: summit, Egan (Udic Haplustolls); shoulder, Ethan (Typic Calciustolls); backslope, Wentworth (Udic Haplustolls); footslope, Trent (Pachic Haplustolls); wetlands, Worthing (Vertic Argiaquolls).

Table 5
Mean initial C (C_{2010}) and mean change in C (ΔC) from 2010 to 2014 for the 0–15 cm depth on cropland undergoing restoration (44°02′ N, 96° 49′ W), by sampling zone. Before analysis, the number 1 was added to all ΔC values and they were then log-transformed. An F-test on transformed values was significant ($p < 0.001$) and mean separation was conducted at $p = 0.05$. Sampling zones were based on modeled historic tillage erosion rates. Zone 1 (> 24 Mg ha^{-1} yr^{-1}, depressions); Zone 2 (6 to 24 Mg ha^{-1} yr^{-1}, footslopes); Zone 3 (6 to −8 Mg ha^{-1} yr^{-1}, nearly level areas); Zone 4 (−8 to −20 Mg ha^{-1} yr^{-1}, upper backslopes); Zone 5 (< −20 Mg ha^{-1} yr^{-1}, upper shoulder positions).

	Sampling zone				
	1	2	3	4	5
ΔC, transformed values	−0.142a	−0.101a	0.008ab	0.054bc	0.175c
ΔC, original values (g · [100 g]$^{-1}$)	−0.124	−0.093	0.013	0.063	0.213
C_{2010} (g · [100 g]$^{-1}$)	2.83	3.01	2.70	2.13	1.88

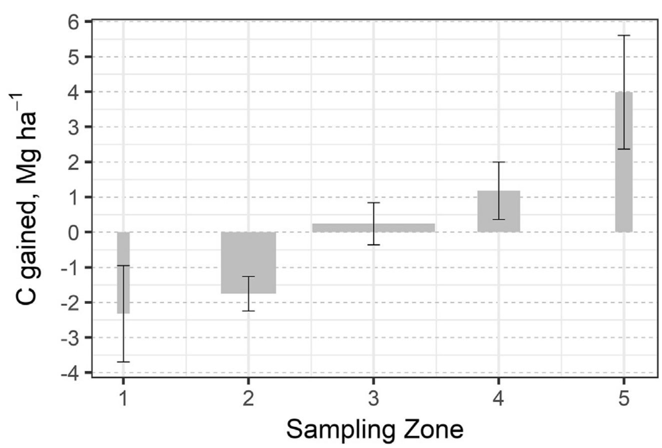

Fig. 10. Change in soil C (Mg ha^{-1}) from 2010 to 2014 (during restoration and rehabilitation; Restoration study) for five sampling zones in the cropland (44°02′ N, 96° 49′ W), to a depth of 15 cm. Zones ranged from 1 (extreme deposition due to tillage erosion) to 5 (extreme soil loss due to tillage). The width of bars indicates the fraction of the cropland represented by each sampling zone. Fractions for zones 1 through 5 were 5%, 22%, 49%, 17%, and 7%, respectively. Across all zones, net gain for the cropland was 0.08 Mg C ha^{-1}. Bulk density was assumed to be 1.25 Mg m^{-3} (Table 4). Error bars show the standard error of the mean. Soil classifications were: summit, Egan (Udic Haplustolls); shoulder, Ethan (Typic Calciustolls); backslope, Wentworth (Udic Haplustolls); footslope, Trent (Pachic Haplustolls); wetlands, Worthing (Vertic Argiaquolls).

the quantity of SOC (Loveland and Webb, 2003). Because POM is typically composed of relatively young SOC compared to the entire SOM fraction, this also suggests the prairie contained younger SOC than the cropland. Nevertheless, significant differences in MAOM between cropland and prairie for most landscape positions and wetland elevations (Fig. 5) indicate that differences in SOM and SOC between cropland and prairie are not due solely to the addition of new SOC, but are also the result of losing older SOM from the cropland.

Because POM is an important source of energy for the soil ecosystem, it is no surprise that microbial activity (as measured by FDA) on the cropland was barely half that of the prairie (Fig. 4). The loss of POM and microbial activity is detrimental for soil structure and nutrient availability. Another indication of the deterioration of the cropland's soil was its decrease in WAS in the uplands and the wetland edge. Wet aggregate stability is relatively sensitive to changes in management and was found to improve after just 2–3 years after re-establishing perennial grass cover in an experiment located on the same cropland (Schumacher, 2011; Zilverberg et al., 2015). These many differences in surface soil properties provided strong support for our first hypothesis, that cultivated fields were degraded relative to virgin prairie of similar topography and soils.

Both uplands and wetlands were subject to the use of heavy machinery and consequent soil compaction. In uplands, only surface bulk densities were elevated in cropland relative to the prairie, whereas both surface and subsoil bulk densities were elevated in the wetlands (Table 4). Cultivated wetlands are especially vulnerable to soil compaction, particularly subsoil compaction. This is because field operations are generally conducted when most of the field is at a suitable moisture content for tillage or harvest operations, but cultivated wetlands, even when drained, often have higher than optimal water content for wheel traffic and tillage. Transmission of stress from wheel loads to the subsoil is particularly sensitive to soil water content (Lamandé and Schjønning, 2011). Additionally, tire inflation pressures and axle loads are typically matched for the drier portions of the field, increasing the probability of subsoil compaction.

