

Carbon and Nitrogen Sequestration in Two Prairie Topochronosequences on Contrasting Soils in Southern Wisconsin

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ABSTRACT.—Prairie restoration has the potential to sequester nitrogen (N) and atmospheric carbon (C) in the soil, but the capability of a site to respond positively to prairie restoration depends on numerous factors such as soil parent material, topography and time. Soil bulk density in the top 10 cm and C and N concentrations at several intervals to a depth of 1 m were measured in a tallgrass prairie topochronosequence at fine- and coarse-textured soil locations to evaluate the role of texture, slope and ecosystem age in controlling C and N sequestration following cessation of cultivation and subsequent prairie restoration. Soil C and N concentrations, contents and C:N ratios were significantly greater in fine-textured soils compared to sites with coarse-textured soil. Soil texture generally did not explain variations in the amounts or rates of C and N sequestration in the restored prairies. Soil surface bulk density was significantly correlated with slope, but not ecosystem age, at sites with coarse-textured soil. Within the limits of this study, neither slope nor ecosystem age were correlated to bulk density at sites with fine-textured soil. Soil C content in the top 25 cm increased significantly as ecosystem age increased for the restored and remnant prairies at the fine-textured location, but not at the coarse-textured location. Results demonstrate that a combination of soil parent material, topography and time since cessation of cultivation control the content and accumulation of C and N following prairie restoration. In the context of this study, the bottom line is that significant C sequestration was not achieved, given the current level and types of restoration management, within two and a half decades following conversion of cultivated cropland to prairie.

INTRODUCTION

In the mid-1800s, humans contributed to the most extensive ecological disturbance to the Upper Midwest since the end of the last ice age, ~11,000 y ago (Paul *et al.*, 1997). Native tallgrass prairies were targeted for food production because the soils were fertile, rich in nutrients and organic matter (Miller, 1997), and could support and sustain human settlement. Consequently, these highly diverse ecosystems were converted to cropland causing rapid depletion of soil nutrients and, particularly, soil carbon (C), from oxidation and release to the atmosphere (Tiessen *et al.*, 1982; Mann, 1986). For example, fewer than 800 ha of the estimated 850,000 ha of pre-settlement native prairie remain in Wisconsin, mostly as scattered remnants of 16 ha or less (Curtis, 1959).

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Conversion of marginal or abandoned croplands to prairie vegetation provides erosion control and habitat for a diverse array of wildlife and is gaining popularity because of prairies' aesthetic value. Prairie vegetation is frequently restored with the goal of returning aboveground biodiversity to the ecosystem, but often without establishing the link to belowground biogeochemical processes that are characteristic of virgin prairies. Prairie restoration has been shown to lead to a gradual buildup of soil C and nitrogen (N) over time (Miller, 1997; Knops and Tilman, 2000). Therefore, conversion of agricultural or abandoned lands to restored prairie has the potential to sequester significant amounts of N and atmospheric C in soil (Fan *et al.*, 1998).

In the 1980s the United States government implemented the Conservation Reserve Program (CRP) to reduce soil loss from highly erodible croplands. Though C sequestration was not an originally defined goal of the CRP, results have shown that cropland returned to natural vegetation can significantly increase C levels in the soil over time (Burke *et al.*, 1989, 1995; Gebhart *et al.*, 1994; Burke *et al.*, 1995; Reeder *et al.*, 1998; Robles and Burke, 1998; Potter *et al.*, 1999). More recently, the United States Department of Agriculture's (USDA) Farm Service Agency (FSA) implemented a Conservation Reserve Enhancement Program (CREP) to provide economic incentives to landowners carrying out eligible environmental conservation practices (USDA-FSA, 2000). Sites enrolled in governmental incentive programs for a minimum specified time and those that have simply been converted forever to less intensive land use offer unique opportunities to assess the impacts of land-use conversion. However, a challenge that researchers face is comparing the impacts of land-use conversion across multiple tracts of land at multiple sites.

Chronosequences and comparisons between adjacent disturbed and undisturbed ecosystems have been used to demonstrate the significance of ecosystem age on C and N dynamics following abandonment from cultivation (Goh *et al.*, 1976; Ihori *et al.*, 1995; Knops and Tilman, 2000). Similarly, the loss of soil organic matter with some agricultural practices has been shown to be significantly related to soil texture (Bauer and Black, 1981; Campbell and Souster, 1982; Burke *et al.*, 1989) and slope (Schimel *et al.*, 1985). Accumulation of soil C and N following cessation of cultivation has also been shown to be significantly affected by texture (Ihori *et al.*, 1995) and plant species composition (Burke *et al.*, 1995; Robles and Burke, 1997; Knops and Tilman, 2000).

Data characterizing the relationship between time since cessation of cultivation and soil C and N contents and their rates of sequestration in restored prairies are minimal. The number of virgin prairies available for reference is few, which means we have small data sets from which we attempt to draw significant inferences. Many prairie remnants are generally of low quality and possibly were not cultivated because the land was undesirable for agriculture. Carbon and N sequestration are affected by the same factors that influence soil formation, such as topography, vegetation, parent material, climate and time (Jenny, 1941). The combination of these factors and other circumstances makes assessment of C and N sequestration in restored prairies challenging. However, understanding future implications of prairie restoration on ecosystem nutrient dynamics can help plan for the potential negative effects of current environmental concerns, such as rising atmospheric carbon dioxide (CO₂) concentrations (Paustian *et al.*, 1997, 1998, 2000).

The question remaining is how much C sequestration can be expected from prairie restoration and what factors control the sequestration of atmospheric C in soil. Therefore, the objective of this study was to characterize soil surface C and N contents with depth in two tallgrass prairie topochronosequences in southern Wisconsin to evaluate the role of soil parent material, topography and time in controlling C and N sequestration following conversion from cultivated agriculture to restored prairie. We hypothesized that soil C and N storage and

sequestration rates are greater in fine- than coarse-textured soil. We also hypothesized that soil C and N sequestration are significantly correlated with slope and ecosystem age.

