

Moisture and vegetation controls on decadal-scale accrual of soil organic carbon and total nitrogen in restored grasslands

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Abstract

Revitalization of degraded landscapes may provide sinks for rising atmospheric CO₂, especially in reconstructed prairies where substantial belowground productivity is coupled with large soil organic carbon (SOC) deficits after many decades of cultivation. The restoration process also provides opportunities to study the often-elusive factors that regulate soil processes. Although the precise mechanisms that govern the rate of SOC accrual are unclear, factors such as soil moisture or vegetation type may influence the net accrual rate by affecting the balance between organic matter inputs and decomposition. A resampling approach was used to assess the control that soil moisture and plant community type each exert on SOC and total nitrogen (TN) accumulation in restored grasslands. Five plots that varied in drainage were sampled at least four times over two decades to assess SOC, TN, and C₄- and C₃-derived C. We found that higher long-term soil moisture, characterized by low soil magnetic susceptibility, promoted SOC and TN accrual, with twice the SOC and three times the TN gain in seasonally saturated prairies compared with mesic prairies. Vegetation also influenced SOC and TN recovery, as accrual was faster in the prairies compared with C₃-only grassland, and C₄-derived C accrual correlated strongly to total SOC accrual but C₃-C did not. High SOC accumulation at the surface (0–10 cm) combined with losses at depth (10–20 cm) suggested these soils are recovering the highly stratified profiles typical of remnant prairies. Our results suggest that local hydrology and plant community are critical drivers of SOC and TN recovery in restored grasslands. Because these factors and the way they affect SOC are susceptible to modification by climate change, we contend that predictions of the C-sequestration performance of restored grasslands must account for projected climatic changes on both soil moisture and the seasonal productivity of C₄ and C₃ plants.

Keywords: *Bromus inermis*, C₄, carbon sequestration, drainage, magnetic susceptibility, restored prairie, soil organic carbon, total nitrogen

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Introduction

Cultivation can deplete native soil organic carbon (SOC) stocks – the largest terrestrial C reservoir – by up to 50% in many systems, particularly in fertile surface soils of temperate grasslands (Tiessen *et al.*, 1982; Mann, 1986; Burke *et al.*, 1989, 1995; Schlesinger & Andrews, 2000; Slobodian *et al.*, 2002; Schnitzer *et al.*, 2006). At least part of the lost SOC can be recovered, however, if the native ecosystem and its characteristic soil properties are reestablished (Baer *et al.*, 2002; McLauchlan, 2006;

Kucharik, 2007; Matamala *et al.*, 2008). Replenishment of SOC stocks contributes to the maintenance of ecosystem structure and function (e.g. Baer *et al.*, 2002; Allison *et al.*, 2005; Matamala *et al.*, 2008) and serves as a sink to partially offset rising atmospheric CO₂ concentrations (Barker *et al.*, 1995; Karlen *et al.*, 1999; Post & Kwon, 2000; Conant *et al.*, 2001; Ogle *et al.*, 2004). Yet, a better understanding of the mechanistic controls on SOC accumulation rates at the landscape level is needed to reliably predict the C sequestration potential of restored ecosystems.

Both abiotic and biotic factors influence the net rate of SOC and total nitrogen (TN) accrual by affecting the ratio of organic matter inputs to mineralization. State

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factors such as climate and vegetation type have long been known to shape the development of soil properties, including SOC and TN, over broad spatial and temporal scales (Jenny, 1941). For example, the climate gradient across the North American Great Plains affects SOC, with greater stocks in cooler and wetter areas to the north and east (Burke *et al.*, 1989). Nonetheless, the relative importance of controlling factors at local spatial scales and decadal temporal scales is poorly understood, thereby limiting quantitative predictions of how native ecosystem restoration will affect SOC and TN accrual rates at any particular location. A number of recent studies have been unable to explicitly attribute SOC accrual rates at the site level to physical features (Brye & Kucharik, 2003; McLauchlan, 2006; McLauchlan *et al.*, 2006; Kucharik, 2007), soil chemistry (McLauchlan *et al.*, 2006), biological factors (McLauchlan *et al.*, 2006) or topography (Brye & Kucharik, 2003; McLauchlan *et al.*, 2006; Matamala *et al.*, 2008). Here, we use sequential sampling over two decades to investigate SOC and TN accrual in perennial grasslands restored on abandoned agricultural fields. To the best of our knowledge, this is the first study to assess both abiotic and biotic drivers of SOC and TN recovery at the landscape scale by repeatedly sampling the same locations in reconstructed grasslands over a time interval relevant to C sequestration accounting.

Soil moisture is a well-known abiotic driver of soil organic matter (SOM) dynamics (Parton *et al.*, 1987; Jenerette & Lal, 2005). Depending on plant adaptations, nonlimiting moisture conditions can promote net primary production (NPP) and, thus, plant residue inputs to the soil system (Sims & Singh, 1978; Sala *et al.*, 1988). In addition, the activity of most soil heterotrophs is inhibited by both high- and low-moisture conditions, which protects organic matter from decomposition (e.g. Linn & Doran, 1984; Bowden *et al.*, 1998). The importance of soil moisture has been demonstrated by comparisons of SOC and TN accumulation rates in restored permanent wetlands and similar vegetation types on well-drained soil (Trumbore & Harden, 1997; Euliss *et al.*, 2006; Meyer *et al.*, 2008). However, the extent to which more subtle variation in drainage can impact SOC and TN recovery rates has yet to be determined in perennial grasslands.

Plant traits also clearly affect SOC and TN cycling (De Deyn *et al.*, 2008), and the diversity of plant species or functional types may affect the rates of SOC and TN accumulation in restored temperate ecosystems. Inputs to soil may be greater in more diverse communities, because high plant diversity may enhance soil fertility (Dybzinski *et al.*, 2008) or improve ecosystem stability and productivity (Hooper *et al.*, 2005). Diversity-enhanced accumulation may also be due in part to

differences in plant residue chemistry that can affect decomposition rates (Silver & Miya, 2001; Dijkstra & Cheng, 2007; Meier & Bowman, 2008) and lead to variation in the transformation of plant residues into SOM. However, the evidence for the effects of grassland plant community diversity on SOM accrual after agricultural abandonment is not conclusive, promoting it in some cases (Fornara & Tilman, 2008; Steinbeiss *et al.*, 2008) and having no effect in others (McLauchlan *et al.*, 2006; Mahaney *et al.*, 2008).

In this study, we use a resampling strategy to explore the degree to which subtle, landscape-scale variation in drainage and vegetation control SOC and TN accrual in restored grasslands. Resampling allows the in-plot study of SOC and TN dynamics over time, providing improved sensitivity over space-for-time substitution methods (i.e. the chronosequence approach) often used to study long-term ecosystem dynamics. The chronosequence approach, which assumes sampling units are identical except for time since treatment commenced (Stevens & Walker, 1970), has been valuable for detecting changes in restored prairies occurring over long time periods (e.g. Jastrow, 1996; Knops & Tilman, 2000; Baer *et al.*, 2002). However, in some cases these studies lack the power to resolve mechanistic controls on SOC and TN dynamics because space and time are confounded (Brye & Kucharik, 2003; McLauchlan, 2006; McLauchlan *et al.*, 2006; Kucharik, 2007; Matamala *et al.*, 2008). In contrast, repeated sampling of the same locations partitions variation arising from space and time to yield more precise estimates of ecosystem processes (Richter *et al.*, 2007). Using the natural ^{13}C tracer from C_4 and C_3 plants at a site with relatively small variation in drainage, we aim to demonstrate the importance of minor differences in moisture and vegetation on decadal-scale SOC and TN accrual. We specifically hypothesize that prairie vegetation with its mixture of C_4 and C_3 plant species will promote faster SOC and TN accumulation than C_3 -only grassland and that these rates will be enhanced by seasonally wet conditions compared with better drained soil. We focus on vegetation and moisture controls on soil processes, as these two factors are sensitive to land-use and climatic changes.