Drainage of wetlands increases their organic matter decomposition rate (Everett, 1983) and the loss of SOC increases bulk density (Everett, 1983; Ewing and Vepraskas, 2006; Fenstermacher et al., 2016). In the Prairie Pothole Region, wetlands surrounded by cultivated land also receive greater amounts of sediment than wetlands surrounded by grassland (Martin and Hartman, 1987). The clay content of sediment deposited in wetlands can increase bulk density of farmed wetlands (Martin and Hartman, 1987) but we did not find evidence of increased clay content (Table 3). Many bulk density samples in the cropped wetland were greater than 1.44 Mg m^{-3}, which was the critical bulk density for wheat in a study on a silty clay loam similar in texture and soil type as in our study (Wilson et al., 2013). At the critical bulk density, mechanical impedance and oxygen availability are both restrictive for root growth. Although critical bulk density can vary by species, this is an indication that bulk density of the cropped wetlands will restrict rooting for at least some species.

Changes in bulk density may also impact wetland hydrology. Increased surface bulk density in the uplands can enhance surface inflow to the wetlands, while increased subsoil bulk density in the wetlands can impede vertical inflow and outflow of groundwater. This effect on the vertical movement of water is particularly important for prairie potholes, where dominant hydrodynamics are vertical (Richardson and Richardson and Brinson, 2000).

4.3. Opportunities and challenges for rehabilitation and restoration

The ecological state-and-transition framework describes both reversible and nonreversible vegetation dynamics (Briske et al., 2005). A site can transition from one state to another when a structural threshold (e.g., caused by fire suppression) or a functional threshold (e.g., caused by soil erosion) is crossed (Briske et al., 2005). Serious ecosystem modification may be difficult or impossible to reverse; consequently, a site's vegetation may diverge from that of the reference site for an indefinite period of time (Briske et al., 2005). In the eroded state, although a complete restoration may not be possible, it could still be possible to rehabilitate a site so that it achieves an alternative but productive and stable state with repaired ecosystem function (Aronson et al., 1993). Nevertheless, an altered vegetation community may have implications for primary productivity, which in turn influences soil properties, including potential for SOC sequestration.

The cropped wetlands in our study may have crossed functional thresholds. Filling drainage ditches often fails to restore wetland hydrology (Vepraskas et al., 2005). High bulk densities, as observed in the cropped wetlands (Table 4), are difficult to reverse. This may be especially important in dry years, when critical bulk densities in the subsoil might prevent roots from reaching a low water table. Also, with drainage ditches filled but the subsoil compacted, the impeded flow to the water table may increase the hydroperiod relative to pre-cultivation conditions. A longer hydroperiod has implications for which species will grow in the wetland and the wetland's net primary productivity.

Despite these challenges, native species (e.g., prairie cordgrass) were successfully introduced to the cropped wetlands (Zilverberg et al., 2014b, 2015). Although subsoil compaction is difficult to reverse, soil compaction near the surface can be improved with time due to greater biological activity, increased organic matter inputs, and abiotic effects such as wetting-drying and freeze-thaw cycles (Hamza and Anderson, 2005). This is especially likely with a species like prairie cordgrass, which has an aggressive system of roots and rhizomes (Boe et al., 2009). Changes in wetland hydrology that increase deep or prolonged flooding could affect the long term viability of a species like prairie cordgrass which does well in wet soils that are not flooded for prolonged periods (Fraser and Kindscher, 2005). If harvest activities for seed and biomass take place and/or grazing is planned, they should be timed to avoid wet periods, else any reduction of soil compaction could easily be reversed (Hamza and Anderson, 2005).

In the cropped uplands, the loss of SOC, TSN, WAS, and microbial activity suggest that primary productivity would be lower after restoration than before cultivation occurred, at least for the short-term. However, because upland bulk density increased only in the soil surface and is unlikely to restrict root growth, there is reason to believe that these conditions could be reversed, albeit over an extended time frame. The best opportunity for recovery lies at the summit and footslope, where clay content did not change (Table 3). The loss of clay at the shoulder and backslope impacts soil nutrient and hydrological properties (e.g., cation exchange capacity, water holding capacity; Brady and Weil, 2008) and has the potential to decrease net primary productivity.

After conversion to native grass agriculture, C replacement was observed on the convex cropland landscape positions most susceptible to erosion (Fig. 10; Table 5). Prior to grassland conversion, dynamic C replacement was likely ongoing. Dynamic replacement occurs in eroding landscapes (Stallard, 1998; Harden et al., 1999) and consists of SOC losses being replaced through a variety of soil processes, including exposure of subsoils with less weathering history; exposure of reactive minerals, including clays with less C saturation; and a potential increase in chemical weathering rates (Doetterl et al., 2016). When erosion is stopped or minimized, as occurs in the conversion of cropland to grassland or the introduction of no-till practices, SOC accretion will continue. At eroded landscape positions, a new SOC steady state (production vs. decomposition of C) will be reached at the SOC saturation point (Six et al., 2002; Stewart et al., 2007; Stockmann et al., 2013). Landscape positions with SOC concentration furthest from the saturation point have the potential for the greatest rates and magnitude of SOC accretion, but accretion slows at all positions as SOC approaches the saturation limit. In southern Ontario, VandenBygaart (2016) showed that the SOC steady state depended on the clay concentration. A clay-SOC relationship has not been developed for the Prairie Pothole Region, but the loss of clay at the shoulder and backslope would likely limit the SOC saturation point relative to that of the reference prairie.

