Ecological Applications, 14(6), 2004, pp. 1680–1694

COMMUNITY- AND ECOSYSTEM-LEVEL CHANGES IN A SPECIES-RICH TALLGRASS PRAIRIE RESTORATION

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Abstract. Changes in the plant community and ecosystem properties that follow the conversion of agriculture to restored tallgrass prairies are poorly understood. Beginning in 1995, we established a species-rich, restored prairie chronosequence where ~3 ha of agricultural land have been converted to tallgrass prairie each year. Our goals were to examine differences in ecosystem properties between these restored prairies and adjacent agricultural fields and to determine changes in, and potential interactions between, the plant community and ecosystem properties that occur over time in the restored prairies. During the summers of 2000–2002, we examined species cover, soil C and N, potential net C and N mineralization, litter mass, soil texture, and bulk density across the 6- to 8-year-old prairie chronosequence and adjacent agricultural fields in southern Minnesota. We also established experimentally fertilized, watered, and control plots in the prairie chronosequence to examine the degree of nitrogen limitation on aboveground and belowground net primary production (ANPP and BNPP). Large shifts in functional diversity occurred within three growing seasons. First-year prairies were dominated by annuals and biennials. By the second growing season, perennial native composites had become dominant, followed by a significant shift to warm-season C_4 grasses in prairies ≥3 yr old. Ecosystem properties that changed with the rise of C_4 grasses included increased BNPP, litter mass, and C mineralization rates and decreased N mineralization rates. ANPP increased significantly with N fertilization but did not vary between young and old prairies with dramatically different plant community composition. Total soil C and N were not significantly different between prairie and agricultural soils in the depths examined (0–10, 10–20, 20–35, 35–50, 50–65 cm). We compared the results from our species-rich prairie restoration to published data on ecosystem function in other restored grasslands, such as Conservation Reserve Program (CRP) and old-field successional sites. Results suggest that rapid changes in functional diversity can have large impacts on ecosystem-level properties, causing community- and system-level dynamics in species-rich prairie restorations to converge with those from low-diversity managed grasslands.

Key words: agriculture; carbon; community; Conservation Reserve Program (CRP); ecosystem; mineralization; nitrogen; restoration; soil; tallgrass prairie.

INTRODUCTION

At the time of European settlement, tallgrass prairie covered more than 68×10^6 ha of the North American Great Plains (Samson and Knopf 1994, Robertson et al. 1997). Because tallgrass prairies areas were so productive for agriculture, they were almost eliminated in North America after European settlement, resulting in substantial changes in community composition and ecosystem processes. In Minnesota, for example, <1% of pre-settlement tallgrass prairie remains (Samson and Knopf 1994, Robertson et al. 1997). The long-term effects of agriculture on soil properties are well known, with most studies in the Midwest indicating a 30–60% decline in soil C and N following decades of cultivation (Hass et al. 1957, Tiessen et al. 1982, Schlesinger 1986, Lal et al. 1999, Potter et al. 1999, Kucharik et al. 2001).

More recently, there have been increasing efforts to return native grasslands to the area of former tallgrass prairie. The Conservation Reserve Program (CRP) has been the impetus for grassland planting over significant areas of the Great Plains (Skold 1989). In addition, both government and private organizations have attempted to restore diverse prairie vegetation in former agricultural sites (Mlot 1990). Both the extreme loss of prairie habitat in the 19th century and the modest return of grasslands in recent years have had a large impact on the ecological characteristics of the affected lands. But these ecological changes are little studied and poorly understood, especially those where agricultural land is converted to prairie. Ecological restoration is important not only for its conservation value, but also because it offers an opportunity to investigate fundamental questions about the structure and function of ecosystems (Dobson et al. 1997).

Manuscript received 8 September 2003; revised 13 February 2004; accepted 24 February 2004. Corresponding Editor: I. C. Burke.

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The different management objectives of prairie restorations and the CRP offer a valuable opportunity for assessing the generality of changes in community structure and system-level processes in managed grassland systems following agriculture. A primary goal of prairie restorations is the reestablishment of native plant species. The few studies of ''complete'' prairie restorations, where species are established in abundances and composition similar to native communities (Cottam and Wilson 1966, Howell and Jordan 1989, Sluis 2002), usually describe how species diversity changes through time (Cottam and Wilson 1966, Sperry 1994, Kindscher and Tieszen 1998, Sluis 2002), although the restoration of ecosystem function is also clearly important (Kindscher and Tieszen 1998, Kucharik et al. 2001). Restorations in Kansas and Illinois suggest that plant diversity declines within 25–35 yr of prairie establishment, even with continual seed supply from native remnants (Kindscher and Tieszen 1998). Even after several decades of restoration, these authors concluded that restored prairies little resemble the species-rich remnants they were intended to model.