MATERIALS AND METHODS

Site locations and descriptions.—Study areas were selected at the Audubon Society's Goose Pond Sanctuary near Arlington (ARL), Wisconsin (43°17'N, 89°22'W) and the International Crane Foundation (ICF) near Baraboo, Wisconsin (43°29'N, 89°44'W) during spring 2000. These locations were selected because they have rare combinations of land management histories that include remnant prairie, cropland, CRP land and restored tallgrass prairie topochronosequences within a relatively small area (*i.e.*, 2 km²). Tallgrass prairie vegetation is common to the prairie ecosystems at each location. However, the prairie ecosystems vary by slope, ecosystem age and soil textural class; loam to silt-loam soils (*i.e.*, fine-textured) at the ARL location and sandy-loam to loamy-sand soils (*i.e.*, coarse-textured) at the ICF location (Mitchell, 1978) (Table 1).

The soils surrounding the fine-textured location developed under the influence of their position in an undulating landscape and past glaciation. Sandy-loam, calcareous glacial till originating from the advancement of the Green Bay ice lobe covered the area during Late Wisconsin time of the Quaternary period in geologic history (Hole, 1980). Although much of the area is presently cultivated, the soils surrounding the fine-textured location developed in a former prairie landscape characterized by native tallgrass prairie species such as big bluestem (*Andropogon gerardii*), little bluestem (*Schizachyrium scoparium*) and side-oats grama (*Bouteloua curtipendula*). Natural and native-American-induced fires periodically recycled nutrients contained in aboveground litter. Five soil series (*i.e.*, Plano, Saybrook, Channahon, Ringwood and Joy) of the six sampled at the fine-textured location are from the same soil association, while the Dresden soil series is from a similar soil association (Mitchell, 1978) (Table 1).

Remnant prairies at the fine-textured location are estimated to be about 3000-y-old (M. Martin, pers. comm., 2000), while restored prairies ranged from 1- to 24-y-old at the time of this study. Plantings for restoration generally occurred in the spring. Prairies at the fine-textured location are mesic tallgrass prairies ranging from 0.5 to 4 ha with dominant species, in no order of abundance, including big bluestem, indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), purple coneflower (*Echinacea purpurea*), goldenrod (*Solidago spp.*) and black-eyed susan (*Rudbeckia hirta*) (Brye, 1999). Prairies at the fine-textured location are subject to prescribed burning approximately every third year. An agricultural field that is annually tilled and planted with maize (*Zea mays*), peas (*Pisum sativum*) or soybeans (*Glycine max*), is adjacent to the oldest restored prairie and within 0.1 to 0.5 km of the other restored prairies.

Oak savanna was the predominant early vegetation type surrounding the 91-ha coarse-textured location (Cochrane and Iltis, 2000). However, the coarse-textured location had been under agricultural influence since European settlement (~1860) until 1979. Presently, approximately 40 ha of the ICF is a mix of restored and remnant tallgrass prairie and oak (*Quercus spp.*) savanna with adjacent cultivated cropland and CRP land. The remnant prairies at the coarse-textured location were never cultivated, but may have been grazed by livestock (J. Barzen, pers. comm., 2000). The coarse-textured location is currently dominated by moderately well-drained to excessively-drained sandy parent materials.

Tallgrass prairie restorations were initiated in plots ranging from 0.2 to 2 ha at the coarse-textured location annually from 1980 to 1996, except for 1987, 1988 and 1993. The dominant grass species in the ICF prairies are little bluestem, big bluestem, side-oats grama, junegrass (*Koeleria cristata*), indiangrass and prairie dropseed (*Sporobolus heteropolis*). The dominant forbs are lead plant (*Amorpha canescens*), thimbleweed (*Anemone cylindrica*), silky

TABLE 1.—Management history, ecosystem age, slope, soil type, and surface texture for the ecosystems sampled at the fine-textured Arlington (ARL) and coarse-textured International Crane Foundation (ICF) locations in southern Wisconsin

Location/Site (Symbol)	Year restored	Ecosystem age	Slope	Soil series/Taxonomic description	Surface texture
Arlington (ARL)		y	%		
Remnant prairie (Ra)	—	~3000	20	Channahon/Lithic Argiudoll	Silt Loam
Remnant prairie (Rb) [†]	—	~3000	1-3	Dresden/Mollic Hapludalf	Loam
Restored prairie (R-24)	1976	24	1-3	Plano/Typic Argiudoll	Silt Loam
Restored prairie (R-10)	1990	10	1-4	Plano/Typic Argiudoll	Silt Loam
Restored prairie (R-5a)	1995	5	0	Plano-Joy/Typic Argiudoll-Aquic Hapludoll	Silt Loam
Restored prairie (R-5b)	1995	5	0	Plano/Typic Argiudoll	Silt Loam
Agricultural field (Ag)	—	>50	0	Plano/Typic Argiudoll	Silt Loam
International Crane Foundation (ICF)					
Remnant prairie (Ra)	—	~3000	10	Wyocena/Typic Hapludalf	Sandy Loam
Remnant prairie (Rb)	—	~3000	25	Gotham/Psammentic Hapludalf	Loamy Sand
Restored prairie (R-20)	1980	20	0	Wyocena/Typic Hapludalf	Sandy Loam
Restored prairie (R-18)	1982	18	5	Wyocena/Typic Hapludalf	Sandy Loam
Restored prairie (R-16)	1984	16	5	Wyocena/Typic Hapludalf	Sandy Loam
Restored prairie (R-14)	1986	14	2	Wyocena/Typic Hapludalf	Sandy Loam
Restored prairie (R-10)	1990	10	0	Wyocena/Typic Hapludalf	Sandy Loam
Restored prairie (R-9)	1991	9	0	Wyocena/Typic Hapludalf	Sandy Loam
CRP Land/Grassland (CRP/R-7)	1993	7	0	Plainfield/Typic Udipsamment	Loamy Sand
Restored prairie (R-6a) [‡]	1994	6	0	Gotham/Psammentic Hapludalf	Loamy Sand
Restored prairie (R-6b)	1994	6	0	Gotham/Psammentic Hapludalf	Loamy Sand
Restored prairie (R-6c)	1994	6	0	Gotham/Psammentic Hapludalf	Loamy Sand
Restored prairie (R-4)	1996	4	10	Wyocena/Typic Hapludalf	Sandy Loam
Agricultural field (Ag)	—	>50	0	Plainfield-Gotham/Typic Udipsamment-Psammentic Hapludalf	Loamy Sand