At a location near our study site, Riedell et al. (2011) found that 9 years after cropland was planted to perennial grasses, soil C accumulated at rates of 0.39 to 0.71 Mg ha^{-1} yr^{-1} in the top 15 cm. This was similar to accumulation rates at our sampling zones 4 and 5 over the course of four years (0.3 to 1.0 Mg ha^{-1} yr^{-1}; Fig. 10). In a study adjacent to Riedell et al. (2011), Pikul et al. (2001) found SOC had increased 0.07% eleven years after grass was planted into cropland, similar to the change in SOC after 4 years in our sampling zone 4. Although these studies took place on soils of similar genetic origin, they lacked slope and did not account for topographic changes. Based on carbon stocks associated with our landscape positions (Fig. 9) and assuming that initially ($\leq$ 6 years after grass seeding) the majority of SOC changes will be near the surface, the changes in soil carbon stocks for our study are within the range predicted from a summary of 68 studies across the world (see Table 1 and Fig. 14 in Minasny et al., 2017).

Contrary to our third hypothesis, soil C accumulation was not observed after tillage ceased and native perennials were planted at our sites of deposition (Table 5). Therefore, across our farm landscape, net C gain over 4 years was just 0.20% ($100 * g\,C * (g\,C)^{-1}$) in the top 15 cm—half that of the ‘4 per mille’ goal (Minasny et al., 2017). Because the rate of SOM oxidation likely slowed down, the most likely explanations for the lack of C accumulation at sites of deposition is that there were higher initial concentrations (Fig. 7) and stocks (Fig. 9) of SOC at depositional positions and the input of OM was less during the period of perennial plant establishment than during annual crop farming. Low OM input during establishment could occur because it takes years for the perennial grasses that were planted to reach their maximum potential productivity and for their root systems to reach full size (Weaver and Zink, 1946a; Zilverberg et al., 2014c, 2015). Moreover, perennial roots can survive across multiple growing seasons

(Weaver and Zink, 1946b). At the time of our second sampling, the roots and perennial organs of these plants were still young (≤ 4–6 years) and probably hadn't experienced maximum rates of turnover yet. Once mature, prairies maintain much larger root systems than annual crops, and therefore perennial prairie plants may contribute greater quantities of organic matter to soil than annual crops, even when aboveground biomass production of fertilized annual crops exceeds that of prairie (Dietzel et al., 2015; Jarchow et al., 2015).

Because nearly all land in the region is privately owned, recovering SOC and soil health by planting perennial species will only be viable if it is also profitable. The sale of C credits could make an important contribution to financial profitability. Our results emphasize the importance of landscape features and historic agricultural practice in establishing realistic baselines for SOC recovery. Recovery will take place at different rates depending upon historic land management and topography, and some landscape positions, such as cropped wetlands, shoulders, and backslopes, may have crossed ecological thresholds that will not support historic SOC levels.

If recovering SOC is an objective, establishment and management of species must be carefully considered. For instance, Ampleman et al. (2014) found that restorations including an abundance of forbs stored significantly more SOC than a restoration dominated by C4 grasses and characterized by more frequent burning. Hay harvests and grazing are likely uses of any perennial species established on former cropland. Timing and intensity of harvests and grazing must be considered to maintain native grass stand viability (Hickman et al., 2004; Mulkey et al., 2006; Smart et al., 2013). In addition, grazing may further redistribute C within the landscape, as animals choose preferred “camping” areas where disproportionately large quantities of excreta are deposited (Haynes and Williams, 1999).

5. Conclusions

A century of farming annual crops in the Prairie Pothole region of North America increased the heterogeneity of lateral SOC distribution across a farm, as the loss of SOC was greater at sites of soil loss than at sites of soil deposition. Simultaneously, farming homogenized the vertical distribution of SOC and total soil nitrogen in the uplands and wetlands by impoverishing SOC concentrations in surface soils, making them similar to soils found deeper in the profile. Eroded landscape positions of the farm lost more stock of SOC (on an equivalent soil mass basis) than depositional positions. At the soil surface, lower concentrations of SOC were associated with reductions in soil quality as measured by changes in composition of SOM (lower POM:SOM ratio), lower wet aggregate stability, and lower microbial activity in the soil surface.

Once tillage ceased and perennial vegetation was planted on the cropland, those soils that had previously experienced the greatest soil losses were soils that gained the most C in the subsequent four years. However, soils that lost less SOC stocks during a century of farming did not accumulate SOC after being planted to perennial vegetation, probably because they were nearer the saturation point for C and because organic inputs were limited during the establishment of perennial vegetation. Thus, the most rapid and extensive accretion of carbon and nitrogen stocks will likely occur at landscape positions that were most eroded.

Rehabilitation and restoration of cropland in the hummocky landscape of the Prairie Pothole Region in North America is most likely to improve SOC stocks and concentrations by targeting the most severely eroded parts of the landscape. Additional research is needed to evaluate whether past farming practices have crossed functional ecological thresholds that could prevent restoration of net primary productivity, SOC concentrations, SOC stocks, and vegetation communities to precultivation levels.