Materials and methods

Site description

The study was carried out in a series of perennial grassland restorations in the National Environmental Research Park (NERP) at Fermi National Accelerator Laboratory (Fermilab, Batavia, IL, USA) (88°14'30"W, 41°50'30"N). The soils are well-aggregated silt loam and

silty clay loam Mollisols (or Alfisols with mollic epipedons); surface soil parent material consists of loess deposits. Average air temperature was 8.9 °C and average annual precipitation was 975 mm for the period from 1971 to 2000. The site is located in the Prairie Peninsula region, where periodic fire and grazing maintained grasslands that encroached on forested lands during the warmer and drier Hypsithermal interval beginning about 8000 BP (King, 1981). Elevation ranges from 225 to 228 m above mean sea level in the study area. Beginning in 1975, long-term agricultural fields in and around the site's particle accelerator were converted to prairie vegetation. To initiate restoration, the land was disked and then seeded with local ecotypes of native prairie species. New prairies were burned 2–3 years after conversion and then annually until the early 1990s. Thereafter, burns were conducted every 1–3 years. Another agricultural field adjacent to the accelerator ring was planted with a mixture of the cool-season grasses, *Bromus inermis* Leyss and *Poa pratensis* L. (referred to as 'brome field' hereafter) and maintained by herbicide applications every 1–3 years until 1984, after which it was mowed biannually (clippings left in place).

Historically, much of the area where Fermilab is located was seasonally wet or even flooded, but installation of drainage tiles early in the twentieth century lowered the water table and allowed reliable cultivation of agricultural fields. Such artificial drainage is common; approximately 37% of cropped land in the US Midwest (the historical distribution of tallgrass prairie) is subsurface drained, contributing to the over 43 million ha of subsurface-drained land in the United States (Madramootoo *et al.*, 2007 and references therein). The construction of Fermilab's accelerator ring and the retention of cooling water restored a seasonally higher water table for the restored prairies located inside the 2-km-diameter ring, but subtle topographic relief causes variation in water table depth and drainage among prairie plots within the ring. In contrast, areas located outside of the accelerator ring (including the brome field) are generally better drained due to functional drainage tiles.

Field sampling

We sampled four restored prairies inside the accelerator ring and a nearby brome field outside the ring (Table 1). Plot soils were topographically associated in the landscape and include Mundelein silt loam (Fine-silty-mixed superactive mesic Aquic Argiudoll), Wauconda silt loam (Fine-silty-mixed superactive mesic Udollic Endoaqualf), and Drummer silt loam (Fine-silty-mixed superactive mesic Typic Endoaquoll). Prairies I and IV

are located in poorly drained areas within the accelerator ring, causing them to be saturated with water during some parts of the year. In contrast, Prairies II and III are situated in somewhat better drained areas. Thus, we grouped prairie plots as 'seasonally saturated' (I and IV) or 'mesic' (II and III). The brome field remains tile drained. All of the selected plots were farmed for over 100 years; cultivation ceased in 1969–1970 when Fermilab was established. The plots then reverted to an old-field condition until planted to grassland. 'Plot age' refers to the time since planting to perennial grassland.

Samples were collected from all five plots in late June or early July of 1985, 1989, 1999, and 2004. All prairies were burned before the 1985 and 1989 growing seasons. None of the prairies were burned successfully before the 1999 growing season, and only the mesic prairies were burned before the 2004 growing season. The brome field was also sampled in 1986, 1988, and 2001. During the initial sampling (Jastrow, 1987), 10 sampling stations were located in each plot by using a stratified random design. In subsequent years, sampling points were located 2.5 m in a random compass direction from the permanent markers placed where 1985 samples were taken.

Aboveground vegetation was clipped to 1–2 cm above the soil surface within a 0.5 m² circular sampling area (0.25 m² area in 1989). Three soil cores (4.8 cm diameter × 20 cm deep) were taken in a predetermined pattern from within the clipped area, sliced into 0–10 and 10–20 cm increments, and pooled by depth increment within each sample area. However, in 1989 (plus 1986, 1988, and 2001 in the brome field) the soil was sampled only to 10 cm. Additional cores (two in 1985 and one in 1989) were collected to quantify belowground biomass by washing. In all years, a separate core was taken for bulk density estimation by using the core method with aluminum rings (Blake & Hartge, 1986), except Prairie IV in 2004 when bulk density was estimated from the three pooled cores because the soil was too wet to use the rings without compaction. Samples were transferred to the laboratory at the end of each day, aboveground biomass was refrigerated until processing (no more than 10 days), and soils were frozen at –20 °C in polyethylene bags.

Laboratory analyses

In 1985 and 1989, aboveground biomass live stems were sorted by species. In 1999, live stems were sorted into 'grass' and 'forb' categories. In 2004, grasses were separated from forbs and then sorted by photosynthetic type (C₄ and C₃). After sorting, all biomass was dried to constant weight at 55–65 °C and weighed. Aboveground biomass collected mid-season does not

Table 1 Plot and soil characteristics of restored prairies and a C₃ brome field used in this study

	Prairie I Spring 1975	Prairie II Fall 1977	Prairie III Spring 1981	Prairie IV Spring 1984	Brome Fall 1971
Planting date					
Area (ha)	3.6	6.5	6.9	2.0	2.0
Soil series	Wauconda & Drummer	Mundelein	Mundelein	Drummer	Mundelein
Elevation (m a.s.l.)	227.0 (<0.1)	227.1 (0.1)	227.2 (0.1)	225.6 (<0.1)	225.9 (0.1)
Decadal-scale moisture class	Seasonally saturated	Mesic	Mesic	Seasonally saturated	Tile drained
<i>Soil 0–10 cm</i>					
Magnetic susceptibility (MS) ($\times 10^{-8} \text{ m}^3 \text{ kg}^{-1}$)	25.8 (0.8) ^{ab}	28.2 (1.9) ^a	30.5 (3.1) ^a	20.6 (0.6) ^b	28.0 (2.3)
Texture (% sand/clay)	25 (1)/10 (1)	24 (1)/13 (2)	21 (1)/16 (3)	25 (2)/19 (3)	26 (1)/9 (<1)
pH	6.30 (0.08)	6.29 (0.10)	6.24 (0.16)	6.95 (0.09)	5.84 (0.07)
Exchangeable Ca ²⁺ (mEq L ⁻¹)	3246 (245)	2991 (298)	2758 (196)	3716 (45)	2921 (198)
Exchangeable Mg ²⁺ (mEq L ⁻¹)	939 (68)	830 (99)	753 (83)	1250 (18)	800 (59)
<i>Soil 10–20 cm</i>					
Texture (% sand/clay)	29 (2)/10 (1)	26 (1)/3 (3)	23 (1)/12 (1)	26 (1)/17 (1)	29 (1)/8 (1)
pH	6.32 (0.10)	6.25 (0.13)	6.15 (0.16)	6.81 (0.07)	5.84 (0.06)
Exchangeable Ca ²⁺ (mEq L ⁻¹)	2982 (265)	2997 (289)	2790 (213)	3726 (33)	3044 (179)
Exchangeable Mg ²⁺ (mEq L ⁻¹)	869 (77)	836 (99)	748 (84)	1220 (13)	790 (52)

For each site, the year at which restoration began, the study surface area, soil series and texture, average elevation of the study area, soil MS, and decadal-scale moisture class is given. Texture, pH, Ca²⁺, and Mg²⁺ were measured on soil sampled in 1985 and MS was measured on soil sampled in 1989. Values for elevation, magnetic susceptibility, % sand, % clay, pH, Ca²⁺, and Mg²⁺ are averages of 9–10 replicates with SE in parentheses. MS data followed by the same letter are not significantly different based on analysis of variance and Tukey–Kramer-adjusted comparison of means and were used to support the observations that determined the decadal-scale moisture classifications (brome not included in test).

represent peak standing crop in prairies, since many species are warm season and continue to add biomass through September. On the other hand, mid-season biomass is a reasonably accurate estimate of peak biomass in the brome field, which has typically set seed by mid-July. A second period of cool season C₃-grass growth occurs in autumn and was excluded from our sampling. Because of this sampling bias and the variation in burn dates among the prairies, we avoided making explicit comparisons of aboveground biomass among grassland types, plots, or across years within a plot.