[†] The soil profile of the Rb remnant at the fine-textured ARL location is shallow, <30 cm to bedrock

[‡] The 6-y-old restored prairie at the coarse-textured ICF location was planted at three levels of species density, low (a), medium (b) and high (c)

aster (*Aster sericeus*) and purple prairie clover (*Petalostemum purpureum*). Each prairie has been subject to several intervals of prescribed burning on an approximate 5-y burn cycle.

Mean annual precipitation for both locations is 790 mm, of which ~30% occurs as snow (Owenby and Ezell, 1992). Mean annual temperature (MAT) for the Arlington region is 7.6 C with a January minimum of -13.8 C and a July maximum of 28.3 C, whereas MAT at the ICF is 6.8 C with an average January minimum of -16.1 C and average July maximum of 26.4 C (Owenby and Ezell, 1992).

Soil sampling protocol, preparation and analyses.—During summer 2000 five soil samples were collected from the top 10 cm in a 181-cm³ core from two remnant prairies, four restored prairies and an adjacent cultivated agricultural field at the fine-textured location and from two remnant prairies, eight restored prairies, an adjacent cultivated agricultural field and an adjacent CRP field at the coarse-textured location (Table 1). Soil samples were dried at 105 C for 24 h for bulk density (BD) determinations.

Multiple soil samples were also collected and composited for one sample per depth per

prairie for soil C and N concentration determinations. At the fine-textured location, five 2-cm diameter soil cores were collected at 25-cm increments to 100 cm. At the coarse-textured location, fifteen 2-cm diameter soil cores were collected from the 0 to 5, 5 to 10, 10 to 25, 25 to 50 and 50 to 100 cm depths. Dry soil samples were mechanically ground to pass through a 2-mm mesh screen and reground by hand with a mortar and pestle to pass a 100-mesh sieve. Total soil C and N concentrations were determined by high-temperature catalytic combustion using a Carlo Erba Model NA 1500 C and N analyzer (CE Instruments, Milan, Italy). All soil C was assumed to be organic C since soil samples were not collected from the transition horizon comprised of calcareous glacial till and therefore did not effervesce upon treatment with dilute hydrochloric acid.

Calculations and statistical analyses.—For the purpose of statistical analyses, soil C and N concentrations measured in the 0 to 5, 5 to 10 and 10 to 25 cm depths at the coarse-textured location were combined using a weighted average by depth interval into a representative value for the 0 to 25 cm depth to facilitate comparison with the fine-textured location. In addition, soil C and N concentrations measured at the fine-textured location for the 50 to 75 and 75 to 100 cm depths were averaged into a representative value for the 50 to 100 cm depth to facilitate comparison with the coarse-textured location.

Soil C and N contents were calculated for the 0 to 25-cm depth by assuming that bulk density in the top 25 cm did not differ significantly from the 0 to 10-cm bulk density for which actual bulk density measurements were obtained. This assumption is reasonable for the ecosystems at both location in this study because, based on hand texturing, noticeable changes in particle size, which are known to significantly affect bulk density (Lal and Kimble, 2001), did not occur within the top 25 cm of the remnant prairies and cultivation during previous land use has uniformly mixed the top soil in the restored prairies. Soil bulk densities are reported as a mean and standard error (SE). Since multiple, representative soil samples were collected and composited per depth from the ecosystems sampled at each location, variability of soil C and N concentration measurements are not available to report.

Amounts of C and N sequestered were calculated as the difference between the C and N contents in the restored prairies and the C and N contents in the adjacent cultivated agricultural field at each location. Carbon and N sequestration rates were calculated by dividing the amounts of C and N sequestered in a restored prairie by the age of the restored prairie (Table 1).

Since the mean age of restored prairies at the two locations did not differ significantly (*i.e.*, 11.0- and 10.5-y old for the fine- and coarse-textured locations, respectively), a one-way analysis of variance was performed to determine the effect of soil texture (*i.e.*, fine- vs. coarse-textured) on soil bulk density, soil C and N concentrations, C:N ratios and on the amount and rate of C and N sequestration, relative to the adjacent cultivated agricultural field in the restored prairies at each location (Minitab, 1997). Multiple regression was used to determine the significance of slope and ecosystem age in controlling soil bulk density, C and N concentrations, C:N ratios and the amounts and rates of C and N sequestration for restored prairies at each location. The sequential sum of squares for each predictor was compared to the model's total sum of squares to determine each predictor's relative contribution to explaining the variability of the measured parameter.

RESULTS

Bulk density.—Soil surface bulk density differed significantly ($P < 0.001$) among the ecosystems sampled at the fine- and coarse-textured locations. Mean soil bulk density in the top 10 cm was the lowest in the shallow-profile Rb remnant [1.31 (SE ± 0.01) g cm⁻³] and highest for the agricultural site [1.51 (SE ± 0.01) g cm⁻³] at the fine-textured location.