Acknowledgments

This research was funded by the South Dakota Agriculture Experiment Station (SD00R336-09), project NC-1178, and EcoSun Prairie Farms Inc. Additional support was provided by the North Central Regional Sun Grant Center at South Dakota State University through a grant from the US Department of Energy Bioenergy Technologies Office under award number DE-FG36-08GO88073 and Conservation Innovation Grant 69-3A75-7-117 from the USDA Natural Resources Conservation Service. We would like to acknowledge the work of Craig Novotny as EcoSun Prairie Farm's manager and restoration ecologist and the Nature Conservancy for permission to sample soils on the Sioux Prairie.

Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at https://doi.org/10.1016/j.catena.2017.09.020. These data include the Google maps of the most important areas described in this article.

References

Adam, G., Duncan, H., 2001. Development of a sensitive and rapid method for the measurement of total microbial activity using fluorescein diacetate (FDA) in a range of soils. Soil Biol. Biochem. 33, 943–951.

Ampleman, M.D., Crawford, K.M., Fike, D.A., 2014. Differential soil organic carbon storage at forb and grass-dominated plant communities, 33 years after tallgrass prairie restoration. Plant Soil 374, 899–913.

Amundson, R., Berhe, A.A., Hopmans, J.W., Olson, C., Sztein, A.E., Sparks, D.L., 2015. Soil and human security in the 21st century. Science 348 (6235), 647.

Aronson, J., Floret, C., LeFloc'h, E., Ovalle, C., Pontanier, R., 1993. Restoration and rehabilitation of degraded ecosystems in arid and semi-arid lands. I. a view from the south. Restor. Ecol. 1, 8–17.

Balesdent, J., Chenu, C., Balabane, M., 2000. Relationship of soil organic matter dynamics to physical protection and tillage. Soil Tillage Res. 53, 215–230.

Bedard-Haughn, A., Jongbloed, F., Akkerman, J., Uijl, A., de Jong, E., Yates, T., Pennock, D., 2006. The effects of erosional and management history on soil organic carbon stores in ephemeral wetlands of hummocky agricultural landscapes. Geoderma 135, 296–306.

Berhe, A.A., Harden, J.W., Torn, M.S., Harte, J., 2008. Linking soil organic matter dynamics and erosion-induced terrestrial carbon sequestration at different landform positions. J. Geophys. Res. 113, G04039.

Berhe, A.A., Harden, J.W., Torn, M.S., Kleber, M., Burton, S.D., Harte, J., 2012. Persistence of soil organic matter in eroding versus depositional landform positions. J. Geophys. Res. Biogeosci. 117, 16.

Boe, A., Owens, V., Gonzalez-Hernandez, J., Stein, J., Lee, D.K., Koo, B.C., 2009. Morphology and biomass production of prairie cordgrass on marginal lands. GCB Bioenergy 1, 240–250.

Brady, N.C., Weil, R.R., 2008. The Nature and Properties of Soils, 14th Ed. Pearson Prentice Hall, Upper Saddle River, NJ.

Richardson, J.L., Brinson, M.M., 2000. Chapter 9: Wetland soils and the hydrogeomorphic classification of wetlands. In: Vepraskas, M.J., Richardson, J.L., Craft, C.B. (Eds.), Wetland Soils: Genesis, Hydrology, Landscapes, and Classification. Lewis Publishers, Boca Raton, FL.

Briske, D.D., Fuhlendorf, S.D., Smeins, F.E., 2005. State-and-transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. Rangel. Ecol. Manag. 58, 1–10.

Cambardella, C.A., Gajda, A.M., Doran, J.W., Wienhold, B.J., Kettler, T.A., 2001. Estimation of particulate and total organic matter by weight loss-on-ignition. In: Lal, R. (Ed.), Assessment Methods for Soil Carbon. Adv. Soil Sci. CRC Press, Boca Raton, FL, pp. 349–359.

Chirinda, N., Elsgaard, L., Thomsen, I.K., Heckrath, G., Olesen, J.E., 2014. Carbon dynamics in topsoil and subsoil along a cultivated toposequence. Catena 120, 20–28.

Core Team, R., 2015. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria(URL http://www.R-project.org/).

Cushing, E.J., Wright, H.E., 1965. Hand-operated piston corers for lake sediments. Ecology 46, 380–384.

De Alba, S., Lindstrom, M., Schumacher, T.E., Malo, D.D., 2004. Soil landscape evolution due to soil redistribution by tillage: a new conceptual model of soil catena evolution in agricultural landscapes. Catena 58, 77–100.

DeLuca, T.H., Zabinski, C.A., 2011. Prairie ecosystems and the carbon problem. Front. Ecol. Environ. 9 (7), 407–413.

Dietzel, R.D., Jarchow, M.E., Liebman, M., 2015. Above- and belowground growth, biomass, and nitrogen use in maize and reconstructed prairie cropping systems. Crop Sci. 55, 1–14.

