

## DYNAMICS OF SOIL NITROGEN AND CARBON ACCUMULATION FOR 61 YEARS AFTER AGRICULTURAL ABANDONMENT

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**Abstract.** We used two independent methods to determine the dynamics of soil carbon and nitrogen following abandonment of agricultural fields on a Minnesota sand plain. First, we used a chronosequence of 19 fields abandoned from 1927 to 1982 to infer soil carbon and nitrogen dynamics. Second, we directly observed dynamics of carbon and nitrogen over a 12-yr period in 1900 permanent plots in these fields. These observed dynamics were used in a differential equation model to predict soil carbon and nitrogen dynamics. The two methods yielded similar results. Resampling the 1900 plots showed that the rates of accumulation of nitrogen and carbon over 12 yr depended on ambient carbon and nitrogen levels in the soil, with rates of accumulation declining at higher carbon and nitrogen levels. A dynamic model fitted to the observed rates of change predicted logistic dynamics for nitrogen and carbon accumulation. On average, agricultural practices resulted in a 75% loss of soil nitrogen and an 89% loss of soil carbon at the time of abandonment. Recovery to 95% of the preagricultural levels is predicted to require 180 yr for nitrogen and 230 yr for carbon. This model accurately predicted the soil carbon, nitrogen, and carbon : nitrogen ratio patterns observed in the chronosequence of old fields, suggesting that the chronosequence may be indicative of actual changes in soil carbon and nitrogen.

Our results suggest that the rate of carbon accumulation was controlled by the rate of nitrogen accumulation, which in turn depended on atmospheric nitrogen deposition and symbiotic nitrogen fixation by legumes. Our data support the hypothesis that these abandoned fields initially retain essentially all nitrogen and have a closed nitrogen cycle. Multiple regression suggests that vegetation composition had a significant influence on the rates of accumulation of both nitrogen and carbon; legumes increased these rates, and C<sub>3</sub> grasses and forbs decreased them. C<sub>4</sub> grasses increased the C:N ratio of the soil organic matter and thereby increased the rate of carbon accumulation, but not nitrogen accumulation.

*Key words:* abandoned fields; carbon cycling; carbon : nitrogen ratio; nitrogen cycling; old fields; soil organic matter; succession.

### INTRODUCTION

Agricultural practices can cause the loss of a large fraction of soil organic matter (Tiessen et al. 1982, Mann 1986, Schlesinger 1986). This, combined with an increase in the amount of land in agriculture over the past 200 years, has led to a decrease in carbon stored in soils and a net release of carbon into the atmosphere (Houghton et al. 1983, Schlesinger 1984), which has strongly influenced atmospheric CO<sub>2</sub> levels (Wilson 1978) and global carbon balances (Houghton et al. 1983, Sellers et al. 1997). Nitrogen lost from soils has decreased soil fertility (Tiessen et al. 1994, Pimentel et al. 1995) and eutrophied the fresh waters that receive this nitrogen (Howarth et al. 1996). Here, we address four questions: (1) What is the quantitative effect of agriculture on levels of soil carbon and nitrogen? (2) How quickly do soil carbon and nitrogen recover after abandonment from agriculture? (3) Does a chronose-

quence of abandoned fields accurately predict this recovery? (4) Does vegetation composition influence the rate of recovery?

Both chronosequences and long-term observational studies of permanent plots have been used to study the effect of time as a soil-forming factor (Stevens and Walker 1970, Jenkinson and Rayner 1977, Jenkinson et al. 1994, Richter et al. 1994), but studies that compare chronosequence soil data with dynamics observed in long-term studies are rare (Turvey and Smethurst 1989). Here we use a 61-yr chronosequence of abandoned agricultural fields and repeated plot sampling over a 12-yr period to quantify soil carbon and nitrogen recovery, and to test the concept of a chronosequence. Because there is no way to know soil carbon and nitrogen conditions at the time that these fields were abandoned, our chronosequence can be interpreted in at least two different ways. First, higher carbon and nitrogen levels of older fields in a chronosequence may indicate that carbon and nitrogen have accumulated through time. Alternatively carbon and nitrogen may not have changed at all, rather fields may have differed in carbon and nitrogen when abandoned, with the fields

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that were abandoned first having higher carbon and nitrogen than those farmed for longer periods. We used periodic resampling of 1900 plots to test between these two hypotheses.

Other studies suggest that losses of soil organic matter caused by agricultural practices range from 16% to 77% (Mann 1986), with a mean of 29% (Schlesinger 1986). Losses are influenced by soil texture with higher losses on sandy soils (Bauer and Black 1981, Campbell and Souster 1982) and with a positive relationship between percentage clay and soil organic matter (Coote and Ramsey 1983, Nichols 1984). These carbon and nitrogen losses are caused by decreased plant organic matter inputs and by increased decomposition and erosion associated with agriculture. Decomposition increases because of a change in aggregate structure of the soil due to cultivation (Laws and Evans 1949, Coote and Ramsey 1983), which influences the physical protection of soil organic matter (Martel and Paul 1974), and increases soil temperatures (Bracken and Greaves 1941). This in turn influences the soil water holding capacity (Laws and Evans 1949), oxygenation (Coote and Ramsey 1983), and activity of extracellular enzymes. These factors lead to an increase in mineralization of soil organic matter and consequent losses of soil organic carbon (Wilson 1978) and nitrogen (Bracken and Greaves 1941, Laws and Evans 1949, Reinhorn and Avnimelech 1974).

Like most studies (Schlesinger 1986), we had no data on soil carbon and nitrogen levels before cultivation, but used two ways to estimate agriculturally induced losses. First we compared each field to adjacent, never-cultivated habitats, via samples stratified around the entire uncultivated margin. Second we measured actual changes within plots over 12 yr to fit a model to predict the steady states and combined this with a chronosequence to predict the conditions at abandonment.