In contrast, the goal of the CRP is to prevent soil erosion and improve water quality (Skold 1989), but studies of CRP grasslands focus on ecosystem processes to determine rates of soil organic carbon (SOC) accumulation and changes in nutrient cycles (Gebhart et al. 1994, Barker et al. 1995, Burke et al. 1995, Reeder et al. 1998, Bruce et al. 1999, Karlen et al. 1999, Baer et al. 2000, 2002). Almost all CRP lands in the historical region of tallgrass prairie were planted to grasses only, lacking the kinds of species diversity characteristic of the original prairie system and are, therefore, better described as ''functional'' restorations (Howell and Jordan 1989, Sluis 2002), where ecosystem processes are strongly controlled by the dominant functional group—warm-season C_4 grasses in many cases. Burke et al. (1995) proposed a conceptual model of nutrient and carbon dynamics in abandoned agricultural fields in northeastern Colorado. They suggested that pools of total soil C would change slowly, requiring up to 100 yr or more before returning to levels of native grasslands. In contrast, pools of active C and N should increase in the first few decades following agricultural abandonment (Barker et al. 1995, Burke et al. 1995, Reeder et al. 1998, Bruce et al. 1999, Karlen et al. 1999, Baer et al. 2000, 2002), although the rate of increase depends on site-specific conditions (community composition, climate, and soils). Mineralizable C often increases following restoration (Burke et al. 1995, Reeder et al. 1998, Karlen et al. 1999, Kucharik et al. 2001, Baer et al. 2002). Available N and net N mineralization have been shown to increase in some studies (Burke et al. 1995, Reeder et al. 1998) but decline following restoration in other studies (Karlen et al. 1999, Baer et al. 2002).

Because species and functional diversity vary greatly between complete restorations in prairies and functional restorations in CRP lands, examining both approaches may make it possible to determine the generality of ecosystem changes in managed grasslands. Although changes in the plant community and soil ecosystem properties have been reported for old-field successional plots at the Cedar Creek Long Term Ecological Research (LTER) site in Minnesota, studies of nonplanted systems may confound soil C and N recovery with that of the plant community. For example, to the extent that these species are colonization limited (Inouye et al. 1987, Tilman 1997), C and N dynamics will lag vegetation changes, possibly explaining slow rates of C and N accumulation in these infertile sites (Knops and Tilman 2000). To date, there have been few studies reporting changes in both community and ecosystem processes in complete prairie restorations (Kindscher and Tieszen 1998).

We used a large-scale prairie restoration in southern Minnesota to examine community and ecosystem changes in several agricultural and tallgrass prairie restoration sites. We utilized a chronosequence of restored tallgrass prairie sites ranging in age from 1 to 8 yr together with adjacent agricultural fields. Our goals were to examine (1) how plant functional groups and ecosystem properties change through time, (2) the extent to which ecosystem processes, such as productivity and C and N cycling, may be functional group dependent, and (3) whether ecosystem processes differ in restored prairies compared to published data from CRP lands with low species richness.

Study Site

The Carleton College Cowling Arboretum consists of 325 ha immediately adjacent to the Carleton College campus in Northfield, Minnesota, USA (Fig. 1). At the time of the General Land Survey in the mid-19th century, the vegetation of the area was a complex mosaic of prairie, closed-canopy forest, and oak savannas and thickets at the prairie–forest border (Grimm 1984). Since European settlement (~1860 AD), the land has been used for cultivation of annual crops, especially corn (*Zea mays*) and soybean (*Glycine max*) in recent decades.

Starting in 1995, large blocks of prairie (mean of ~3 ha) have been planted in these cultivated areas each year (Fig. 1). Seeding took place in late fall of each year. Since germination did not occur until the following spring, we designated individual restorations by their first growing season rather than the year seed was planted. Hereafter, we refer to prairie restorations and agricultural sites by the two-digit year of first growing season (i.e., the 95, 96, 97. . . , 07 prairies). Seeds for each restoration were collected from local (within 20 km of the Arboretum) prairie remnants. Bulk prairie seed was collected by haying at a 13-ha prairie remnant located 11 km from the Arboretum, which has a diverse flora of prairie plants (over 200 plant species known; M. J. McKone, *unpublished data*). Populations of the