Similarly, mean bulk density was the lowest for the 14-y-old restored prairie (R-14) [1.41 ($SE \pm 0.05$) $g\ cm^{-3}$] and highest for the agricultural site [1.91 ($SE \pm 0.04$) $g\ cm^{-3}$] at the coarse-textured location.

Soil surface bulk density for the restored and remnant prairies was significantly higher ($P = 0.011$) in the coarse- than fine-textured soil. Bulk density in the restored prairies increased significantly ($P = 0.01$) as slope increased at the coarse-textured location (Fig. 1), whereas addition of ecosystem age did not improve the multiple regression model. Neither slope nor ecosystem age were significantly correlated with soil surface bulk density in the restored prairies at the fine-textured location.

Soil carbon.—Soil C concentration and content in the top 25 cm, averaged across restored and remnant prairies, were significantly higher ($P < 0.001$) in the fine- than coarse-textured soil. Soil C concentration ranged from 15.5 to 37.3 $g\ kg^{-1}$ in the top 25 cm for the restored and remnant prairies at the fine-textured location (Table 2), while soil C content ranged from 5.1 to 12.2 $kg\ C\ m^{-2}$ (data not shown). Soil C concentration ranged from 5.6 to 12.2 $g\ kg^{-1}$ in the top 25 cm for the restored and remnant prairies at the coarse-texture location (Table 2), while soil C content ranged from 2.1 to 4.5 $kg\ C\ m^{-2}$ (data not shown).

Neither slope nor ecosystem age, by themselves or combined as sequential predictors, were significantly linearly related to soil C concentration or C:N ratio in the 0–25, 25–50, 50–100, or 0–100 cm depth interval and soil C content in the 0–25 cm depth interval for the restored prairies of the fine- or coarse-textured locations (Table 3). However, in general, ecosystem age explained a higher proportion of the variations by depth in soil C concentration, C:N ratio and C content than did slope (Table 3). When remnant prairies are included with restored prairies, soil C concentration for the fine-textured and soil C:N ratio in the top 25 cm for the coarse-textured location increased, while soil C concentration in the top 25 cm at the coarse-textured location significantly decreased, significantly ($P < 0.1$; Note: with a small number of observations, such as in this study, statistical significance may be more appropriately established at the 10 rather than 5% level) as ecosystem age increased (Fig. 2). The contrasting results between locations relate to differences in infiltration capacities with subsequent drainage. Decreasing soil C, with a concomitant increase in soil C:N ratio, in the top 25 cm at the coarse-textured location are consistent with a higher infiltration capacity and greater redistribution of solutes, particularly soluble C, to the subsoil for a coarse- than fine-textured soil.

Soil texture did not affect the amount of C sequestered or the rate of C sequestration in the restored prairies at either location. The mean C sequestration rate in the top 25 cm was 0.12 ($SE \pm 0.05$) and 0.07 ($SE \pm 0.02$) $kg\ C\ m^{-2}\ y^{-1}$ in the fine- and coarse-textured soils, respectively. The amount and rate of C sequestered declined, though not significantly, as ecosystem age increased in the restored prairies at the fine-textured location (Fig. 3). Neither slope nor ecosystem age were related to the amount or rate of C sequestered in the restored prairies at either location.

Soil nitrogen.—Prairie soil N concentration and content were significantly higher ($P < 0.001$) in the fine- than coarse-textured soil. Soil N concentration in the top 25 cm ranged from 1.5 to 3.3 $g\ kg^{-1}$ for the restored and remnant prairies at the fine-textured location (Table 2), while soil N content ranged from 0.5 to 1.1 $kg\ N\ m^{-2}$. Soil N concentrations in the top 25 cm at the coarse-textured location ranged from 0.4 to 1.0 $g\ kg^{-1}$ (Table 3), while soil N content ranged from 0.2 to 0.4 $kg\ N\ m^{-2}$. Neither slope nor ecosystem age were significantly correlated with soil N concentration or content in the restored prairies at either location.

The C:N ratio in the restored and remnant prairies was significantly higher ($P < 0.013$) in the coarse- than fine-textured soil in the 0–25 and 25–50 cm layers. Neither slope nor ecosystem age was a significant predictor of the soil C:N ratio in any layer for the restored