Finally, studies of abandoned agricultural fields suggest that soil organic matter increases after cessation of farming (Prince et al. 1938, Inouye et al. 1987a, Burke et al. 1995), much as it accumulates during primary succession (Crocker and Major 1955, Olson 1958). The agricultural abandonment of large areas, like the eastern United States (Hart 1968), has the potential to be a significant sink for carbon (Fan et al. 1998). By documenting the accumulation of soil carbon and nitrogen during secondary succession, our data provide information that may better explain such dynamics.

## METHODS

### *Study site*

Cedar Creek Natural History Area, the site of this study, is located 45 km north of Minneapolis, Minnesota (45°24' N, 93°12' W). It has a midcontinental climate with hot, humid summers and cold winters. This results in a large annual difference between the

warmest and coldest month (34°C) and a relatively small diurnal difference in temperature in the winter (10°C) and in the summer (14°C). The average dates of the last spring freeze and the first fall freeze are 9 May and 27 September, respectively. The average annual precipitation is 775 mm (1950–1993), of which 72% occurs from May through October. Soils were formed from a sandy glacial outwash during the end of the last glacial period and are low in organic matter, nitrogen, clay, and water-holding capacity (Grigal et al. 1974). All fields in this study are on well-drained sands of the Sartell, Nymore, or Zimmerman series, with 1–5% silt, 1–4% clay, and 92–97% sand (Grigal et al. 1974).

Settlement in this area started in the late 19th century, with most fields first cultivated in 1890 to 1910 (Pierce 1954). Common crops on the Minnesota sandplain, which includes Cedar Creek, were potatoes, corn, rye, wheat, and increasingly, after a dairy industry developed, alfalfa. Before 1930 manure was only used on selective, accessible fields and little or no inorganic fertilizer was applied to fields through the 1960s (Pierce 1954; D. Bosanko, *personal communication*). Fields at Cedar Creek were abandoned after as little as 1 yr of cultivation or as much as 80 yr of agriculture, but on average after 10–20 yr (Pierce 1954).

Chronosequence studies of abandoned agricultural fields undergoing secondary succession at Cedar Creek have been used to document that soil nitrogen (Inouye et al. 1987a), soil carbon (Johnston et al. 1996), above-ground litter biomass (Inouye et al. 1987a), and plant nitrogen (Gleeson and Tilman 1990) increase with field age. These hypothetical increases corresponded with changes in nitrogen availability (Pastor et al. 1987, Zak et al. 1990), vegetation composition, with a sequence of dominance from annual forbs to C<sub>3</sub> grasses to C<sub>4</sub> grasses (Inouye et al. 1987a), vegetation structure (Gleeson and Tilman 1990), and soil microbial dynamics (Zak et al. 1990). Nitrogen is the most limiting nutrient for plant growth during the entire successional sequence (Tilman 1984, 1987).

### *Soil samples*

Soils were sampled in 1983, 1989, and 1995 in the chronosequence of 19 old fields. In 1983, 100 permanent quadrats were established in each field along four parallel, 40 m long transects spaced 25 m apart. On each transect, 25 quadrats of 1 × 0.5 m were spaced 1.5 m apart (Inouye et al. 1987a). A 2.5 cm wide by 10 cm deep soil core was taken in the center of each quadrat, dried and archived. In addition, three other fields were sampled in 1983 and one in 1995. These four additional fields were sampled with the same transect-quadrat setup. The three sampled in 1983 were subsequently converted into a fertilization experiment (Tilman 1987) and a new chronosequence field, abandoned in 1989 was added in 1995.

We also sampled soils of never-cultivated, upland

habitats adjacent to each old field. This native vegetation consisted mainly of oak savanna or oak-dominated forest. Eight samples, collected ~5–10 m in from the field margin for each side at which a field had adjacent undisturbed land, were taken in April 1997, processed, and analyzed following the same protocol as other soil samples. These plots were stratified around the entire uncultivated margin of each field. Two sets of two fields were located next to each other and only four samples were collected for each field.

#### *Nitrogen and carbon analysis*

All soil samples were dried to constant dry mass at 55°C, sifted through a 1-mm sieve, and ground in a coffee mill. All chronosequence samples were analyzed on the same Carlo Urba NA 1500 elemental analyzer (CE Elantech Incorporated, Lakewood, New Jersey) for total nitrogen and carbon. All the 1983 and 1989 samples were analyzed in 1989–1990. The 1995 samples were analyzed in 1995–1996. To assure that no qualitative differences occurred in our analysis between 1989–1990 and 1995–1996, in 1997 we reran two samples per transect from each field for each year, resulting in 454 samples. Regressions comparing the results of initial analysis with the results of the rerun showed no significant effects of the date of analysis for either carbon, nitrogen, or the C:N ratio. These three simple linear regressions had slopes of 1.005 (SE 0.009) for nitrogen, 1.014 (SE 0.006) for carbon, and 1.016 (SE 0.013) for C:N, with  $R^2$  of 0.965, 0.968, 0.928, respectively, and none of the intercepts were significantly different from zero. Rerun samples were averaged with the original sample before analysis. In addition, the 66 highest and lowest samples from the 5700 point data set were rerun again in 1997. We found a strong, linear, one-to-one relation with the original data, with  $R^2$  of 0.929 for carbon and 0.930 for nitrogen, slopes of 0.923 (SE 0.032) and 0.941 (SE 0.032), and none of the intercepts were significantly different from zero. Nine of these reruns were used to replace the original data because the original samples had a C:N ratio markedly higher or lower than any of the other samples. All others were averaged with the original data.

Eight soil samples per field (two per transect) were collected by depth in 1983 (0–5, 6–10, 11–20, 21–40, 41–60 cm) and analyzed in 1984 (Inouye et al. 1987a, b). Soil data were converted from a mass basis to an area basis, using the empirical formula of Wedin and Tilman (1990): bulk density = 1.509 – 1.03(% soil nitrogen),  $R^2 = 0.98$ ,  $P < 0.001$ .