Doetterl, S., Cornelis, J.T., Six, J., Bode, S., Opfergelt, S., Boeckx, P., Van Oost, K., 2015. Soil redistribution and weathering controlling the fate of geochemical and physical

carbon stabilization mechanisms in soils of an eroding landscape. Biogeosciences 12, 1357–1371.
Doetterl, S., Berhe, A.A., Nadeu, E., Wang, Z.G., Sommer, M., Fiener, P., 2016. Erosion, deposition and soil carbon: a review of process-level controls, experimental tools and models to address C cycling in dynamic landscapes. Earth Sci. Rev. 154, 102–122.
Ellert, B.H., Janzen, H.H., McConkey, B.G., 2001. Measuring and comparing soil carbon storage. In: Lal, R. (Ed.), Assessment Methods for Soil Carbon. CRC Press, Boca Raton, pp. 131–146.
Everett, K.R., 1983. Histosols. In: Wilding, L.P., Smeck, N.E., Hall, G.F. (Eds.), Pedogenesis and Soil Taxonomy II: The Soil Orders. Elsevier Scientific Publishers, Amsterdam, pp. 1–53.
Ewing, J.M., Vepraskas, M.J., 2006. Estimating primary and secondary subsidence in an organic soil 15, 20, and 30 years after drainage. Wetlands 26, 119–130.
Fenstermacher, D.E., Rabenhorst, M.C., Lang, M.W., McCarty, G.W., Needelman, B.A., 2016. Carbon in natural, cultivated, and restored depressional wetlands in the Mid-Atlantic coastal plain. J. Environ. Qual. 45, 743–750.
Fiener, P., Dlugoss, V., Van Oost, K., 2015. Erosion-induced carbon redistribution, burial and mineralisation Is the episodic nature of erosion processes important? Catena 133, 282–292.
Fraser, A., Kindscher, K., 2005. Spatial distribution of *Spartina pectinata* transplants to restore wet prairie. Restor. Ecol. 13, 144–151.
Gajda, A.M., Doran, J.W., Kettler, T.A., Wienhold, B.J., Pikul Jr., J.L., Cambardella, C.A., 2001. Soil quality evaluations of alternative and conventional management systems. In: Lal, R. (Ed.), Assessment Methods for Soil Carbon. CRC Press, Boca Raton, pp. 381–400.
Gee, G.W., Bauder, J.W., 1986. Particle Size Analysis. In: Klute, A. (Ed.), Methods of Soil Analysis. Soil Science Society of America. Madison, WI, pp. 383–411.
Grossman, R.B., Reinsch, T.J., 2002. 2.1 Bulk density and linear extensibility. In: Dane, J.H., Topp, G.C. (Eds.), Methods of Soil Analysis: Part 4. Physical Methods. SSSA Book Series 5.4 Soil Science Society of America, Madison, WI, pp. 201–228.
Guzman, J.G., Al-Kaisi, M., 2010. Landscape position and age of reconstructed prairies effect on soil. J. Soil Water Conserv. 65, 9–21.
von Haden, A.C., Dornbush, M.E., 2016. Prairies thrive where row crops drown: a comparison of yields in upland and lowland topographies in the upper Midwest US. Agronomy 6 (32), 1–12.
Hamza, M.A., Anderson, W.K., 2005. Soil compaction in cropping systems: a review of the nature, causes and possible solutions. Soil Tillage Res. 82, 121–145.
Harden, J.W., Sharpe, J.M., Parton, W.J., Ojima, D.S., Fries, T.L., Huntington, T.G., Dabney, S.M., 1999. Dynamic replacement and loss of soil carbon on eroding cropland. Glob. Biogeochem. Cycles 13, 885–901.
Martin, D.B., Hartman, W.A., 1987. The effect of cultivation on sediment composition and deposition in prairie pothole wetlands. Water Air Soil Pollut. 34, 45–53.
Haynes, R.J., Williams, P.H., 1999. Influence of stock camping behavior on the soil microbiological and biochemical properties of grazed pastoral soils. Biol. Fertil. Soils 28, 253–258.
Heimerl, K., 2011. Comparisons of soil within a till plain across contrasting land uses. M.S. thesis. South Dakota State University, Brookings, SD.
Hickman, K.R., Hartnett, D.C., Cochran, R.C., Owensby, C.E., 2004. Grazing management effects on plant species diversity in tallgrass prairie. J. Range Manag. 57, 58–65.
High Plains Regional Climate Center, 2016. Available at: http://climod.unl.edu/ (accessed 23 Aug. 2016).
Hu, Y.X., Kuhn, N.J., 2016. Erosion-induced exposure of SOC to mineralization in aggregated sediment. Catena 137, 517–525.
Hu, Y.X., Berhe, A.A., Fogel, M.L., Heckrath, G.J., Kuhn, N.J., 2016. Transport-distance specific SOC distribution: does it skew erosion induced C fluxes? Biochemistry 128, 339–351.