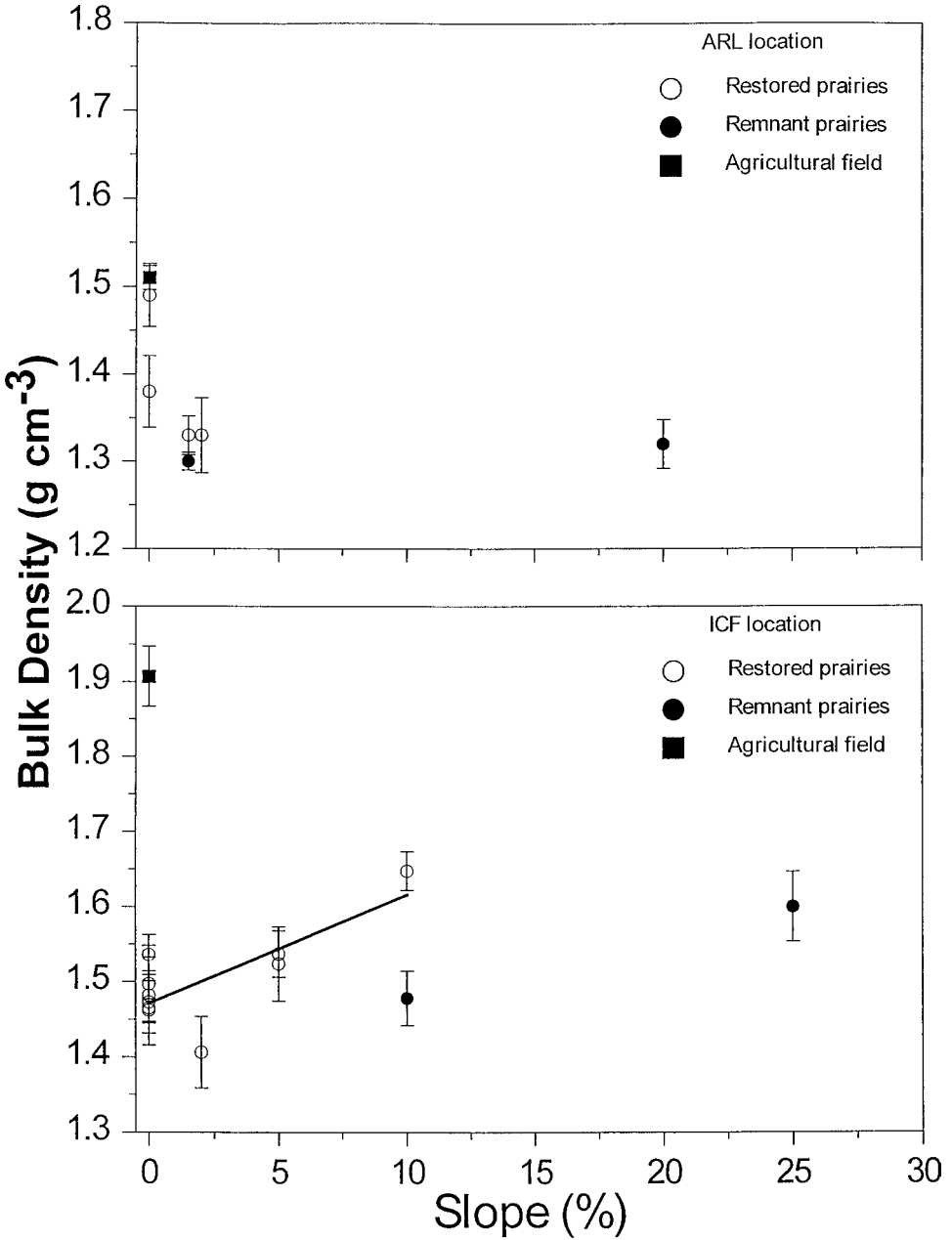


FIG. 1.—Relationship between soil bulk density (BD) for the top 10 cm and slope for the restored and remnant prairies at the fine-textured ARL and coarse-textured ICF locations. Standard error bars are plotted for replicate measurements. The linear regression model for the restored prairies at the coarse-textured ICF location is $BD = 0.0145 \times (\% \text{ slope}) + 1.47$, $r^2 = 0.59$, $P = 0.01$

TABLE 2.—Soil C and N concentrations by depth for the ecosystems at the fine-textured ARL and coarse-textured ICF locations. See Table 1 for complete description of ecosystem symbols

Location/Site	Soil C concentrations (g kg ⁻¹)			Soil N concentration (g kg ⁻¹)		
	0–25 cm	25–50 cm	50–100 cm	0–25 cm	25–50 cm	50–100 cm
Arlington (ARL)						
Ra	21.5	8.5	11.7	2.1	0.8	0.4
Rb [†]	37.3	—	—	3.3	—	—
R-24	15.5	5.7	3.6	1.5	0.6	0.3
R-10	20.9	7.7	3.9	1.9	0.7	0.4
R-5a	16.0	8.6	7.5	1.5	0.8	0.7
R-5b	18.9	7.3	3.9	1.8	0.7	0.4
Ag	14.2	5.1	3.0	1.5	0.6	0.4
International Crane Foundation (ICF)						
Ra	5.6	1.9	1.8	0.4	0.1	0.1
Rb	5.9	2.6	1.8	0.4	0.2	0.1
R-20	12.2	3.3	2.1	1.0	0.2	0.1
R-18	7.1	2.9	1.8	0.6	0.2	0.1
R-16	7.6	2.4	1.6	0.5	0.2	0.1
R-14	9.6	4.1	2.5	0.8	0.3	0.3
R-10	6.2	2.5	2.0	0.5	0.1	0.1
R-9	10.0	3.7	3.1	0.9	0.3	0.2
CRP/R-7	8.3	3.1	1.9	0.8	0.2	0.2
R-6a [‡]	8.2	2.8	1.7	0.7	0.2	0.1
R-6b	6.3	1.8	1.8	0.5	0.1	0.1
R-6c	7.3	2.8	1.5	0.6	0.2	0.1
R-4	7.0	3.8	1.9	0.6	0.3	0.1
Ag	5.7	2.1	1.5	0.5	0.2	0.1

[†] The soil profile of the Rb remnant at the fine-textured ARL location is shallow, <30 cm to bedrock

[‡] The 6-y-old restored prairie at the coarse-textured ICF location was planted at three levels of species density, low (a), medium (b) and high (c)

prairies at the either location (Table 2). However, the soil C:N ratio in the top 25 cm for the restored and remnant prairies combined at the fine-texture location did not correlate with slope or ecosystem age, but the soil C:N ratio in the top 25 cm for the restored and remnant prairies combined at the coarse-textured location increased significantly ($P = 0.026$) as slope increased (Fig. 2E).

Soil texture was unrelated to the amount or rate of N sequestered in the restored prairies at either location. The mean N sequestration rate in the top 25 cm was <0.01 ($SE \pm <0.01$) and < -0.01 ($SE \pm <0.01$) kg N m⁻² y⁻¹ in the fine- and coarse-textured soils, respectively. The amount and rate of N sequestered declined, though not significantly, as ecosystem age increased in the restored prairies at the fine-textured location (Fig. 3). Neither slope nor ecosystem age explained variation in the amount or rate of N sequestered in the restored prairies at either location.