#### *Vegetation*

The 19 chronosequence old fields were also periodically sampled for plant cover. We used these plant percent cover data to determine if soil changes correlated with vegetation changes. The sampling protocols were given by Inouye et al. (1987a) and the location of each plot was identical to the sample locations of

the soil samples used in this paper. Cover of each plant species, bare ground, and litter, which totaled 100% for each plot, was visually estimated in late July in 1983, 1989, and 1994. From these cover estimates, the abundance of five functional groups was calculated: C<sub>3</sub> grasses, C<sub>4</sub> grasses, cryptogams, forbs, and legumes. The cover of ferns, woody plants, and sedges was excluded from our analysis because their average covers were extremely low and most plot values were zero.

#### *Statistical analysis*

The chronosequence was analyzed as field averages, whereas changes relative to plot vegetation composition or plot soil quality were analyzed for each plot, as these were the basic sampling units. We lost some samples from 1983 and the total sample size was 1720 out of 1900 quadrats. The annual instantaneous rates of change in soil carbon and nitrogen were estimated for each plot for the time interval from 1983 to 1995:

$$\left(\frac{dN}{dt}\right)\frac{1}{N} = \left(\ln\frac{N_{95}}{N_{83}}\right)\frac{1}{12}. \quad (1)$$

This gives rates of change for nitrogen (N) with units of yr<sup>-1</sup>. Comparable analyses give the rates for carbon (C). These rates of change can be used to predict the long-term dynamics of carbon and nitrogen in these soils. To do this, it is necessary to determine how these rates of change depend on the ambient carbon or nitrogen levels in each plot. We determined the dependence of rates of change on the soil carbon or nitrogen data of 1989. This ensured that the data were not autocorrelated (Atchley et al. 1976, Knops et al. 1997). The observed dependence of the rates of soil carbon and nitrogen change on total soil carbon and nitrogen provides empirically derived differential equation models that can be used to predict the long-term dynamics of carbon and nitrogen at Cedar Creek. Such predictions can be compared with the levels observed in the chronosequence to test if the chronosequence is a valid measure of the dynamics of carbon and nitrogen. Note that the model does not use any information on field ages. It depends only on the observed rates of carbon and nitrogen change and how these rates depend on ambient carbon and nitrogen. Thus its predictions are completely independent of the chronosequence analysis and predictions. The dynamic model's predicted equilibrium levels of carbon and nitrogen can also be compared to levels observed in never-cultivated habitats at field margins to test the predictive ability of the model.

All statistics were performed with SPSS 7.5 for Windows (Norusis 1993). The differential equation model was numerically solved with Mathematica 3.0 for Unix (Wolfram 1996). Multiple regression analysis was used to examine the effect of vegetation on soil carbon or nitrogen dynamics. The extent of collinearity was determined for each regression analysis (Norusis 1993). No data set had serious collinearity problems, based

TABLE 1. Multiple backwards elimination regression for the dependence of soil carbon, soil nitrogen, and the carbon : nitrogen ratio in 1995 on field age and the abundances of major plant functional groups.

Variable	Carbon			Nitrogen			Carbon : Nitrogen		
	Parameter estimate	<i>P</i>	Partial correlation	Parameter estimate	<i>P</i>	Partial correlation	Parameter estimate	<i>P</i>	Partial correlation
Intercept	0.292	0.000		0.0295	0.000		10.98	0.000	
Field age	0.0130	0.000	0.422	0.000753	0.000	0.377	0.0481	0.000	0.378
C <sub>3</sub> grasses	0.00656	0.000	0.130	0.000867	0.000	0.252	-0.0427	0.000	-0.198
C <sub>4</sub> grasses	0.00411	0.000	0.098	0.000189	0.003	0.068	0.0348	0.000	0.195
Forbs	0.00318	0.010	0.059	0.000358	0.000	0.100	-0.0176	0.001	-0.078
Legumes	eliminated			eliminated			eliminated		
Cryptograms	-0.0128	0.000	-0.257	-0.000817	0.000	-0.249	-0.0341	0.000	-0.167

Notes: Carbon regression: df = 5, 1894;  $F = 169.9$ ,  $P = 0.000$ ,  $R^2 = 0.308$ . Nitrogen regression: df = 5, 1894;  $F = 173.4$ ,  $P = 0.000$ ,  $R^2 = 0.312$ . Carbon : nitrogen ratio regression: df = 5, 1894;  $F = 214.3$ ,  $P = 0.000$ ,  $R^2 = 0.360$ .

on the following criteria: variance inflation factors were  $<1/(1 - R^2)$ , eigenvalues were not close to zero, condition index values were not large (e.g.,  $>30$ ), and variance proportions were not close to one (Freund and Littell 1991).

## RESULTS

### *Dynamics observed over 12 yr within fields*

We calculated the average carbon and nitrogen content of each field in 1983 and 1995. We used these to calculate the accumulation rate for each field as the instantaneous rate of change ( $\text{yr}^{-1}$ ) for the time period from 1983 to 1995 in Eq. 1. Field accumulation rates varied from 0.0009 to 0.0295  $\text{yr}^{-1}$ , with a mean of 0.0167  $\text{yr}^{-1}$  (i.e., 1.67% per year) for carbon and from -0.0017 to 0.0233  $\text{yr}^{-1}$  with a mean of 0.0130  $\text{yr}^{-1}$  (i.e., 1.28% per year) for nitrogen. Fields differed significantly in both carbon and nitrogen accumulation (Kruskal-Wallis; carbon  $\chi^2 = 218$ ,  $n = 19$ ,  $P < 0.000$ , nitrogen  $\chi^2 = 209$ ,  $n = 19$ ,  $P < 0.000$ ), but there was no significant relationship between the accumulation rate of either carbon or nitrogen and field age ( $n = 19$ , carbon  $P = 0.903$ , nitrogen  $P = 0.360$ ).