After thawing in a refrigerator overnight, soil cores were passed through an 8 mm sieve to remove roots and rhizomes, which, in 1999 and 2004, were rinsed free of soil, oven dried, and quantified for mass. In 1985 and 1989, roots and rhizomes were isolated from the extra cores collected for that purpose by washing and flotation over a 0.5 mm sieve (Cook *et al.*, 1988; Reinhardt & Miller, 1990) and biomass removed during soil processing was discarded. Data from 1999 and 2004 were corrected to account for the mass of roots that were not removed during soil processing through the 8 mm sieve by using information from a group of samples where roots were collected by both methods. Nonetheless, interpretation of belowground biomass data was constrained to within-year comparisons because collection methods were not consistent across sampling

years. The sieved soil was dried at 55 °C for 24–48 h, crushed with a rolling pin, and passed through a 2 mm sieve. Remaining root pieces longer than 3–4 mm were discarded. A subsample of the sieved soil was pulverized in a ball mill (Spex CertiPrep, Metuchen, NJ, USA) for elemental analyses and magnetic susceptibility determination.

Soils were analyzed for total C and TN contents by dry combustion with a Carlo Erba NC2500 elemental analyzer (Milan, Italy) and for $\delta^{13}\text{C}$ with a Finnegan MAT Delta Plus XL isotope ratio mass spectrometer (Bremen, Germany). Total C was equivalent to organic C since no carbonates were present (i.e. there was no effervescence after addition of 6 N HCl). Soil organic C, TN, and belowground biomass stocks were calculated on an equivalent mass basis to account for declining soil bulk density over time (Ellert & Bettany, 1995). The lightest mass of soil (Prairie IV in 2004, 96 kg m⁻² at 0–10 cm and 111 kg m⁻² at 10–20 cm) was used as the equivalent (Wander *et al.*, 1998; Gál *et al.*, 2007). The proportions of C₄- and C₃-derived C were calculated by using a two-endmember mixing model with measured average biomass values of –12.1‰ (SE 0.3‰) and –26.5‰ (SE 0.3‰) as the C₄- and C₃-endmembers, respectively. The endmembers were determined based on root, rhizome and shoot samples of common plant species at Fermilab [*Andropogon gerardii* Vitman, *Bromus*

inermis Leyss., *Coreopsis tripteris* L., *Panicum virgatum* L., *Phalaris arundinacea* L., *Poa pratensis* L., *Solidago altissima* L., and *Sorghastrum nutans* (L.) Nash].

Soil pH, exchangeable Ca, exchangeable Mg, and texture analyses were conducted on 2 mm sieved soil samples collected in 1985 and were performed at the University of Wisconsin – Madison Soil and Plant Analysis Laboratory. Soil pH was measured in a 1:1 soil: water slurry. Exchangeable Ca and Mg were extracted using ammonium acetate and measured using flame photometry (Schulte *et al.*, 1987). Texture was determined by the hydrometer method, without organic matter oxidation (Bouyoucos, 1962).

Soil magnetic susceptibility was determined for samples from 0 to 10 cm depth collected in 1989 and 2004. A Bartington MS2 magnetic susceptibility meter was used with an MS2B dual frequency attachment. Magnetic susceptibility (MS), the ratio of induced magnetism to the intensity of the field applied, can be used as a proxy for long-term soil moisture across transects with relatively uniform soil parent materials (Maher, 1998; Grimley *et al.*, 2004). Aided by microorganisms, ferrimagnetic minerals can readily dissolve in anaerobic soil, where Fe (III) is reduced to Fe (II). Thus, Fe-reduced soils worldwide have consistently lower MS values than adjacent well drained soils, other soil forming factors being similar (Le Borgne, 1955; Vadyunina & Babanin, 1972; Mullins, 1977; Maher, 1986; Yu *et al.*, 1986; Maher, 1998; Grimley *et al.*, 2004). The advantage of MS measurements is that they can be made rapidly and nondestructively on field or archived samples to provide a proxy for long-term drainage conditions (Grimley *et al.*, 2004, 2008).

Magnetic susceptibility reflects soil moisture conditions that have been in place over longer time scales than the drainage changes induced by engineering and construction of the accelerator ring at Fermilab. Thus, to fully explore soil moisture controls on SOC and TN accumulation, we used both a gradient approach based on measured MS and a categorical approach where we grouped plots using field observations of topography and drainage patterns to capture more recent changes in soil moisture regime (i.e. 'seasonally saturated' prairies, I and IV, vs. 'mesic' prairies, II and III).

Statistical analyses

Net changes in soil stocks (SOC, TN, C₃-C, and C₄-C) within each plot were assessed using paired *t*-tests (1985 vs. 2004). A one-way analysis of variance (ANOVA) was used to compare net change in SOC and TN stocks in seasonally saturated prairies (I and IV), mesic prairies (II & III) and brome (groupings based on field observations of decadal scale drainage patterns). ANOVA

was used to test for plot differences in MS to provide support for the moisture groupings based on field observations (Table 1). Plot differences in SOC and TN stocks at the start of the study were also compared by ANOVA.

Soil organic C, TN, C:N ratio, C₄-C, and C₃-C at each depth were regressed against plot age (i.e. time since planting) for each plot. The slopes of these regressions were then regressed against log MS (representing long-term drainage patterns), as were the net changes in C₄-C and C₃-C in each plot. The net change in SOC and the rate of C:N change for each plot were also regressed against net change in C₄- and C₃-C.

Repeated measures mixed model ANOVA (PROC MIXED; SAS System, version 8.01, SAS Institute, Cary, NC, USA) was used to test for differences in SOC and TN accumulation rates between prairies in the two moisture groups. Moisture classification, sampling date, and the treatment by date interaction were treated as fixed effects with sampling date as the repeated measure and plot as a random effect. A spherical spatial covariance structure was used because it gave the best fit on the basis of Akaike's information criterion.

Regression parameters were calculated using SIGMAPLOT version 8.0 (Systat Software Inc., San Jose, CA, USA) and all other statistical tests were carried out using SAS. Post hoc treatment comparisons were made by using the Tukey–Kramer-adjustment to minimize experiment-wise Type I errors. Nonnormal data were log-transformed before analysis and all effects and comparisons were considered significant at $\alpha \leq 0.1$ because of limited replication in a field setting and the desire to minimize the chances of failing to detect differences (Type II error) in such a system. Specific *P*-values are reported in the text, and tiered significance is denoted with asterisks in tables (** $P < 0.05$, * $0.05 < P < 0.10$) so that readers wishing to evaluate our results more stringently may do so (Villalpando *et al.*, 2009).