DISCUSSION

Soil carbon and nitrogen dynamics.—Soil C and N concentrations in the top 1 m and soil C and N contents in the top 25 cm were significantly higher in the fine- than coarse-textured soil. On average, soil C and N contents in the top 25 cm at the coarse-textured location were 15 and 35%, respectively, of those at the fine-textured location indicating that variations in

TABLE 3.—Summary of multiple regression analysis with slope and ecosystem age as sequential predictors of soil carbon (C) concentrations and carbon:nitrogen (C:N) ratios at various depths to 1 m and soil C content for the 0 to 25-cm depth for the restored tallgrass prairies at the fine-textured ARL and coarse-textured ICF locations

Location/Soil property	Depth (cm)	Slope [†]		Ecosystem age		Whole model	
		% of Sum of squares [‡]	P-value	% of Sum of squares	P-values	Adjusted R ²	P-value
Arlington (ARL)							
C concentration	0–25	10.8	0.347	67.3	0.330	0.342	0.468
	25–50	20.5	0.813	59.6	0.334	0.401	0.447
	50–100	35.6	0.734	3.4	0.852	0.000	0.781
	0–100 [§]	16.8	0.783	60.1	0.354	0.306	0.481
C:N ratio	0–25	3.1	0.438	83.8	0.239	0.609	0.361
	25–50	0.1	0.203	95.4	0.136	0.866	0.211
	50–100	<0.1	0.512	68.7	0.378	0.062	0.559
	0–100 [§]	1.9	0.901	0.6	0.951	0.000	0.987
C content	0–25	0.1	0.269	91.8	0.183	0.758	0.284
International Crane Foundation (ICF)							
C concentration	0–25	8.0	0.330	25.6	0.117	0.170	0.194
	25–50	7.9	0.435	0.7	0.810	0.000	0.698
	50–100	3.4	0.598	1.4	0.738	0.000	0.819
	0–100	2.7	0.604	13.3	0.293	0.000	0.498
C:N ratio	0–25	14.3	0.252	15.9	0.214	0.127	0.238
	25–50	9.9	0.368	8.0	0.403	0.000	0.454
	50–100	0.9	0.779	3.5	0.602	0.000	0.835
	0–100	0.3	0.897	2.2	0.685	0.000	0.907
C content	0–25	2.6	0.581	23.1	0.153	0.071	0.305

[†] The model was fit with slope as the first predictor and ecosystem age as the next sequential predictor

[‡] The percent of the total sum of squares that is accounted for by each predictor as it appears in the model

[§] Values for the 0–100 cm depth interval represent a composite sample for the profile

soil C and N between the contrasting locations are related to differences in the amount of precipitation that infiltrates the soil surface to subsequently cause a portion of the soluble C and N to leach deeper in the soil profile.

The fine-textured prairies with slopes $\geq 5\%$ had noticeably higher soil C:N ratios in deeper soil layers. Soil C and N concentration tended to decrease, though not significantly, with depth in the fine-textured prairies with a slope $< 5\%$. In contrast, soil C and N concentrations at depth in the fine-textured prairies on $> 5\%$ slope tended to be similar to C and N concentrations at shallower depths or to increase at depths greater than 50 cm (Table 2). One explanation is that downward water movement through the profile (*i.e.*, drainage) was limited due to increased runoff, consequently decreasing the amount of soluble C redistributed lower in the soil profile. However, greater infiltration of precipitation and less runoff, which can result in higher rates of soil organic matter decomposition, at the coarse-textured location may partially explain the poor correlation between slope and soil C and N contents because of soluble C redistribution in the profile and loss due to leaching. These results demonstrate the significant effect soil texture and slope can have on C and N contents in restored prairie soils.

Soil carbon and nitrogen sequestration.—In similar studies, Potter *et al.* (1999) and Knops and