### *Dynamics observed over 12 yr within plots*

The functional group composition of the vegetation in the fields (C<sub>3</sub> grasses, C<sub>4</sub> grasses, forbs, legumes, and cryptograms) differed significantly among fields; bare ground and forbs decreased, and sedges, C<sub>4</sub> grasses, and woody plants increased with field age. A multiple regression with backward elimination showed that field age and the average cover at the three sampling dates of C<sub>3</sub> grass, C<sub>4</sub> grass, and forbs had a positive significant influence on the total soil carbon and nitrogen in 1995. Legume abundance had no influence on soil carbon or nitrogen and cryptograms had a negative effect (Table 1). The C:N ratio in 1995 was also significantly and positively related to field age and to the C<sub>4</sub> grass abundance, but negatively to C<sub>3</sub> grass, forb, and cryptogram abundance (Table 1). Thus, in addition to an increase with time in the soil nitrogen and carbon, the vegetation composition also was correlated with

the actual levels of soil carbon, nitrogen, and the C:N ratio of the soil organic matter.

When the plot-by-plot instantaneous rates of carbon and nitrogen change were determined for all 1720 plots, the accumulation rates of both carbon and nitrogen (1983 to 1995) were significantly and negatively related to the actual carbon and nitrogen in the plots (1989) (Eqs. 2 and 4, Fig. 1). Thus, the rate of nitrogen and carbon accumulation declines as nitrogen and carbon accumulate (Eqs. 3 and 5, Fig. 2). The integrated forms of these equations (Eqs. 3 and 5) also include the average total soil carbon and nitrogen in newly abandoned fields ( $C_0 = 0.418$  and  $N_0 = 0.0431$ ), which we directly observed from field measurements:

$$\frac{dC}{Cdt} = 0.0217 \left( 1 - \frac{C}{3.754} \right) \quad (2)$$

$$C_{(t)} = \frac{3.754}{1 + 7.981e^{-0.0217t}} \quad (3)$$

$$\frac{dN}{Ndt} = 0.0223 \left( 1 - \frac{N}{0.1715} \right) \quad (4)$$

$$N_{(t)} = \frac{0.172}{1 + 2.979e^{-0.0223t}} \quad (5)$$

The annual rates of both carbon and nitrogen accumulation were also significantly influenced by plant species composition. The carbon accumulation rates had a significantly positive partial correlation with C<sub>4</sub> grass and legume abundance, significantly negative with C<sub>3</sub> grasses and forb abundance, and none with the cryptogram abundance (Table 2). For the rate of nitrogen accumulation, we found a significantly positive partial correlation with legume abundance, C<sub>3</sub> grass, and forb abundance and none with C<sub>4</sub> grass and cryptogram abundance (Table 2). This vegetation influence on the rate of accumulation corroborates the pattern of the vegetation correlation with the actual levels of soil carbon and nitrogen (Table 1).

### *Patterns observed in the chronosequence*

Soil total carbon, nitrogen, and the carbon : nitrogen ratio (C:N) all were significantly positively correlated

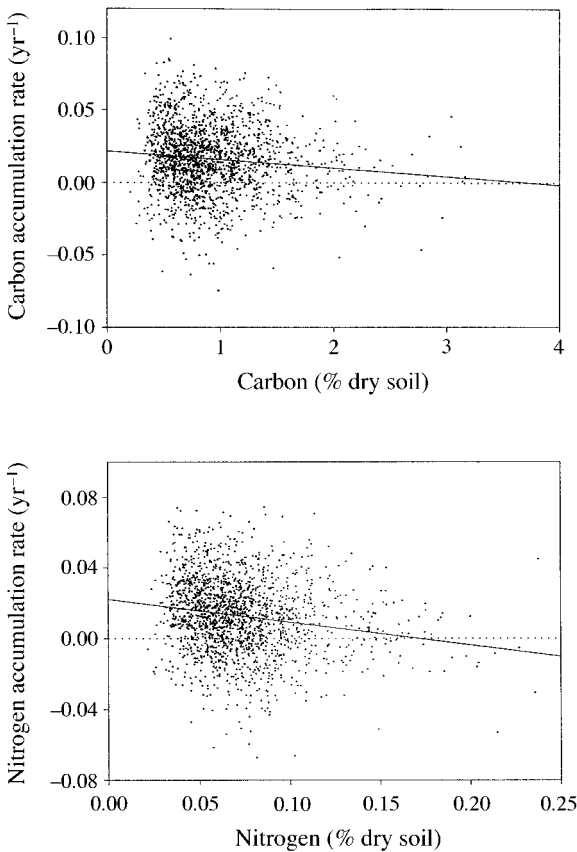


FIG. 1. Carbon and nitrogen accumulation from 1983 to 1995 vs. 1989 soil carbon and nitrogen. Accumulation is calculated as  $[\ln(C_{95}/C_{83})]/12$ . The best-fit regression for carbon is  $y = 0.02170 - 0.0058x$ ,  $P < 0.000$ ,  $R^2 = 0.011$ ,  $n = 1718$ ; for nitrogen it is  $y = 0.02227 - 0.130x$ ,  $P < 0.000$ ,  $R^2 = 0.032$ .

with field age since abandonment (Table 1). We found no differences among the three sampling dates in the dependence of carbon, nitrogen, or the C:N ratio on field age (Table 3). This supports the hypothesis that the chronosequence accurately captures the increase in soil carbon and nitrogen with time and that the fields at abandonment date did not differ in their initial soil carbon and nitrogen.

Based on the chronosequence, field average soil nitrogen in the 0–10 cm depth increased with field age, but there was no change in the 10–60 cm depth horizon (Fig. 3). Soil from the 10–60 cm depth horizon contained 170 g N/m<sup>2</sup>, whereas nitrogen in the 0–10 depth increased from 58 g at abandonment to 108 g N/m<sup>2</sup> at 60 yr. This implies that the amount of nitrogen in the 0–10 horizon increases from 25% to 39% of the total soil profile down to 60 cm.