Results

Soil moisture effects on SOC and TN

In the surface 10 cm, seasonally saturated prairies gained more than twice as much SOC as the brome field over the two decades of the study, while SOC gains in mesic prairies were intermediate, an effect that appears to be ecologically significant although not statistically significant (Fig. 1). After net SOC losses at depth are factored in, however, the amount of SOC accrued over the entire 0–20 cm increment by seasonally saturated prairies was more than double that of the mesic prairies or brome ($P = 0.02$). This difference was

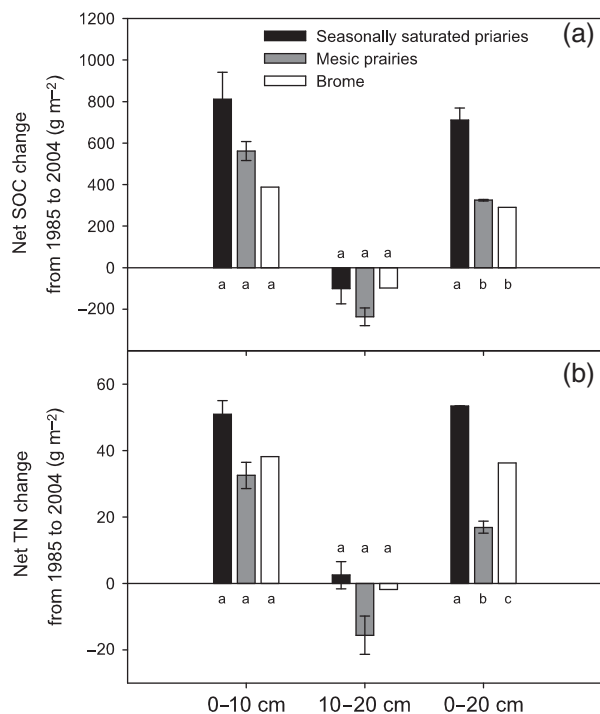


Fig. 1 Net change in SOC (a) and TN (b) from 1985 to 2004 in seasonally saturated prairies (I and IV), mesic prairies (II and III), and C₃ brome field at 0–10, 10–20, and 0–20 cm (based on equivalent mass – see ‘Materials and methods’). Error bars are SE. Within each depth increment, bars indicated by the same letter are not significantly different ($P < 0.05$) on the basis of analysis of variance and the Tukey–Kramer-adjusted pair-wise comparisons.

not attributable to starting stocks, because there were no significant differences in SOC or TN at the first sampling in 1985 (based on one-way ANOVAS of 1985 stocks). Results were similar for TN, except that the brome field gained similar amounts of TN as the mesic prairies at 0–10 cm with little net TN loss at 10–20 cm, resulting in a twofold overall increase in TN in brome with respect to the mesic prairies over the entire 20 cm profile. Seasonally saturated prairies gained nearly 50% more TN than brome and three times as much as mesic prairies (Fig. 1).

Soil organic C and TN accrued linearly over the duration of the study, with 88–98% (SOC) and 77–98% (TN) of within-plot variation at 0–10 cm described by time since planting (Fig. 2a and c). There were no significant trends at the 10–20 cm depth, except for slow SOC losses in Prairie IV and the brome field (Fig. 2b and d). The seasonally saturated prairies tended to have the most rapid SOC and TN accrual (mean rate of 42.1 g C and 2.6 g N m⁻² yr⁻¹ in plots I and IV vs. 30.6 g C and 1.9 g N m⁻² yr⁻¹ in plots II and III), however, the interaction of moisture with time was not significant for SOC ($P = 0.60$) or TN ($P = 0.55$). Soil organic C appeared to

outpace TN accumulation in the prairies, and three of the four plots had significant linear increases in C:N ratios (Fig. 2a and c, Table 2). In contrast, the relative rates of SOC and TN accrual were similar in the brome field (Fig. 2a and c, Table 2). At 10–20 cm, C:N ratios tended to narrow over time, but significant trends occurred only in Prairie II and the brome field.

Soil MS (i.e. a proxy for long-term soil moisture as described in ‘Materials and methods’) ranged from 17 to 48 × 10⁻⁸ m³ kg⁻¹ (typical for poorly to moderately well-drained loessal soils in northern Illinois; Table 1) and did not change from near the beginning of the study in 1989 to its conclusion in 2004 (data not shown). There was an inverse relationship between SOC accumulation rate and soil MS (Fig. 3). Because low soil MS reflects long-term poorly drained conditions (among similar areas with uniform soil parent material), the relationship between SOC accrual and MS indicates that higher soil moisture was correlated with faster SOC accumulation. There was no such relationship between MS and TN or C:N ratio (not shown).

Plant community composition effects on SOC and TN

In the surface 10 cm of prairies, SOC accrued from both C₄ and C₃ sources, except in the mesic Prairie II where the net increase in C₃-C was not significant (Table 3). In contrast, with only C₃ vegetation in the brome field, a net gain in C₃-C was accompanied by a net loss of C₄-derived C. These increases translated to significant linear rates of accrual for C₄-derived C in Prairies I, II, and IV and C₃-derived C in Prairies II and IV, and in brome (Table 3). Soil C from C₄ sources was highly correlated with total SOC accumulation, whereas C₃-C showed no such relationship (Fig. 4). In addition, the rate of change in C:N over the sampling period was directly related to the net change in C₄-C but inversely related to the net change in C₃-C (Fig. 5). A strong relationship also existed between soil MS and C₄-C but not with C₃-C (Fig. 6).

Above- and belowground biomass showed interannual variation typical for young restored prairies, and long-term SOC accrual did not respond to short-term changes in plant biomass. Aboveground biomass ranged from 230 to 904 g dw m⁻² (Table 4). The average contribution from grasses was 57% and average contribution from C₄ species was 38% but varied widely (Table 4). *Melilotus alba*, a nonnative biennial legume, had a mast year in 2004 regionally. This phenomenon contributed to the above average aboveground biomass and reduced proportion of C₄ plants in Prairies I–III in 2004 (34%, 18%, and 16% of aboveground biomass, respectively; not shown). For comparison to SOC and TN values, belowground biomass is reported as