IUSS Working Group WRB, 2015. World reference base for soil resources 2014, (update 2015). International soil classification system for naming soils and creating legends for soil maps. In: World Soil Resources Reports No. 106. FAO, Rome Available at: http://www.fao.org/3/a-i3794e.pdf, Accessed date: 26 July 2017.
Jarchow, M.E., Liebman, M., Dhungel, S., Dietzel, R., Sundberg, D., Anex, R.P., Thompson, M.L., Chua, T., 2015. Trade-offs among agronomic, energetic, and environmental performance characteristics of corn and prairie bioenergy cropping systems. GCB Bioenergy 7, 57–71.
Johnson, R.R., Higgins, K.F., 1997. Wetland Resources of Eastern South Dakota. South Dakota State University, Brookings, SD, USA.
Johnson, W.C., Boettcher, S.E., Guntenspergen, G.R., 2004. Influence of weather extremes on the water levels of glaciated prairie wetlands. Wetlands 24, 385–398.
Johnson, W.C., Werner, B., Guntenspergen, G.R., Voldseth, R.A., Millett, B., Naugle, D.E., Tulbure, M., Carroll, R.W.H., Tracy, J., Olawsky, C., 2010. Prairie wetland complexes as landscape functional units in a changing climate. Bioscience 60, 128–140.
Johnston, C., 2014. Beaver pond effects on carbon storage in soils. Geoderma 213, 371–378.
Kemper, W.D., Rosenau, R.C., 1986. Aggregate stability and size distribution. In: Klute, A. (Ed.), Methods of Soil Analysis, Part I. Physical and Mineralogical Methods, 2nd ed. SSSA Book Ser. 5.1. SSSA ASA, Madison, pp. 435–442.
Kirkels, F., Cammeraat, L.H., Kuhn, N.J., 2014. The fate of soil organic carbon upon erosion, transport and deposition in agricultural landscapes - a review of different concepts. Geomorphology 226, 94–105.
Lal, R., 2008. Carbon sequestration in soil. CAB Reviews 3 (030), 1–20 perspectives in agriculture, veterinary science, nutrition and natural resources.
Lal, R., 2015. Restoring soil quality to mitigate soil degradation. Sustainability 7 (5), 5875–5895.
Lamandé, M., Schjønning, P., 2011. Transmission of vertical stress in a real soil profile. Part III: effect of soil water content. Soil Tillage Res. 114, 78–85.
Li, Y., Quine, T.A., Yu, H.Q., Govers, G., Six, J., Gong, D.Z., Wang, Z., Zhang, Y.Z., Van Oost, K., 2015. Sustained high magnitude erosional forcing generates an organic carbon sink: test and implications in the Loess Plateau, China. Earth Planet. Sci. Lett. 411, 281–289.
Lindstrom, M.J., Schumacher, J.A., Schumacher, T.E., 2000. TEP: a tillage erosion prediction model to calculate soil translocation rates from tillage. J. Soil Water Conserv. 55, 105–108.
Linn, D.M., Doran, J.W., 1984. Effect of water-filled pore space on carbon dioxide and nitrous oxide production in tilled and nontilled soils. Soil Sci. Soc. Am. J. 48, 1267–1272.
Lobb, D.A., 2011. Understanding and managing the causes of soil variability. J. Soil Water Conserv. 66, 175A–179A.
Loveland, P., Webb, J., 2003. Is there a critical level of organic matter in the agricultural soils of temperate regions: a review. Soil Tillage Res. 70, 1–18.
Minasny, B., Malone, B.P., McBratney, A.B., Angers, D.A., Arrouays, D., Chambers, A., Chaplot, V., Chen, Z.S., Cheng, K., Das, B.S., Field, D.J., Gimona, A., Hedley, C.B., Hong, S.Y., Mandal, B., Marchant, B.P., Martin, M., McConkey, B.G., Mulder, V.L., O'Rourke, S., Richer-de-Forges, A.C., Odeh, I., Padarian, J., Paustian, K., Pan, G., Poggio, L., Savin, I., Stolbovoy, V., Stockman, U., Sulaeman, Y., Tsui, C.C., Vagen, T.G., van Wesemail, B., Winowiecki, L., 2017. Soil carbon 4 per mille. Geoderma 292, 59–86.
Mulkey, V.R., Owens, V.N., Lee, D.K., 2006. Management of switchgrass-dominated Conservation Reserve Program lands for biomass production in South Dakota. Crop Sci. 46, 712–720.
Novotny, C., 2008. Fly ash in sediments as a marker to estimate pre-agricultural bathymetry of glaciated prairie wetlands. M.S. thesis. South Dakota State University, pp. 110.
O'Connell, J.L., Daniel, D.W., McMurry, S.T., Smith, L.M., 2016. Soil organic carbon in playas and adjacent prairies, cropland, and Conservation Reserve Program land of the High Plains, USA. Soil Tillage Res. 156, 16–24.