#### *Patterns observed in never cultivated adjacent fields*

Soil from the habitats adjacent to the field also differed significantly among the locations for carbon, ni-

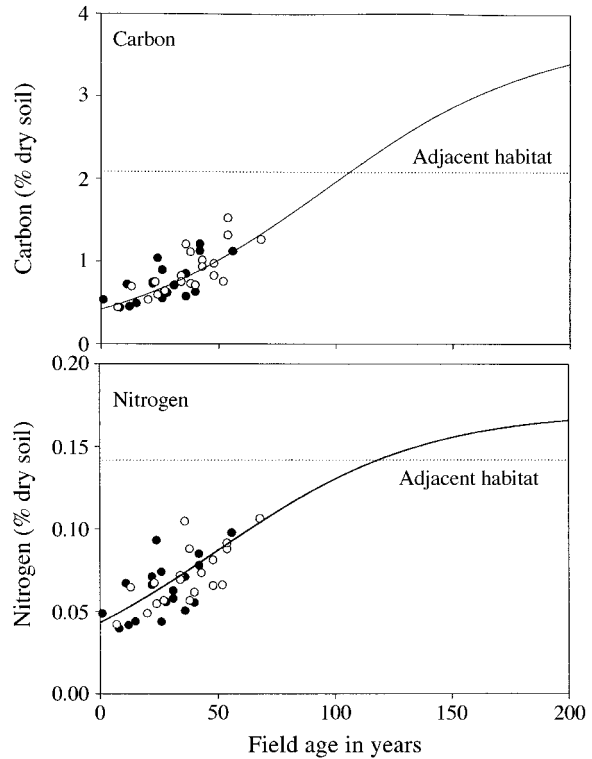


FIG. 2. Modeled carbon ( $dC/Cdt$ ) and nitrogen ( $dN/Ndt$ ) accumulation and actual field averages of carbon and nitrogen vs. field age. The logistic curves are calculated from the changes within a plot from 1983 to 1995 (e.g., Fig. 1). Curves are drawn from a logistic curve with the following parameters for nitrogen:  $r = 0.0223$ ,  $K = 0.1715$ ,  $N_0 = 0.0431$ . For carbon the parameters are:  $r = 0.0217$ ,  $K = 3.754$ ,  $N_0 = 0.418$  (Eqs. 3 and 5). The  $N_0$  values were estimated from the average intercepts of the two sampling years vs. field age. Open circles indicate 1995 data and solid circles indicate 1983 chronosequence data. The stippled line is the median of the adjacent habitats for all fields.

trogen, and C:N ratio (Kruskal-Wallis; carbon  $\chi^2 = 30.5$ ,  $n = 19$ ,  $P = 0.046$ , nitrogen  $\chi^2 = 33.4$ ,  $n = 19$ ,  $P = 0.021$ , C:N  $\chi^2 = 57.4$ ,  $n = 19$ ,  $P < 0.000$ ), but this was not correlated with field age (regression  $df_{17,1}$ ; carbon  $F = 1.004$ ,  $P = 0.330$ ; nitrogen  $F = 1.658$ ,  $P = 0.215$ ; C:N  $F = 0.388$ ,  $P = 0.542$ ). Thus, the chronosequence patterns in carbon and nitrogen are unlikely to be caused by landscape patterns in soil organic matter. The coefficient of variation for carbon and nitrogen within the adjacent habitat samples was consistently much higher than within the fields (cv carbon old field 0.46 vs. adjacent habitat 1.05, nitrogen 0.38 vs. 0.87), whereas variation within the C:N ratio was similar (cv 0.15 vs. 0.13). These cv values are corrected for a sample size of 2000 for the old fields and 136 for the adjacent habitats (Sokal and Rohlf 1995). Therefore, we used the median values of the adjacent habitats as a comparison with the steady state predictions of the model.

TABLE 2. Multiple backwards elimination regression for the dependence of carbon or nitrogen accumulation rate from 1983 to 1995 on soil carbon or nitrogen in 1989, field age, and the major plant functional groups.

Variable	Carbon accumulation			Nitrogen accumulation		
	Parameter estimate	<i>P</i>	Partial correlation	Parameter estimate	<i>P</i>	Partial correlation
Intercept	0.0268	0.000		0.0282	0.000	
Nitrogen, 1989	not included			-0.0897	0.000	-0.104
Carbon, 1989	-0.00514	0.000	-0.089	not included		
Field age, 1989	eliminated			-0.000108	0.017	-0.057
C <sub>3</sub> grasses	-0.00295	0.000	-0.090	-0.000240	0.000	-0.095
C <sub>4</sub> grasses	0.000167	0.015	0.059	eliminated		
Forbs	-0.000336	0.000	-0.098	-0.000242	0.001	-0.080
Legumes	0.000599	0.004	0.070	0.000577	0.002	0.074
Cryptograms	eliminated			eliminated		

Notes: Carbon regression: df = 5, 1712; *F* = 20.7, *P* = 0.000, *R*<sup>2</sup> = 0.057. Nitrogen regression: df = 5, 1712; *F* = 17.7, *P* = 0.000, *R*<sup>2</sup> = 0.046.

## DISCUSSION

### *Chronosequence, sequential sampling, and adjacent habitats*

There are several ways to estimate the dynamics and eventual equilibrium levels of soil organic matter after a prolonged disturbance, such as cultivation. Direct observation over the necessary century or two is impractical. Alternatively, this can be done indirectly (1) by using measured rates of change for analytical predictions, or (2) by inference based on a chronosequence, or (3) by comparing disturbed areas to adjacent undisturbed areas. Each of these indirect methods makes different assumptions about the process of soil recovery; (1) assumes that relatively short time measurements of rates of accrual (e.g., 12 yr) and the dependence of these rates on pool sizes can accurately predict long term changes, (2) assumes that fields only differ in their age, undergo the same successional sequence, and that organic matter losses were not correlated with abandonment date, and (3) assumes that initially fields and adjacent habitats were similar, that uncultivated adjacent areas have not changed, and that cultivated fields will recover to a state similar to adjacent undisturbed habitats.