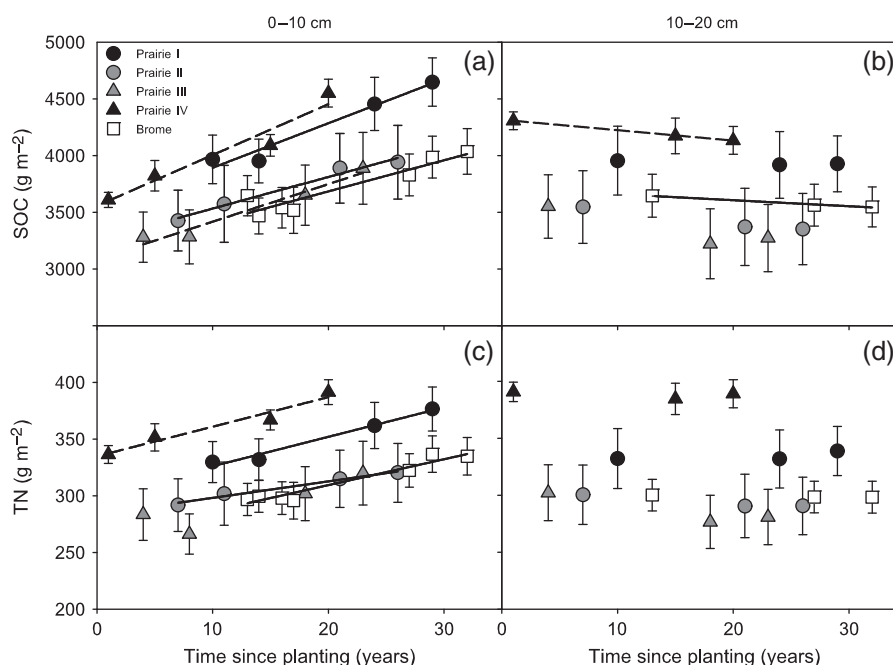


Fig. 2 Soil organic carbon (SOC) and total nitrogen (TN) accretion in restored prairies and C_3 brome field from 1985 to 2004. Circles and triangles represent plots of different age within a moisture category. Each symbol represents plot level means ($n = 9-10$) and error bars are SE. SOC and TN values are based on equivalent mass (see 'Materials and methods'). (a) SOC accretion at 0–10 cm. Prairie I: intercept = 3500.3 ± 118.5 , slope = 39.2 ± 5.7 , $r^2 = 0.96$, $P = 0.02$. Prairie II: intercept = 3253.8 ± 56.0 , slope = 27.9 ± 3.1 , $r^2 = 0.98$, $P = 0.01$. Prairie III: intercept = 3085.1 ± 75.1 , slope = 33.3 ± 4.9 , $r^2 = 0.96$, $P = 0.02$. Prairie IV: intercept = 3558.1 ± 103.6 , slope = 44.9 ± 8.1 , $r^2 = 0.94$, $P = 0.03$. Brome: intercept = 3136.1 ± 104.0 , slope = 27.5 ± 4.6 , $r^2 = 0.88$, $P < 0.01$. (b) SOC accretion at 10–20 cm. Prairie IV: intercept = 4315.6 ± 4.7 , slope = -9.2 ± 0.3 , $r^2 = 0.99$, $P = 0.02$. Brome: intercept = 3712.5 ± 14.9 , slope = -5.3 ± 0.6 , $r^2 = 0.99$, $P = 0.07$. (c) TN accretion at 0–10 cm. Prairie I: intercept = 300.1 ± 5.7 , slope = 2.6 ± 0.3 , $r^2 = 0.98$, $P = 0.01$. Prairie II: intercept = 283.6 ± 2.8 , slope = 1.5 ± 0.2 , $r^2 = 0.98$, $P = 0.01$. Prairie III: intercept = 262.3 ± 13.8 , slope = 2.3 ± 0.9 , $r^2 = 0.77$, $P = 0.13$. Prairie IV: intercept = 334.8 ± 5.4 , slope = 2.6 ± 0.4 , $r^2 = 0.95$, $P = 0.03$. Brome: intercept = 263.8 ± 6.0 , slope = 2.3 ± 0.3 , $r^2 = 0.93$, $P < 0.01$. (d) TN accretion at 10–20 cm. No plot had a significant regression.

g dw m^{-2} on the basis of equivalent mass. Belowground biomass varied from plot to plot and year to year, ranging from 162 to 1951 g dw m^{-2} in the top 10 cm in 1985 and from 978 to 1787 g dw m^{-2} by 2004 (Table 5). In 1985 when the prairies were relatively young, prairie belowground biomass was directly related to time since planting (slope = $194 \text{ g dw m}^{-2} \text{ yr}^{-1}$, $r^2 = 0.99$, $P < 0.01$). By 2004, however, belowground biomass was no longer related to plot age (slope = $-80 \text{ g dw m}^{-2} \text{ yr}^{-1}$, $r^2 = 0.72$, $P = 0.15$). In fact, belowground biomass was greatest in Prairie IV and essentially equal in Prairies I–III. As expected, more biomass was found near the surface than in the deeper soil layer. In 1985, 60–73% of the biomass in the 0–20 cm increment occurred in the surface 10 cm and this increased to 78–86% by 2004 (Table 5).

Depth distribution

The depth distribution of SOC and TN stocks changed over time irrespective of soil moisture (Table 6). At the

start of the study in 1985, the three oldest plots, Brome and Prairies I and II, had a ratio of SOC_{0-10} to SOC_{10-20} very close to 1, indicating that SOC stocks were essentially equal at 0–10 and 10–20 cm. The two youngest plots (Prairies II–IV) had ratios < 1 in 1985, indicating that they had more SOC at depth. Ratios increased over time and by 2004 all plots had 10–20% more SOC at 0–10 cm than at 10–20 cm (Table 6).

Discussion

Soil moisture

Our results indicate that even small topographic variation (Table 1) and its impacts on drainage and soil moisture conditions can influence SOC and TN accretion rates over decadal scales (Figs 1, 2a, c, and 3). In the surface 10 cm, the seasonally saturated prairies tended to accrete SOC and TN about 30% faster than the mesic prairies or brome field (Fig. 2a and c). Sustained over two decades, this difference in accretion rate led to

Table 2 Soil C:N ratios in restored prairies and C₃ brome field for each sampling date at 0–10 and 10–20 cm depths (based on equivalent mass – see 'Materials and methods')

	Prairie I	Prairie II	Prairie III	Prairie IV	Brome
<i>0–10 cm</i>					
1985	12.0 (0.1)	11.8 (0.2)	11.7 (0.2)	10.7 (0.1)	12.3 (0.1)
1989	11.9 (0.2)	11.8 (0.2)	12.3 (0.2)	10.9 (0.1)	11.9 (0.1)
1999	12.3 (0.1)	12.4 (0.1)	12.2 (0.2)	11.2 (0.1)	11.9 (0.1)
2004	12.4 (0.1)	12.3 (0.1)	12.2 (0.1)	11.6 (0.1)	12.1 (0.1)
Intercept	11.7 (0.1)	11.5 (0.2)	11.8 (0.3)	10.6 (0.1)	11.9 (0.3)
Slope	0.02 (0.01)*	0.03 (0.01)*	0.02 (0.02)	0.04 (0.01)**	<0.01 (0.01)
<i>r</i> ²	0.85	0.88	0.34	0.92	<0.01
<i>10–20 cm</i>					
1985	11.9 (0.1)	11.7 (0.2)	11.8 (0.2)	11.0 (0.1)	12.1 (0.1)
1999	11.8 (0.1)	11.5 (0.1)	11.6 (0.3)	10.9 (0.1)	11.9 (0.1)
2004	11.6 (0.1)	11.4 (0.2)	11.6 (0.1)	10.6 (0.1)	11.9 (0.1)
Intercept	12.1 (0.2)	11.9 (<0.1)	11.8 (0.1)	11.1 (0.1)	12.3 (<0.1)
Slope	−0.02 (0.01)	−0.02 (<0.01)**	−0.01 (<0.01)	−0.02 (0.01)	−0.01 (<0.01)*
<i>r</i> ²	0.82	>0.99	0.78	0.90	0.99

The 10–20 cm depth increment was not collected in 1989. Values are plot level means with SE in parentheses, $n = 9–10$. Regression parameters are for linear relationships of C:N ratio as a function of time since planting (years) and statistical significance is indicated by ** $P < 0.05$ and * $0.05 < P < 0.10$.

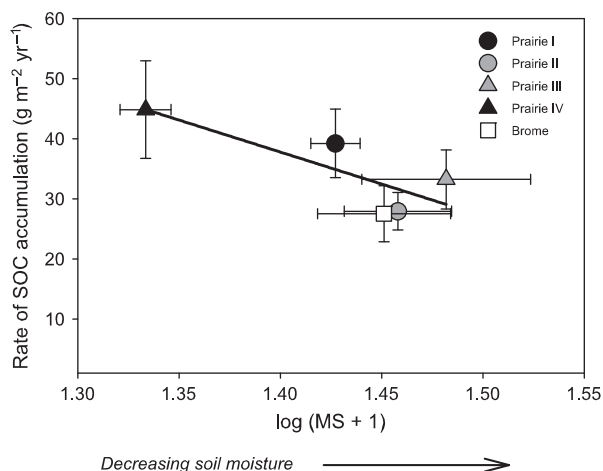


Fig. 3 Relationship between the rate of soil organic carbon (SOC) accumulation in the surface 10 cm (regression slopes in Fig. 2a) and transformed soil magnetic susceptibility ($\log(MS + 1)$) at 0–10 cm in restored prairies and C₃ brome field. Lower magnetic susceptibility (MS) indicates higher soil moisture. Circles and triangles represent plots of different age within a moisture category. Each symbol represents plot level means ($n = 9–10$) and error bars are SE. Intercept = 186.8 ± 61.4 , slope = -106.5 ± 42.9 , $r^2 = 0.67$, $P = 0.09$.

significant net increases in SOC stocks in the seasonally saturated prairies that were more than double the gains observed in the mesic prairies or brome field over the entire 20 cm profile (Fig. 1). These results were a consequence of both smaller net accrual of SOC and TN in the surface 10 cm and larger net losses at 10–20 cm in