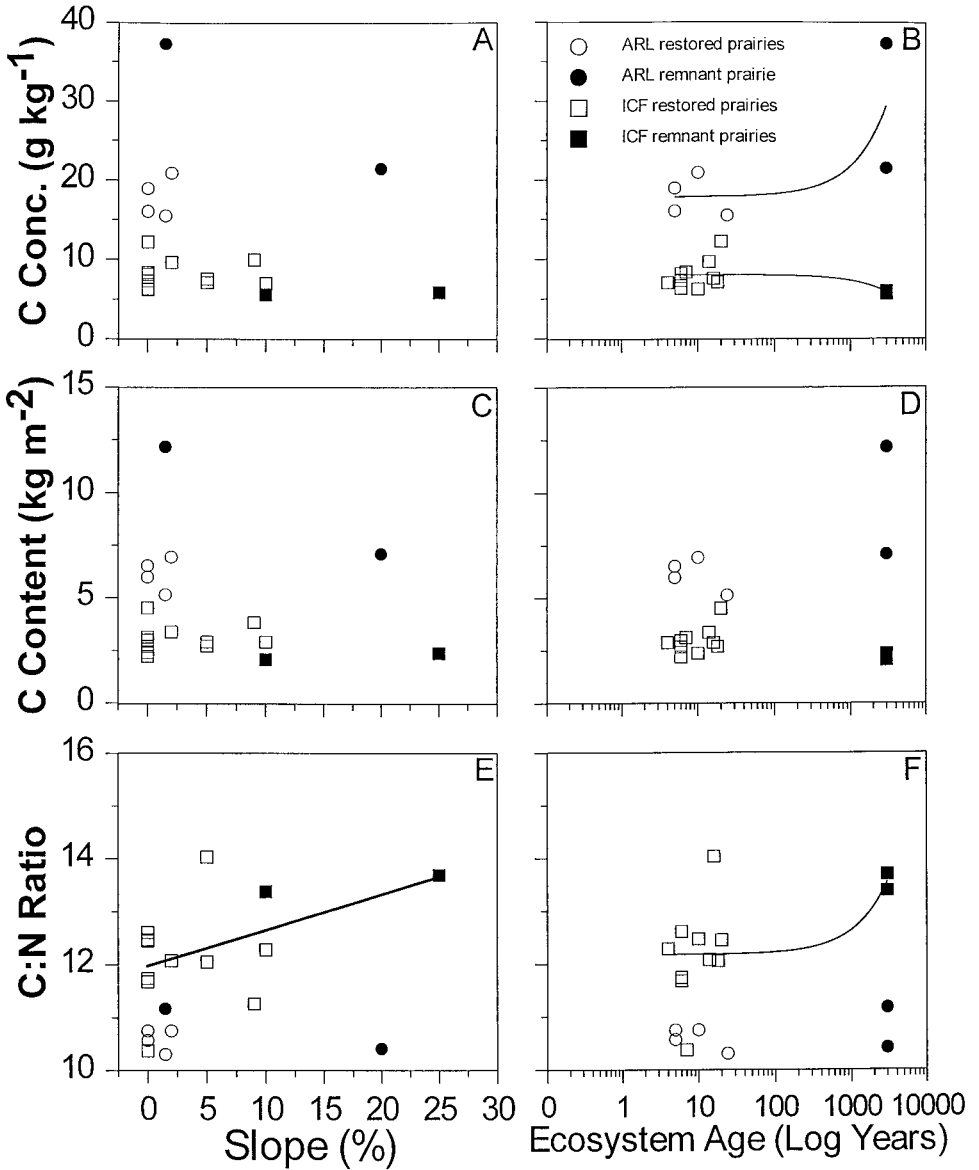


FIG. 2.—Relationship between soil C concentration (A, B), content (C, D) and C:N ratio (E, F) in the top 25 cm and slope and ecosystem age for restored and remnant prairies at the fine-textured ARL and coarse-textured ICF locations. The linear regression models for soil C concentration in the restored and remnant prairies are soil C concentration = $0.00387 \times (\text{ecosystem age in years}) + 17.8$, adjusted $r^2 = 0.442$, $P = 0.090$ and soil C concentration = $0.000804 \times (\text{ecosystem age in years}) + 8.17$, adjusted $r^2 = 0.160$, $P = 0.097$ for the fine-textured ARL and coarse-textured ICF locations, respectively. The linear regression models for soil C:N ratio in the restored and remnant prairies of the coarse-textured ICF location are soil C:N ratio = $0.0817 \times (\% \text{ slope}) + 12.0$, adjusted $r^2 = 0.297$, $P = 0.031$ and soil C:N ratio = $0.000482 \times (\text{ecosystem age in years}) + 12.1$, adjusted $r^2 = 0.233$, $P = 0.054$

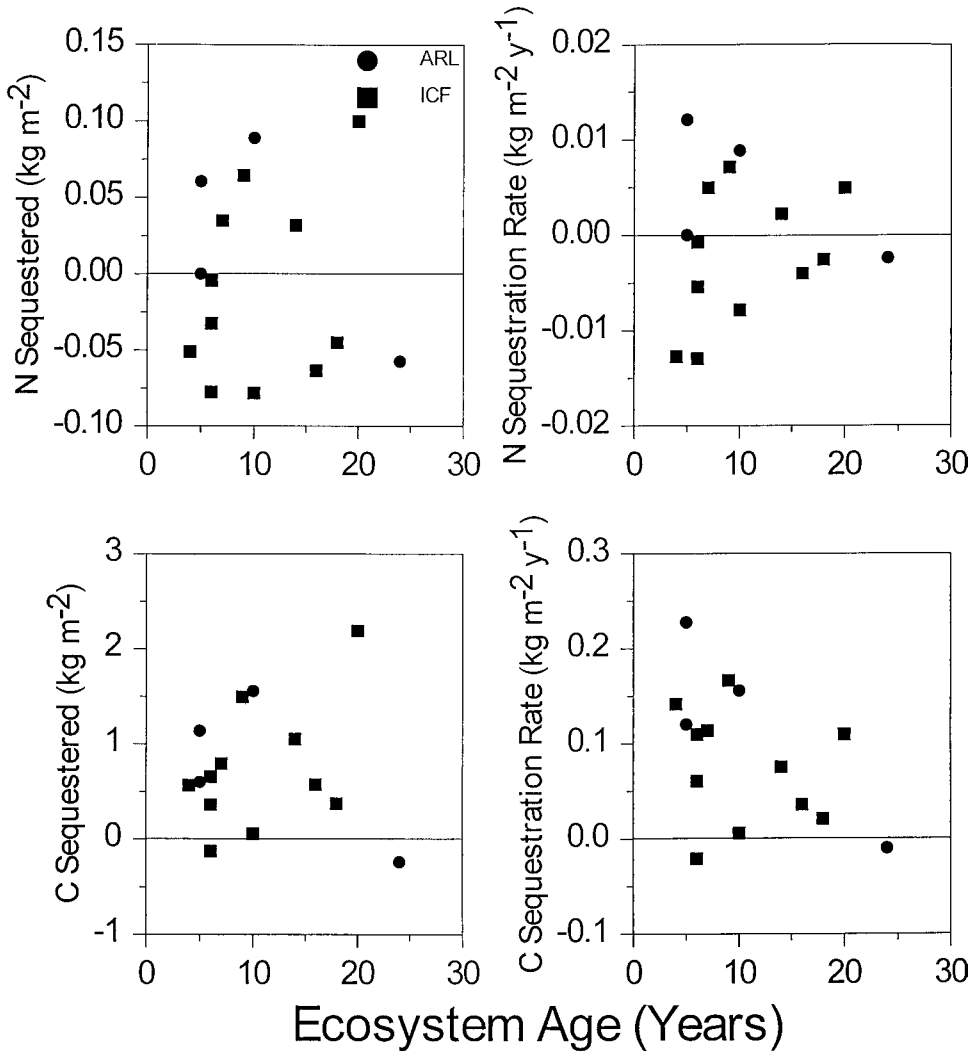


FIG. 3.—Relationship between amount and rate of C and N sequestered in the top 25 cm and ecosystem age for the restored prairies at the fine-texture ARL and coarse-textured ICF locations