We found good agreement between the apparent dependence of soil carbon and nitrogen on time since abandonment observed in the chronosequence fields and the dynamics independently predicted by observation of carbon and nitrogen dynamics over 12 yr

within plots (Eqs. 2–5, Fig. 2). Note that the curves shown in Fig. 2 are the dynamics predicted by Eqs. 3 and 5, whereas the data points are from the chronosequence. The similarity of these independent approaches suggests that both the chronosequence and the dynamic approach accurately describe the dynamics of soil carbon and nitrogen recovery. Using changes in soil carbon ( $dC/Cdt$ ) or nitrogen ( $dN/Ndt$ ) within plots, relative to the nitrogen or carbon in each plot, the best simple model to fit the data was a logistic model (Eqs. 2 and 4, Fig. 2). This model predicted an eventual steady state of 0.17% soil nitrogen and 3.75% soil carbon, with a C:N ratio of 21.9 (Eqs. 3 and 5). According to the model, 95% of the steady state is reached after 180 years for nitrogen and after 230 years for carbon. The logistic model predicts an increase to ~1.5% soil carbon and 0.11% soil nitrogen after 61 years, which is similar to that observed in the chronosequence for the same time period (Fig. 2). The never-cultivated adjacent habitats had a mean soil total nitrogen level of 0.182% and a median of 0.134%, which agrees reasonably well with the prediction of 0.17% made independently by the soil model. Soil total carbon, in contrast, was substantially lower in the adjacent habitats than projected by the soil model; the mean was 2.99% with a median of 2.08%, compared with a prediction of 3.75%. This also was reflected in the observed C:N ratio of 16.0 (median 15.7), vs. the predicted C:N ratio of 21.9. However, our logistic

TABLE 3. Type III General Linear Model, univariate analysis of variance of the average field total soil carbon, total soil nitrogen, and the carbon : nitrogen ratio vs. sampling date (e.g., 1983, 1989, 1995), with the actual field age as a covariate.

Source	df	Carbon		Nitrogen		Carbon : Nitrogen	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Corrected model	3	20.3	0.000	14.7	0.000	9.0	0.000
Intercept	1	45.4	0.000	94.9	0.000	857.4	0.000
Field age	1	52.7	0.000	38.7	0.000	21.8	0.000
Sampling date	2	1.3	0.283	0.6	0.528	1.5	0.240
Error	57						

Note: For carbon, *R*<sup>2</sup> = 0.517; for nitrogen, *R*<sup>2</sup> = 0.437; for C : N *R*<sup>2</sup> = 0.322.

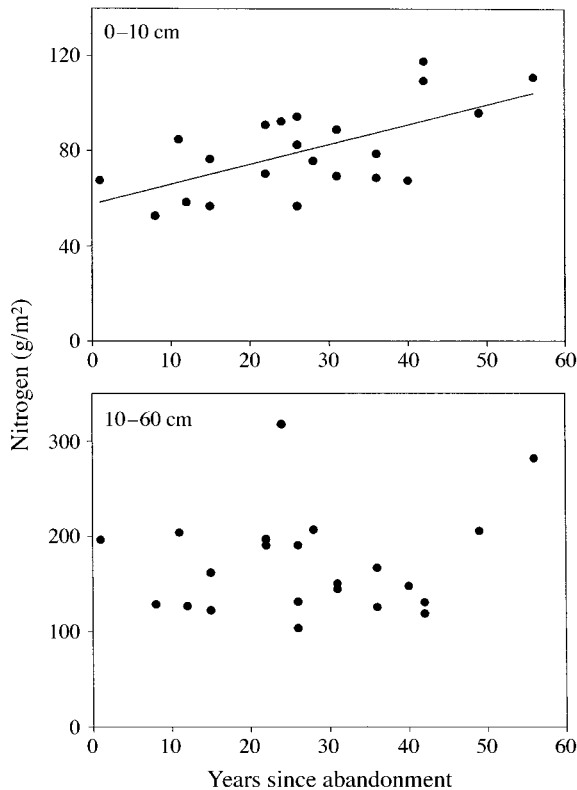


FIG. 3. Soil nitrogen ( $\text{g/m}^2$ ) from 0–10 and 10–60 cm deep. These data are based on Inouye et al. (1987a, b), who reported mass-based data from a subset of the fields presented here. Data are averaged by field ( $n = 8$  per field), and the regression slope is from a linear regression: 0–10 cm,  $df = 1, 20, F = 13.17, P = 0.002, R^2 = 0.367$ ; 10–60 cm,  $df = 1, 20, F = 0.36, P = 0.555, R^2 = 0.018$ .

growth curve was based on plot data only from the first 61 years after field abandonment, a period of dominance by herbaceous vegetation. Patterns that may occur later in succession, such as the invasion of trees into these fields, are not incorporated into the logistic model because tree invasion is extremely slow (Inouye et al. 1987a, 1994). Thus, this discrepancy may be caused by the difference between the herbaceous vegetation in the old fields vs. the woody vegetation of the adjacent habitats. The trees dominating in the forest have a much higher allocation to aboveground biomass than the grasses. For instance experimental plots planted with *Schizachyrium scoparium* had an above/belowground biomass ratio of 0.61 six years after planting, whereas *Quercus ellipsoidalis* had a ratio of 1.17 and *Pinus strobus* of 2.29 (J. M. H. Knops and D. Tilman, unpublished data). This results in more carbon in standing aboveground biomass and in surface litter, not yet incorporated into the mineral soil organic matter. In addition, the  $\text{C}_4$  grasses often have a higher C:N ratio than tree leaf litter, which is reflected in the higher predicted C:N ratio of the logistic regression. Consistent with this, Richter et al. (1995) who examined car-

bon accumulation over 34 years in a pine forest, found that nearly all of the carbon accumulated in the plant biomass and forest floor and Hamburg (1984) found only a small increase in soil organic matter over 70 years. Thus, our model, which is fit to the observed rates of change during a 12-yr interval in fields younger than 61 years, may not predict soil organic matter patterns after a successional transition from grassland to forest occurs.

We found that field age, but not the chronosequence sampling dates, influenced soil carbon and nitrogen patterns (Table 3). This, combined with the field observations that soil organic matter losses are most rapid immediately after cultivation and level off over time reaching a lower steady state (Jenkinson and Rayner 1977, Schlesinger 1986), which is incorporated in models accurately describing soil organic matter dynamics (Houghton et al. 1983, Parton et al. 1988, Smith et al. 1997), makes it unlikely that the chronosequence soil carbon and nitrogen pattern is caused by differences in cultivation duration.