Table 3 Rate and net change of C₄- and C₃-derived soil organic carbon from 1985 to 2004 in restored prairies and C₃ brome field at 0–10 cm depth ($\text{g C m}^{-2} \text{yr}^{-1}$ based on equivalent mass – see 'Materials and methods')

	Rate	<i>r</i> ²	Net change
<i>Prairie I</i>			
C ₄ -C	22 (3)**	0.96	450 (136)**
C ₃ -C	17 (9)	0.65	233 (93)**
<i>Prairie II</i>			
C ₄ -C	19 (3)**	0.95	351 (108)**
C ₃ -C	9 (<1)**	0.99	164 (122)
<i>Prairie III</i>			
C ₄ -C	3 (12)	0.04	212 (92)*
C ₃ -C	30 (16)	0.63	396 (194)*
<i>Prairie IV</i>			
C ₄ -C	30 (8)*	0.88	654 (109)**
C ₃ -C	14 (1)**	0.99	287 (88)**
<i>Brome</i>			
C ₄ -C	−15 (5)	0.80	−229 (51)**
C ₃ -C	38 (9)**	0.91	618 (101)**

*Plot level means ($n = 9–10$) shown with SE in parentheses. Rate based on linear regressions of C₄-C or C₃-C in each plot as a function of time since planting. Significant rate (i.e. regression slope) and net change (based on paired *t*-test) are indicated by ** $P < 0.05$ and * $0.05 < P < 0.10$.

mesic prairies compared with seasonally saturated prairies (Figs 1 and 2).

Soil moisture likely controls SOM accumulation via its influence and feedback on biotic mechanisms

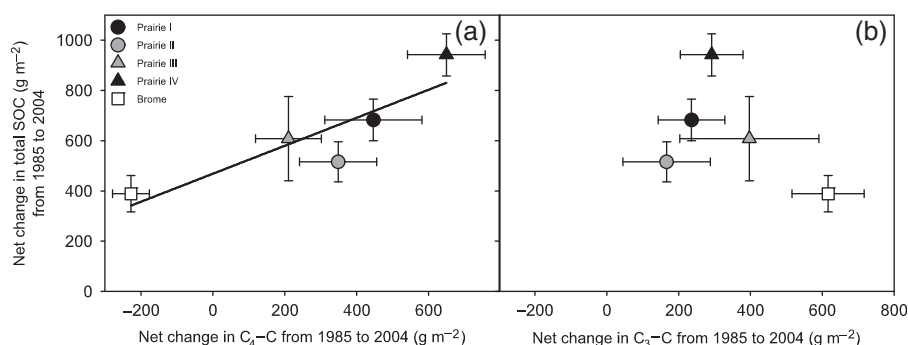


Fig. 4 Relationship between net change from 1985 to 2004 in total SOC in the surface 10 cm (based on equivalent mass – see ‘Materials and methods’) and the net change in (a) C_4 -C: intercept = 468.2 ± 70.2 , slope = 0.56 ± 0.17 , $r^2 = 0.78$, $P = 0.05$ and (b) C_3 -C: intercept = 817.9 ± 226.2 , slope = -0.56 ± 0.60 , $r^2 = 22$, $P = 0.42$. Circles and triangles represent plots of different age within a moisture category. Each symbol represents plot level means ($n = 9$ –10) and error bars are SE.

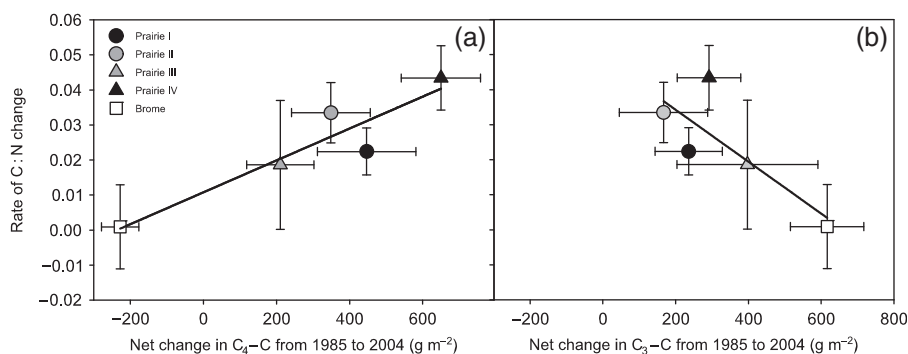


Fig. 5 Relationship between rate of C:N ratio change (regression slopes in Table 2) in the surface 10 cm of restored prairies and C_3 brome field and (a) net change in C_4 -C from 1985 to 2004: intercept = 0.011 ± 0.004 , slope = $5 \times 10^{-5} \pm 1 \times 10^{-5}$, $r^2 = 0.87$, $P = 0.02$ and (b) net change in C_3 -C from 1985 to 2004: intercept = 0.049 ± 0.012 , slope = $-7 \times 10^{-5} \pm 3 \times 10^{-5}$, $r^2 = 0.66$, $P = 0.095$ in the same plots. Circles and triangles represent plots of different age within a moisture category. Each symbol represents plot level means ($n = 9$ –10) and error bars are SE.

because it can affect both the quantity of plant inputs to soils and decomposition of those inputs. A higher water table throughout the growing season could promote plant production by easing moisture limitation during midsummer, leading to greater or more sustained organic matter inputs to soil (Knapp *et al.*, 1993). On the other hand, the periodic seasonal inundation and shallow water table observed in the seasonally saturated prairies could create partial hypoxic conditions that can inhibit microbial activities that mineralize SOM, reducing the efficiency of decomposition (Greenwood, 1961; Smith & Tiedje, 1979; Sextone *et al.*, 1985; Neckles & Neill, 1994; Trumbore & Harden, 1997). Unfortunately, no measures of time-integrated plant biomass inputs at scales relevant to the SOC and TN accrual were available for this study. Further experiments are needed to specifically partition the relative contributions of increased plant production and slowed decomposition to the observed effects of soil moisture on SOC and TN accrual.

Plant community

On average, the prairies accrued more SOC and TN at a faster rate in the surface 10 cm than the brome field (Fig. 2a and c). Prescribed fire may have supplied black C to the soil in prairies, increasing their SOC accrual rate compared with the unburned brome field (Glaser & Amelung, 2003; Dai *et al.*, 2005). Nonetheless, it is unlikely that black C alone can explain our findings (Dai *et al.*, 2005; Knicker, 2007), and other ecological mechanisms are probably more important. For instance, compared with the brome field the prairies had higher functional and species diversity, which has been shown to enhance SOC stocks in a variety of systems (Piper, 1998; Russell, 2002; Russell *et al.*, 2004) including grasslands (Fornara & Tilman, 2008; Steinbeiss *et al.*, 2008). One means by which diversity could increase SOC is through ecological complementarity, which enhances NPP and thus detrital inputs (Cardinale *et al.*, 2007). At our site, differences in SOC accrual could be related