Tilman (2000) showed how the use of chronosequences can yield C and N sequestration rates on lands returned to natural vegetation after previous intensive agriculture in Texas and Minnesota, respectively. However, the use of chronosequences in assessing soil nutrient dynamics over time is not without potential flaws (Knops and Tilman, 2000).

The underlying assumption of a chronosequence is that the ecosystems only differ in age. Many studies that use chronosequences do not know predisturbance or time-of-abandonment soil C and N levels (Schlesinger, 1986; Knops and Tilman, 2000). Therefore, apparent changes in soil C and N following prairie restoration, relative to adjacent disturbed

areas, may be due to differences that existed at the time of restoration rather than the result of accumulation over time after removing the disturbance (Knops and Tilman, 2000). Even if the soil C and N contents are greater in older ecosystems of the same type, this may not necessarily show that significant C or N sequestration has occurred. We have tried to minimize error in this analysis by carefully defining study areas that are small (*i.e.*, $\sim 2 \text{ km}^2$), but still contain the rare combination of cultivated cropland and remnant and restored prairies necessary to conduct this assessment.

Potter *et al.* (1999) analyzed native prairies and restored grasslands 7 km apart and showed significant, positive, linear relationships between ecosystem age and C sequestration. In contrast, we found little to no correlation between ecosystem age and the amounts or rates of C and N sequestered in fine- or coarse-textured soils. Knops and Tilman (2000) used a chronosequence of abandoned agricultural fields compared with direct soil C sampling on coarse-textured soils over a 12-y period to test the concept of using a chronosequence to estimate C and N accumulation. They found that total soil C, N and C:N ratio were significantly positively correlated with ecosystem age (*i.e.*, field age since abandonment), annual rates of C and N accumulation were significantly correlated with species composition and the amount of C and N in the soil was negatively correlated with the rate of C and N accumulation (Knops and Tilman, 2000). Similarly, Burke *et al.* (1995) demonstrated significantly higher soil C and N contents in abandoned fields, relative to adjacent cultivated fields, and that soil N recovered faster than C once the disturbance by cultivation was removed.

The results of this study in southern Wisconsin are similar to those of previous studies in that soil C concentration in the top 25 cm of the restored and remnant prairies at the fine-textured location were significantly correlated with ecosystem age, but not slope (Fig. 2). However, the C:N ratio in the top 25 cm of the restored and remnant prairies was correlated with slope, but not ecosystem age, at the coarse-textured location (Fig. 2). Therefore, slope and ecosystem age influence soil C and N dynamics at the coarse- and fine-textured locations, respectively. Although, with less clay content, which is known to stabilize soil organic matter, decomposition rates would be expected to be slightly higher in coarse- than fine-textured soils. Despite a lack of statistical power due to a small size to draw a significant inference, decline in the amount and rate of C and N sequestered as ecosystem age increased in the restored prairies at the fine- and coarse textured locations (Fig. 3) suggests that the C and N sequestration potential decreases over time as the amount of soil C and N reaches a new equilibrium following restoration from cultivation.

Soil C and N contents in the top 25 cm of the restored prairies were positively correlated (r ranged from 0.86 to 0.90), though not significantly, with the rates of soil C and N sequestration at the fine-textured and significantly positively correlated (r ranged from 0.70 to 0.88; $P < 0.02$) at the coarse-textured locations. However, the amount of soil C and N have been shown to negatively affect the rate of C and N accumulation in a coarse-textured soil in Minnesota (Knops and Tilman, 2000).

The 24-y-old restored prairie (R-24), located immediately adjacent to the agricultural field at the fine-textured location, is losing C faster than it is gaining C for reasons not yet known (Brye *et al.*, 2002). For this particular restored prairie, significant C sequestration following cessation of cultivation was temporary and probably limited to within the first 5 to 10 y after the initial landuse conversion. However, the decline of soil organic C two decades after abandonment has been previously documented (Christian and Thompson, 2000). This supports the observations that C sequestration rates decreased, though not significantly, as ecosystem age increased at the fine-textured location (Fig. 3), which in turn indicates that C accumulation rates can be high initially, but then decrease over time. It seems that the current approach to prairie restoration has not found the balance between the

aboveground structure and belowground biogeochemistry necessary to sustain C or N sequestration beyond a few years.

A primary concern of future policy makers centers on having access to quantitative assessments of C and N sequestration and the potential for future land-use change. Soil surface bulk density and soil C and N concentration, content and C:N ratio were significantly affected by soil texture and appeared to be related to the amount of precipitation infiltration and solute leaching that occurred at the two locations. Results demonstrate that the combination of soil parent material (*i.e.*, texture), topography (*i.e.*, slope) and amount of time elapsed since abandonment of cultivation (*i.e.*, ecosystem age) control the content and accumulation of soil C and N following prairie restoration. In the context of this study for restored prairies on contrasting soils in southern Wisconsin, significant C sequestration has not been achieved, given the current level and types of restoration management, within two-and-a-half decades following conversion of cultivated cropland to prairie. Further research will be required to evaluate the impact of different restoration management practices on C sequestration potential.

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