Burke et al. (1995) compared adjacent shortgrass prairie with both currently cultivated fields and fields abandoned 50 years ago. Their study showed that the soil in the top 10 cm of native grassland had 80% more carbon and 87% more nitrogen than the cultivated soil and that 50-yr-old abandoned field soil had 20% more carbon and 35% more nitrogen than the cultivated soil. These recovery rates are substantially lower than ours (Fig. 2), but are similar to our results in showing faster recovery of nitrogen than of carbon. Their dominant species, *Bouteloua gracilis*, has a much lower productivity than the dominant species at Cedar Creek (Parton et al. 1987, Tieszen et al. 1997). Consequently, the amount of input into the soil was much lower, which may well lengthen the recovery time.

#### Rate of nitrogen and carbon accumulation

There are four likely long-term sources for increasing nitrogen in soil of the abandoned fields: atmospheric deposition, symbiotic fixation, asymbiotic fixation, and redistribution within the soil profile. The annual net increase of nitrogen over 12 yr, averaged over all fields, was  $1.23 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$  in the top 10 cm and ranged from  $-0.15$  to  $1.93 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$  for these fields. The annual atmospheric deposition of nitrogen is not precisely known, but the National Atmospheric Deposition Programs reports a wet deposition for central Minnesota of  $0.4\text{--}0.5 \text{ g N}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$  and dry deposition can substantially increase this amount (Heil et al. 1988). This indicates that atmospheric deposition could potentially account for most of the average increase in soil nitrogen seen over our 12-yr sampling period. However, the absolute amount of nitrogen was also significantly, positively correlated with field legume occurrence (measured as average cover in 1983, 1989, and 1994; Pearson correlation 0.444,  $n = 19$ , one-tailed test  $P < 0.05$ ). Thus, at least in some fields,

TABLE 4. Simple regressions of field average carbon or nitrogen vs. field age for the 1983 and 1995 chronosequences.

Dependent variable	N	Intercept		Slope		R <sup>2</sup>
		Estimate	P	Estimate	P	
Carbon, 1983	19	0.434 ± 0.093	0.000	0.012 ± 0.003	0.001	0.457
Carbon, 1995	20	0.359 ± 0.117	0.007	0.14 ± 0.003	0.000	0.563
Nitrogen, 1983	19	0.043 ± 0.007	0.000	0.00075 ± 0.000	0.007	0.361
Nitrogen, 1995	20	0.042 ± 0.008	0.000	0.00080 ± 0.000	0.001	0.492
C:N, 1983	19	10.6 ± 0.5	0.000	0.041 ± 0.016	0.024	0.267
C:N, 1995	20	9.8 ± 0.8	0.000	0.061 ± 0.019	0.006	0.319

Notes: Field ages used are years since abandonment at the time of sampling. C:N averages are average ratios. The carbon accumulation rate is  $[\ln(C_{95}/C_{83})]/12$ , with units of  $\text{yr}^{-1}$ . Note that this is based on field means. Nitrogen accumulation was calculated similarly. The table reports the intercepts and slopes  $\pm$  one standard error, *P* values, and the overall *R*<sup>2</sup> of the regression.

symbiotic nitrogen fixation probably contributed nitrogen. Asymbiotic nitrogen fixation may also be important (McKone and Biesboer 1986, Eisele et al. 1989, Abbadie et al. 1992).

Total soil carbon on average had an annual increase of  $19.7 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ , with a range of  $1.2\text{--}36.2 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$  in the top 10 cm. This rate is relatively high (Schlesinger 1990), but similar rates have been reported for northern forest ecosystems (Bormann and Sidle 1990, Bormann et al. 1995) and Cedar Creek has substantially more atmospheric nitrogen input than ecosystems farther west in the Great Plains (Shannon and Sisterson 1992). Standing aboveground biomass in 14 of these fields from 1988 through 1995 averaged  $117 \text{ g/m}^2$ . Assuming 43% carbon in the plant biomass, this equals  $50.3 \text{ g C/m}^2$  as an estimate of primary productivity. Proportional root biomass is 0.8 (Gleeson and Tilman 1994), but we lack data on root turnover. Assuming 50% turnover per year, primary productivity would be  $151 \text{ g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ . Thus, whereas the inputs of nitrogen seem to be largely immobilized in soil organic matter, much of the fixed carbon may be released as  $\text{CO}_2$  during the decomposition process.

One alternative explanation for the nitrogen accumulation in the 0–10 cm deep soil is that some of the increase in soil nitrogen in the 0–10 cm depth is due to mining of deeper soil nitrogen. We only sampled the deeper soil layers in 1983, thus we are unable to follow profile changes over time. The chronosequence data does show an increase, in relation to abandonment age, for soil nitrogen in the 0–10 cm depth, but not for the 10–60 cm depth (Fig. 3), and there was no significant relationship between abandonment age and soil nitrogen for the entire soil profile (simple regression,  $F = 1.935$ ,  $n = 22$ ,  $P = 0.180$ ), when we used field averages. However, this seems unlikely because abandoned fields are dominated by grasses, which have most roots in the upper soil horizons, and when we analyze all replicates together, we do find a significant positive correlation with field age (simple regression,  $F = 5.896$ ,  $n = 182$ ,  $P = 0.016$ ).