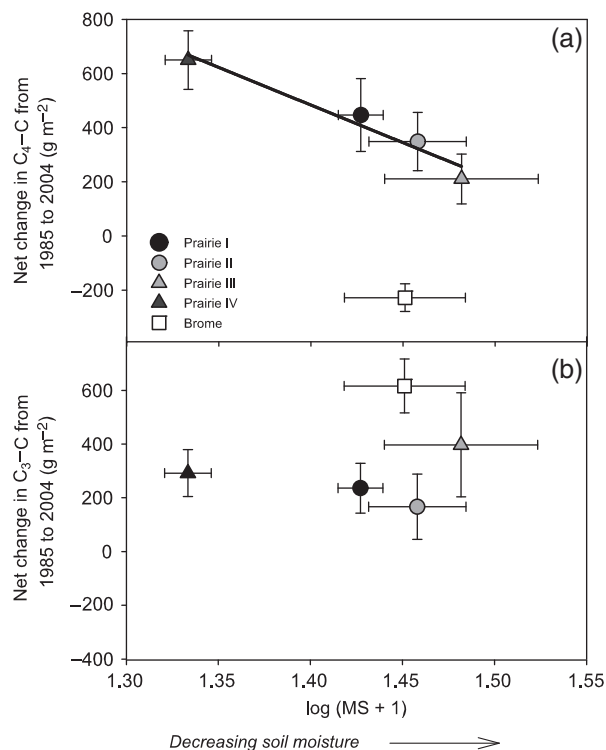


Fig. 6 Relationship between the net change from 1985 to 2004 of (a) C_4 -derived C and soil magnetic susceptibility (MS): intercept = 4366.4 (608.7) slope = -2773.4 (426.8) $r^2 = 0.95$ $P = 0.02$ and (b) C_3 -derived C and soil MS: intercept = 78.7 (1503.3) slope = 136.2 (1054.1) $r^2 = 0.01$ $P = 0.91$ in restored prairies and C_3 brome field. Lower MS indicates higher soil moisture. C_4 - and C_3 -C were calculated based on equivalent mass (see 'Materials and methods'). Circles and triangles represent plots of different age within a moisture category. Each symbol represents plot level means ($n = 9$ –10) and error bars are SE.

to NPP, because aboveground biomass standing stocks averaged over all years were higher in prairies than in brome (487 vs. 310 g dw m^{-2} , $P < 0.01$; Table 4). Further, the difference in NPP was probably even greater than the difference in June/July biomass standing stocks (sampling in June/July occurred closer to the time of peak production in brome than in prairies). Yet, in several studies in temperate climates, monocultures of highly productive grasses such as *P. virgatum* or *Miscanthus × giganteus* did not produce significant increases in SOC stocks compared with controls after 5–16 years (Garten & Wullschlegel, 1999; Hansen *et al.*, 2004; Clifton-Brown *et al.*, 2007; Schneckenberger & Kuzyakov, 2007). Thus, high NPP is not always enough to induce significant SOC accrual. Diversity could also enhance SOC by providing inputs with more chemical complexity and greater spatial and temporal heterogeneity (Meier & Bowman, 2008), which might help build SOC (Silver & Miya, 2001; Russell *et al.*, 2007). The

Table 4 Aboveground biomass in restored prairies and C_3 brome field in each sampling year

	Prairie I			Prairie II			Prairie III			Prairie IV			Brome		
	AGBM (g m ⁻²)	Grass (%)	C ₄ (%)	AGBM (g m ⁻²)	Grass (%)	C ₄ (%)	AGBM (g m ⁻²)	Grass (%)	C ₄ (%)	AGBM (g m ⁻²)	Grass (%)	C ₄ (%)	AGBM (g m ⁻²)	Grass (%)	C ₄ (%)
1985	481 (29)	84 (6)	83 (6)	408 (29)	50 (8)	43 (8)	290 (28)	60 (10)	27 (12)	428 (74)	48 (10)	36 (9)	230 (19)	100 (0)	0
1989	481 (47)	88 (4)	79 (6)	391 (36)	51 (9)	32 (10)	301 (50)	69 (7)	51 (10)	276 (41)	34 (8)	18 (6)	324 (39)	100 (0)	0
1999	357 (31)	70 (8)	–	348 (29)	57 (5)	–	630 (85)	62 (7)	–	761 (112)	84 (3)	–	327 (34)	89 (6)	0
2004	904 (237)	24 (9)	7 (2)	732 (117)	40 (9)	28 (8)	750 (136)	46 (9)	12 (5)	303 (27)	51 (7)	35 (8)	359 (17)	86 (6)	0

Values are plot level means with SE in parentheses, $n = 9$ –10. Biomass from C_4 plants was not quantified separately in 1999.

Table 5 Belowground biomass in restored prairies and C₃ brome field at 0–10 cm depth (based on equivalent mass – see ‘Materials and methods’) and relative depth distribution of belowground biomass (ratio of BGBM_{0–10 cm} to BGBM_{10–20 cm}) in each sampling year

	Prairie I		Prairie II		Prairie III		Prairie IV		Brome	
	g m ⁻²	Ratio	g m ⁻²	Ratio	g m ⁻²	Ratio	g m ⁻²	Ratio	g m ⁻²	Ratio
1985	1951 (260)	2.7 (0.2)	1211 (319)	2.5 (0.2)	764 (121)	2.7 (0.3)	162 (45)	1.5 (0.2)	996 (81)	3.1 (0.2)
1989	1168 (293)	–	907 (130)	–	820 (94)	–	499 (96)	–	900 (92)	–
1999	1324 (143)	5.1 (0.4)	1469 (114)	6.7 (0.3)	1197 (92)	4.0 (0.1)	1250 (136)	3.9 (0.3)	945 (52)	3.4 (0.1)
2004	978 (89)	3.5 (0.8)	1114 (76)	5.2 (0.3)	1100 (77)	5.4 (0.7)	1787 (322)	5.4 (0.8)	1010 (44)	6.0 (0.7)

Values are plot level means with SE in parentheses, $n = 9$ –10. The 10–20 cm depth increment was not collected in 1989.

Table 6 Relative depth distribution of SOC (ratio of SOC_{0–10 cm} to SOC_{10–20 cm} based on equivalent mass – see ‘Materials and methods’) in restored prairies and C₃ brome field for sampling years when both depth increments were collected

	Prairie I	Prairie II	Prairie III	Prairie IV	Brome
1985	1.03 (0.05)	0.98 (0.02)	0.93 (0.02)	0.84 (0.01)	1.00 (0.02)
1999	1.16 (0.03)	1.18 (0.04)	1.16 (0.04)	0.99 (0.02)	1.08 (0.01)
2004	1.20 (0.03)	1.19 (0.02)	1.20 (0.02)	1.10 (0.02)	1.14 (0.02)
Rate	0.009 (<0.001)**	0.012 (0.003)	0.015 (0.002)*	0.013 (0.003)	0.007 (0.002)
r^2	>0.99	0.94	0.99	0.96	0.95

The rate shown is the slope of linear regression for depth distribution as a function of time since planting. Values are plot level means with SE in parentheses, $n = 9$ –10. Significant rates are indicated by ** $P < 0.05$ and * $0.05 < P < 0.10$.

diverse residue quality of plants characteristic of tall-grass prairie (warm-season C₄ grasses, cool-season C₃ grasses and warm- and cool-season C₃ forbs) may thus encourage rapid SOC recovery.

In addition to its role in complementarity, phenology may directly enhance SOC in prairies compared with brome. C₃ grasses are active in cool, moist times early and late in the growing season whereas C₄ grasses and many prairie forbs (C₃) are active throughout hotter and drier periods (Ode *et al.*, 1980; Ehleringer & Monson, 1993; Ogle *et al.*, 2003). With higher functional diversity (e.g. C₃/C₄ mixture), organic matter inputs can be sustained for longer portions of the year (Buyanovsky *et al.*, 1987; Fornara & Tilman, 2008), increasing the likelihood of organic matter entering the soil during periods of reduced mineralization. Thus, the combination of the seasonal distribution of diverse inputs and greater NPP may have contributed to greater SOC accrual in prairies compared with brome (Fig. 1).