Ode, D.J., 1978. Nature Conservancy Stewardship Master Plans for Five Prairies in Eastern South Dakota. Report to the Nature Conservancy. Midwest Regional Office, Minneapolis, Minnesota.
Olson, K.R., Gennadiyev, A.N., Kovach, R.G., Lang, J.M., 2013. The use of fly ash to determine the extent of sediment transport and deposition on a nearly level western Illinois landscape. Soil Sci. 178, 24–28.
Olson, K.R., Gennadiyev, A.N., Kovach, R.G., Schumacher, T.E., 2014. Comparison of prairie and eroded agricultural lands on soil organic carbon retention (South Dakota). Open J. Soil Sci. 4, 136–150.
Papiernik, S.K., Lindstrom, M.J., Schumacher, T.E., Schumacher, J.A., Malo, D.D., Lobb, D.A., 2007. Characterization of soil profiles in a landscape affected by long-term tillage. Soil Tillage Res. 93, 335–345.
Pennock, D.J., 2003. Multi-site assessment of cultivation-induced soil change using revised landform segmentation procedures. Can. J. Soil Sci. 83, 565–580.
Pikul Jr., J.L., Schumacher, T.E., Vigil, M., 2001. Nitrogen use and carbon sequestered by corn rotations in the northern corn belt, U.S. Sci. World 1 (S2), 707–713.
Quinton, J.N., Govers, G., Van Oost, K., Bardgett, R.D., 2010. The impact of agricultural soil erosion on biogeochemical cycling. Nat. Geosci. 3, 311–314.
Ramankutty, N., Evan, A.T., Monfreda, C., Foley, J.A., 2008. Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. Glob. Biogeochem. Cycles 22, GB1003.
Rejman, J., Iglik, I., Paluszek, J., Rodzik, J., 2014. Soil redistribution and crop productivity in loess areas (Lublin Upland, Poland). Soil Tillage Res. 143, 77–84.
Richardson, J.L., Arndt, J.L., Freeland, J., 1994. Wetland soils of the prairie pothole. Adv. Agron. 52, 121–171.
Riedell, W.E., Osborne, S.L., Schumacher, T.E., Pikul Jr., J.L., 2011. Grassland canopy management and native tallgrass species composition effects on C and N in grass canopies and soil. Plant Soil 338, 51–61.
Ruehlmann, J., Körschens, M., 2009. Calculating the effect of soil organic matter concentration on soil bulk density. Soil Sci. Soc. Am. J. 73, 876–885.
Samson, F.B., Knopf, F.L., 1994. Prairie conservation in North America. Bioscience 44, 418–421.
Schumacher, T.E., 2011. Precision conservation using multiple cellulosic feedstocks. In: NRCS 69-3a75-7-117 Final Report, Final Report, Available at: http://www.nrcs.usda.gov/Internet/FSE_DOCUMENTS/stelprdb1046770.pdf accessed 11.08.2016.
Schumacher, T.E., Lindstrom, M.J., Schumacher, J.A., Lemme, G.D., 1999. Modeling spatial variation in productivity due to tillage and water erosion. Soil Tillage Res. 51, 331–339.
Schumacher, T., Eynard, A., Chintala, R., 2015. Rapid cost-effective analysis of microbial activity in soils using modified fluorescein diacetate method. Environ. Sci. Pollut. Res. 22 (6), 4759–4762. http://dx.doi.org/10.1007/s11356-014-3922-4.
Sherrod, L.A., Gunn, G., Peterson, G.A., Kolberg, R.L., 2002. Inorganic carbon analysis by modified pressure-calcimeter method. Soil Sci. Soc. Am. J. 66, 299–305.
Six, J., Conant, R.T., Paul, E.A., Paustian, K., 2002. Stabilization mechanisms of soil organic matter: implications for C-saturation of soils. Plant Soil 241, 155–176.
Slobodian, N., Van Rees, K., Pennock, D., 2002. Cultivation-induced effects on belowground biomass and organic carbon. Soil Sci. Soc. Am. J. 66, 924–930.
Smart, A.J., Scott, T.K., Clay, S.A., Clay, D.E., Ohrtman, M., Mousel, E.M., 2013. Spring clipping, fire, and simulated increased atmospheric nitrogen deposition effects on tallgrass prairie vegetation. Rangel. Ecol. Manag. 66, 680–687.
Smith, P., House, J.I., Bustamante, M., Sobocka, J., Harper, R., Pan, G.X., West, P.C., Clark, J.M., Adhya, T., Rumpel, C., Paustian, K., Kuikman, P., Cotrufo, M.F., Elliott, J.A., McDowell, R., Griffiths, R.I., Asakawa, S., Bondeau, A., Jain, A.K., Meersmans, J., Pugh, T.A.M., 2016. Global change pressures on soils from land use and management. Glob. Chang. Biol. 22 (3), 1008–1028.
Soil Survey Staff, Natural Resources Conservation Service, United States Department of Agriculture, 2017. Official Series Descriptions. Available at: https://soilseries.sc.