#### *Rate of carbon and nitrogen accumulation related to soil carbon, nitrogen, and the vegetation composition*

Carbon and nitrogen levels and the C:N ratio increased along the chronosequence time series (Fig. 2,

Table 1). However, in addition to the time factor and the amount of soil carbon and nitrogen, the vegetation also varied along the chronosequence, potentially influencing the rate of accumulation. A multiple regression showed that the rate of carbon accumulation was negatively dependent on soil carbon and on the abundance of  $\text{C}_3$  grasses and forbs, and positively dependent on the abundances of  $\text{C}_4$  grasses and legumes (Table 2). The rate of nitrogen accumulation was not influenced by the abundance of  $\text{C}_4$  grasses, was negatively related to soil nitrogen, field age, and the abundance of  $\text{C}_3$  grasses and forbs, and positively related to legumes abundance. This discrepancy between positive effect on carbon and no effect on nitrogen of  $\text{C}_4$  grass abundance can be explained by the change of C:N ratio over time (Table 4), which changes the stoichiometry of carbon relative to nitrogen over the successional gradient.  $\text{C}_4$  grasses produce higher C:N and are able to produce more biomass under nitrogen-limiting conditions (Epstein et al. 1997). This litter decomposes more slowly (Wedin and Tilman 1990), resulting in a higher carbon accumulation rate. The positive influence of legumes is likely caused by their fixation of atmospheric nitrogen. This supports suggestions that legumes are important in the accumulation of soil organic matter in old fields (Prince et al. 1938, Odum 1960, Ritchie and Tilman 1995) and areas undergoing primary succession (Crocker and Major 1955). The negative influence of  $\text{C}_3$  grass and forb abundance on both carbon and nitrogen accumulation might either be caused by their relatively rapidly decomposing litter (Swift et al. 1979), or by their lower productivity relative to  $\text{C}_4$  grasses (Tilman and Wedin 1991). The amounts of nitrogen and carbon both had a negative effect on the rate of accumulation, which implies a decreasing rate of increase as soil organic matter accumulates. Field age was negatively correlated with the rate of nitrogen accumulation, which implies that another factor correlated with field age influences the rate of nitrogen, but not carbon accumulation. Possible factors for this are either a decrease in inputs of nitrogen, such as a decrease in symbiotic or asymbiotic nitrogen fixation with field age, or an increase in nitrogen losses.



### *Soil C:N ratio and vegetation composition*

The different influence of  $C_4$  grass abundance on the rate of carbon and nitrogen accumulation leads to the question: can vegetation composition influence the stoichiometry of elements in the soil and thereby have a qualitative influence on the soil organic matter. We tested this by regressing the C:N ratio of the soil in 1995 against the vegetation composition measured in 1983, 1989, and 1994 (Table 1). We found an increasing C:N ratio with field age and  $C_4$  abundance and a negative influence of  $C_3$  grass and forb abundance. This corroborates the contrasting pattern for  $C_4$  grasses with the rate of carbon and nitrogen accumulation and suggests that vegetation composition influences the C:N ratio of soil organic matter and the stoichiometry of element cycling.

We also found that the amount of soil carbon and nitrogen was positively influenced by the abundance of forbs,  $C_3$  and  $C_4$  grasses, but not influenced by legumes and negatively influenced by cryptogams. This strongly documents that the major three functional groups have a positive influence on the soil organic matter, most likely through their litter inputs (Gorham et al. 1979) and that the soil organic matter increases with time, which is the same pattern that we observed along the chronosequence (Fig. 2) and has been documented in other ecosystems (Goh et al. 1976).

### *Soil carbon and nitrogen after cultivation*

Prairies lose a large amount of organic matter and nitrogen during cultivation. Our data show an average concentration of 0.043% nitrogen and 0.42% carbon at abandonment from agriculture, which implies a net loss during agriculture of 75% of original nitrogen and 89% of original carbon in the top 10 cm (Fig. 2). Most literature studies documenting such losses in temperate grasslands use comparisons with adjacent uncultivated virgin prairies and show an average loss of 28.6%, which is equivalent to 5.5 kg C/m<sup>2</sup> from a steady state of 19.2 kg C/m<sup>2</sup> in the entire soil profile (Schlesinger 1986). Our steady state for carbon is 3.75% and for nitrogen is 0.172% in the top 10 cm, which is equivalent to a total of 5 kg C/m<sup>2</sup> with a loss of 4.45 kg carbon. Our estimate is therefore high, but not extreme. Most of the carbon losses are specifically from the top soil levels and losses from sandy soils are likely to be higher because soil organic matter can form decomposition recalcitrant complexes with clay minerals (Nichols 1984).

### *Mechanisms controlling the rate of carbon and nitrogen accumulation*

After abandonment, fields at Cedar Creek contain soil with a C:N ratio of 11. This implies that a highly decomposed soil organic matter fraction with a C:N signature close to the microbial turnover signature (Waksman 1924) is the only fraction left. This is con-

sistent with observations that the lighter, easily decomposable soil organic matter fraction has a higher C:N ratio than the recalcitrant pools and that the lighter fraction declines most sharply under agricultural practices (Porter et al. 1964, Martel and Paul 1974, Spycher et al. 1983). Litter inputs have a much higher C:N ratio, in the order of 40–60 (Wedin and Tilman 1996) and this ratio tends to decrease over time in decomposing litter, as carbon is mineralized and nitrogen is retained. We measured the soil organic matter that is smaller than 1 mm, which includes recalcitrant soil organic matter and partly decomposed intermediate pools of soil organic matter. This retained recalcitrant soil organic matter pool and an increasing intermediate soil organic matter pool, with a higher C:N ratio results in the observed increase in C:N ratio of the soil organic matter over time (Fig. 2). This results in an immobilization of all the nitrogen inputs into the soil organic matter, as the lighter soil organic matter fractions with a higher C:N ratio increase in the first 61 years after field abandonment. This supports the hypothesis that abandoned fields initially retain nitrogen inputs and essentially have a closed nitrogen cycle. However, eventually long-term nitrogen losses have to reach an equilibrium with nitrogen inputs and our logistic regression implies that this balance is reached after about 300 years (Fig. 2). This is analogous to a similar pattern observed in forest ecosystems during primary succession (Odum 1969) and supports the hypothesis of low nitrogen retention in old-growth systems (Vitousek and Reiners 1975, Gorham et al. 1979). This also supports the conclusion of Hedin et al. (1995) “that losses of nitrogen from old-growth forest ecosystems are not exclusively subject to . . . direct biotic control, but are also subject to indirect biotic control associated with the long-term accumulation, humification, and leaching of soil organic nitrogen during ecosystem succession.” This interplay among biotic biomass production, organic matter decomposition, and the nature of the litter–soil, organic matter pool controls ecosystem carbon and nitrogen dynamics.

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