Within the species-rich prairies, the C₄ vegetation appeared to be particularly important for SOC accumulation. Each prairie (except Prairie III) accrued about twice as much C₄-derived SOC as C₃-C (Table 3). That response was independent of the C₄ contribution to

aboveground biomass because there was generally not twice as much C₄ biomass compared with C₃ biomass (Table 4). Total SOC gains were best predicted by the dynamics of C₄-derived C (Fig. 4), which is consistent with other reports and suggests that C₄-C is a critical driver of total SOC in warm- to cool-temperate systems (Knops & Tilman, 2000; Fornara & Tilman, 2008). The change in soil C:N ratio over time (Table 2) also occurred at rates predicted by the net change in C₄-C and C₃-C (Fig. 5; Mahaney *et al.*, 2008). These dynamics depend on a combination of the relative amount of C₄ and C₃ inputs and their potentially different decomposability. Native prairie species, especially C₄ grasses, produce root tissue of lower nutritional quality (higher C:N ratio) for microbial decomposers compared with C₃ plants (Hessen *et al.*, 2004; Huang *et al.*, 2004). Furthermore, compared with brome, mixed C₄/C₃ prairie ecosystems have a higher proportion of coarse roots (i.e. roots > 1 mm in diameter; Reinhardt & Miller, 1990), which generally decompose slower than fine roots (Gill & Jackson, 2000; Matamala *et al.*, 2003). Thus prairie root residues may have greater opportunity to become stabilized SOM (see Sollins *et al.*, 1996). High stabilization of C₄-derived SOM can also be inferred from the brome plot, where old C₄-C appeared to be

remarkably persistent even though C_4 inputs were eliminated by 1971 (Fig. 4a).

There was a strong inverse relationship between the net accrual of C_4 -C and soil MS (Fig. 6a). All prairies supported similar, generally mesic plant communities seasonally dominated by C_4 grasses, and soil moisture can be rather low in the surface soils of even seasonally saturated prairies during parts of the growing season. Mesic prairies were generally better drained and often had lower water tables than seasonally saturated prairies. Thus, the relationship between C_4 -C and soil moisture is likely a combined function of (1) higher productivity in the seasonally saturated plots because more moisture is available for growth at times of stress and (2) limited organic matter decomposition during the wettest periods. A relationship between C_3 -C and soil moisture (Fig. 6b) was not apparent perhaps because C_3 -derived inputs are more likely to be suppressed in the seasonally saturated prairies, because the timing of inundation coincides with the peak of C_3 growth in the spring and thus may inhibit it. Another possible reason is that functional diversity of C_3 plants is higher than that of C_4 grasses in prairies and may have shifted over time. The resulting variations in root morphology and the chemistry of C_3 plants thus might have obscured any relationship between C_3 -C and moisture.

Depth distribution

The bulk of SOC and TN accumulation occurred in the surface 10 cm and compensated for SOC and TN losses or lack of change below 10 cm (Figs 1 and 2). Our findings below 10 cm are consistent with depth responses in other studies (Baer *et al.*, 2002; Russell *et al.*, 2005; Kucharik, 2007; Steinbeiss *et al.*, 2008) and may be largely attributable to changes in input rates during restoration. After cessation of tillage, plant inputs at depth are greatly reduced compared with the continual delivery of fresh crop residues to deeper layers under conventional tillage (Yang *et al.*, 2008). On the other hand, biomass proliferation near the surface is much greater in perennial grasslands than in cultivated fields (e.g. Slobodian *et al.*, 2002). Drainage also may have influenced the variable response of SOC by depth because changing moisture conditions within the soil profile can promote different decomposition rates at different depths (Gill *et al.*, 1999). Indeed, the net SOC losses at 10–20 cm were especially pronounced in the mesic prairies where SOM decomposition may have occurred faster due to better soil aeration (Fig. 1).

Conversion from conventional row-crop agriculture to perennial grasslands also led to a partial recovery of the natural depth stratification of SOC found in native

grasslands. The ratio of SOC at 0–10 cm compared with SOC at 10–20 cm steadily increased with time from 0.84 to 1.2 (Table 6). Recovery of shallow SOC may be partly due to the depth distribution of the expansive system of roots and rhizomes in perennial grasslands, which results in much greater inputs at the surface than at depth (Dahlman & Kucera, 1965; Risser *et al.*, 1981; Matamala *et al.*, 2008). Belowground biomass at our site was four times greater, on average, at 0–10 cm than at 10–20 cm (Table 5), in line with SOC increases seen at 0–10 cm. Furthermore, the generally increasing C:N at 0–10 cm and decreasing C:N at 10–20 cm over time (Table 2) is consistent with a build-up of fresh organic matter (with higher C:N ratios; e.g. Baldock *et al.*, 1992; Gregorich *et al.*, 1996) at the surface and a depletion of fresh material at depth. Hence, our results suggest that inputs from the restored grasslands were greater than decomposition or leaching of crop-derived SOM at the surface, while lower root biomass inputs at depth could not overcome such losses. However, this loss may dampen and reach steady state as root stocks build up at depth over time (Steinbeiss *et al.*, 2008).

Implications and conclusions

This study documents interactive moisture and vegetation controls on net SOC gains of restored prairies that lost native SOC stocks due to past agricultural activities. Our findings indicate that SOC and TN accrued at linear rates during the 19-year interval of the study in grasslands that ranged in age from 20 to 32 years at the study's close. Linear rates of SOC and TN accrual will not be sustained over time as soils of restored prairies approach steady state (Jenny, 1941; Olson, 1963; Jastrow, 1996; Six *et al.*, 2002; Post *et al.*, 2004; Kucharik, 2007; Matamala *et al.*, 2008). Our data suggest that total SOC accumulation in temperate grasslands is enhanced by inputs and stabilization of C_4 plant material (Table 3 and Fig. 4) and promoted by high soil moisture (Figs 1, 3, and 6). Both of these SOC-controlling factors may be influenced by rising atmospheric CO_2 concentrations and associated changes in climate for the temperate grasslands of North America. Changes in climate and CO_2 expected over the course of the current century may alter the current proportion of C_3 and C_4 plants (Sage & Kubien, 2003; von Fischer *et al.*, 2008). Further, there may be shifts in the seasonal distribution of precipitation and the intensity and pattern of precipitation events, potentially leading to reduced soil moisture during the growing season through several interacting mechanisms (Wuebbles & Hayhoe, 2004; Christensen *et al.*, 2007; Meehl *et al.*, 2007). Therefore, the SOC and TN accrual rates observed here are not as likely to occur as rapidly in future grassland restorations unless

appropriate adaptive management strategies are implemented to compensate for climatic and atmospheric changes. Such caution is particularly important given recent interest in the use of perennial grasslands for sustainable and C-negative biofuel energy (Tilman *et al.*, 2006), the use of which has been encouraged for marginal, often well-drained land. Given the divergence in SOC accrual that can arise from subtle differences in drainage, hydrology should be taken into account when forecasting SOC sequestration in such management scenarios. Furthermore, the broad distribution of sub-surface-drained cropland in this region offers an opportunity to reverse historical SOC losses due to cultivation and improved drainage, potentially sequestering substantial C if vegetation is returned to native ecosystems (Tilman *et al.*, 2006) together with reducing the flow from drain tile systems (Jastrow *et al.*, 2007).

In summary, SOC and TN accumulation rates appear to be controlled by an interaction of biotic and abiotic processes. Seasonally saturated prairies accrued double the SOC and triple the TN accumulated by mesic prairies in the top 20 cm of soil. Although the field comprised of cool-season grasses also gained SOC, it tended to do so at a slower rate than restored prairies with their mixed C₄/C₃ plant communities. We found the C₄ component of the prairie vegetation to be a more important contributor to total SOC than C₃ vegetation, an effect that may be enhanced by soil moisture given the strong relationship we observed between moisture and C₄-derived C but not C₃-C. These differences were most pronounced in the surface 10 cm, where most of the SOC and TN accumulation occurred. Combined with a small SOC loss in the 10–20 cm layer, the buildup of SOC appeared to be regenerating a depth-stratified SOC profile similar to never-tilled prairies. We hypothesize that tallgrass prairies may provide a stronger sink for atmospheric C than cool-season grasslands, especially if they are established on poorly drained land or if drain tiles are plugged or broken during restoration. Further research to better isolate and understand these interacting mechanisms is needed to maximize our ability to predict the performance of perennial grasslands as C sinks and to take full advantage of the C benefits of prairie restorations and herbaceous perennial bioenergy crops in a changing climate.

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