egov.usda.gov/osdname.aspx, Accessed date: 26 July 2017.
South Dakota Geological Survey, 2009. South Dakota Geology Available at: http://www.sdgs.usd.edu/geologyofsd/geosd.html, Accessed date: 15 May 2011.
Soil Survey Staff, 1985. Soil Survey of Moody County, South Dakota. In: USDA Natural Resources Conservation Service (NRCS). U.S. Government Printing Office, Washington, DC.
Stallard, R.F., 1998. Terrestrial sedimentation and the carbon cycle: coupling weathering and erosion to carbon burial. Glob. Biogeochem. Cycles 12, 231–257.
Stewart, R.E., Kantrud, H.A., 1971. Classification of natural ponds and lakes in the glaciated prairie region. U.S. Fish and Wildlife Service, Washington, DC.
Stewart, C.E., Paustian, K., Conant, R.T., Plante, A.F., Six, J., 2007. Soil carbon saturation: concept, evidence and evaluation. Biochemistry 86, 19–31.
Stockmann, U., Adams, M.A., Crawford, J.W., Field, D.J., Henarkaarchchi, N., Jenkins, M., Minasny, B., McBratney, A.B., Remy de Courcelles, V., Singh, K., Wheeler, I., Abbott, L., Angers, D.A., Baldock, J., Bird, M., Brookes, P.C., Chenu, C., Jastrow, J.D., Lal, R., Lehmann, J., O'Donnell, A.G., Parton, W.J., Whitehead, D., Zimmermann, M., 2013. The knowns, known unknowns and unknowns of sequestration of soil organic carbon. Agric. Ecosyst. Environ. 164, 80–99.
Szalai, Z., Szabo, J., Kovacs, J., Meszaros, E., Albert, G., Centeri, C., Szabo, B., Madarasz, B., Zachary, D., Jakab, G., 2016. Redistribution of soil organic carbon triggered by erosion at field scale under subhumid climate, Hungary. Pedosphere 26, 652–665.
Thomas, G.W., 1996. Soil pH and soil acidity. In: Sparks, D.L., Page, A.L., Heimke, P.A., Loeppert, R.H., Solatanpour, P.N., Tabatabai, M.A., Johnston, C.T., Sumner, M.E. (Eds.), Methods of Soil Analysis. Part Vol. 3. Chemical Methods, Soil Science Society of America, Madison, pp. 475–490.
Van der Valk, A., 1989. Northern Prairie Wetlands. Iowa State University Press, Ames, pp. 400.
Van Hemelryck, H., Govers, G., Van Oost, K., Merckx, R., 2011. Evaluating the impact of soil redistribution on the in situ mineralization of soil organic carbon. Earth Surf. Process. Landf. 36, 427–438.
Van Oost, K., Govers, G., Desmet, P., 2000. Evaluating the effects of changes in landscape structure on soil erosion by water and tillage. Landsc. Ecol. 15, 577–589.
Van Oost, K., Quine, T.A., Govers, G., De Gryze, S., Six, J., Harden, J.W., Ritchie, J.C., McCarty, G.W., Heckrath, G., Kosmas, C., Giraldez, J.V., da Silva, J.R.M., Merckx, R., 2007. The impact of agricultural soil erosion on the global carbon cycle. Science 318, 626–629.
Van Oost, K., Six, J., Govers, G., Quine, T.A., De Gryze, S., 2008. Soil erosion: a carbon sink or source? Response. Science 319, 1042.
VandenBygaart, A.J., 2016. The potential to regain organic carbon in degraded soils: a boundary line approach. Can. J. Soil Sci. 96, 351–353.
Vepraskas, M.J., Huffman, R.L., Kreiser, G.S., 2005. Hydrologic models for altered landscapes. Geoderma 131, 287–298.
Liebowitz, S.G., Vining, K.C., 2003. Temporal connectivity in a prairie pothole complex. Wetlands 23, 13–25.
Weaver, J.E., Zink, E., 1946a. Annual increase of underground materials in three range grasses. Ecology 27, 115–127.
Weaver, J.E., Zink, E., 1946b. Length of life of roots of ten species of perennial range and pasture grasses. Plant Physiol. 21, 201–217.
Werner, B., Tracy, J., Johnson, W.C., Voldseth, R.A., Guntenspergen, G.R., Millett, B., 2016. Modeling the effects of tile drain placement on the hydrologic function of farmed prairie wetlands. J. Amer. Water Res. Assoc. 52, 1482–1492.
Wiaux, F., Cornelis, J.T., Cao, W., Vanclooster, M., Van Oost, K., 2014. Combined effect of geomorphic and pedogenic processes on the distribution of soil organic carbon quality along an eroding hillslope on loess soil. Geoderma 216, 36–47.
Wickham, H., 2009. ggplot2: elegant graphics for data analysis. Springer, New York.
Wilson, M.G., Sasal, M.C., Caviglia, O.P., 2013. Critical bulk density for a mollisol and a vertisol using least limiting water range. Geoderma 192, 354–361.
Wright, C.K., Wimberly, M.C., 2013. Recent land use change in the Western Corn Belt threatens grasslands and wetlands. Proc. Natl. Acad. Sci. 110, 4134–4139.
Zhang, J.H., Wang, Y., Li, F.C., 2015. Soil organic carbon and nitrogen losses due to soil erosion and cropping in a sloping terrace landscape. Soil Res. 53, 87–96.
Zilverberg, C., Johnson, W.C., Archer, D., Kronberg, S., Schumacher, T., Boe, A., Novotny, C., 2014a. Profitable prairie restoration: the EcoSun Prairie Farm experiment. J. Soil Water Conserv. 69, 22A–25A.
Zilverberg, C.J., Johnson, W.C., Boe, A., Owens, V., Archer, D., Novotny, C., Volke, M., Werner, B., 2014b. Growing *Spartina pectinata* in previously farmed prairie wetlands for economic and ecological benefits. Wetlands 34, 853–864.
Zilverberg, C.J., Johnson, W.C., Owens, V., Boe, A., Schumacher, T., Reitsma, K., Hong, C.O., Novotny, C., Volke, M., Werner, B., 2014c. Biomass yield from planted mixtures and monocultures of native prairie vegetation across a heterogeneous farm landscape. Agric. Ecosyst. Environ. 186, 148–159.
Zilverberg, C.J., Johnson, W.C., Archer, D., Schumacher, T., Boe, A., 2015. The EcoSun Prairie Farm: an Experiment in Bioenergy Production, Landscape Restoration, and Ecological Sustainability. South Dakota State University, Brookings, SD, pp. 96.