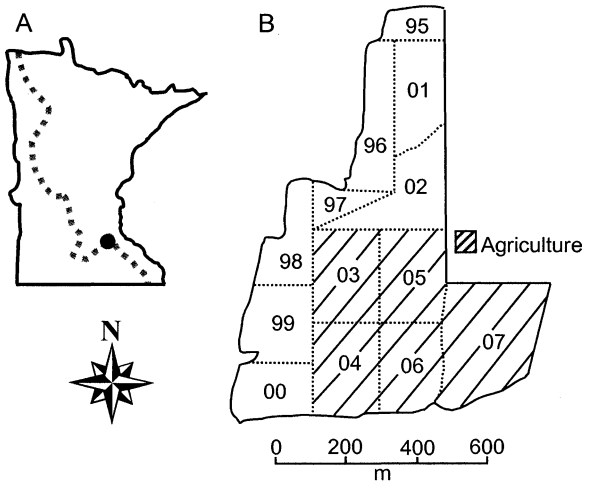

FIG. 1. (A) Location of the Cowling Arboretum study sites in Northfield, Minnesota, USA, relative to the position of the modern prairie–forest border (dotted line). (B) Close-up map of prairie restoration sites, which are identified by a two-digit designation indicating the first growing season (95–07). Future restoration sites still in agriculture through 2002 are shown with hatching.

long-lived prairie plants in the remnant probably changed relatively little among years. However, the composition of seeds planted each year could have varied due to differences in exact location hayed within the remnant and to annual variation in the rate of flowering and fruiting of different species. Native grasses were consistently abundant in the bulk seed from hay, but we supplemented this with hand-collected seed to ensure that all functional groups (see Table 1) were well represented. On average, hand-collected seed added 10–20% bulk mass to the seed collected by haying. A mean of 36 hand-collected species were added each year, including multiple species of legumes, perennial composites, and other perennial forbs.

In most years, prairies to be seeded in the fall were fallow for the preceding growing season. Final site preparation and planting were done by Prairie Restorations, Inc. (Princeton, Minnesota, USA). After plowing and disking, a mix of the bulk and hand-collected seed was planted with a broadcast seeder towed by a tractor. In the first growing season, the newly planted prairies were mowed to suppress the heavy growth of annual agricultural weeds from the soil seed bank. Mowing sometimes occurred in the second year as well, depending on the density of weeds. During the period of soil sampling, all but one of the agricultural fields (01–06) were planted in corn using conventional chisel-plow tillage—the exceptions being the 07 field, which was planted to soybeans, and the 02 field, in which <10% was planted to alfalfa (*Medicago sativa*).

The planted prairie restorations were managed by fire as soon as there was sufficient biomass accumulation, typically in spring of the third year. Some restorations are burned each year, with a mean of 3–4 yr between fires at a particular site. In 2000 and 2001, we reduced fire as much as possible to eliminate variability in net primary production (NPP), C, and N cycling associated with this treatment.

Soils types were variable across the chronosequence (NRCS Soil Conservation Service 1983, *available online*;[2] NRCS Soil Survey Division 2002, *available online*).[3] Soils in the majority of prairie restorations (97–00) and agricultural sites (02–07) (Fig. 1) were classified as Ostrander series, which are deep and well-drained soils that formed in a mantle of silty or loamy sediments with firm loam glacial till beginning between depths of 90–150 cm. Soils in the 96 and 01 restorations (Fig. 1) were classified as Kanaranzi series, which are very deep and well-drained soils that formed in a loamy mantle over sandy sediments. Soils in the 95 restoration were classified as Wadena series, which are well-drained soils that formed in glacial outwash consisting of a 60–100-cm loamy mantle over sandy sediments.

METHODS

In 2000, we established 12 permanent vegetation and soil sampling plots in each of the restored prairies and agricultural fields slated for restoration ($n = 156$). Each permanent plot (1.5 × 2.0 m) consisted of three contiguous 0.5 × 2.0 m quadrats. Vegetation surveys were conducted in the two outer quadrats, and soil properties were sampled from the inner quadrat.

Vegetation sampling

Plant community composition was sampled in mid- to late summer (late July to early September) of 2000 and 2002 in the 2-m^2 area of each permanent plot. We visually estimated cover for each species in the plots using cover classes according to Daubenmire (1959), except that we divided Daubenmire's 0–5% cover class into two classes (0–1% and 2–5%). Nomenclature follows Kartesz (1994).

Vegetation data were summarized by functional group (Table 1). The groups annuals/biennials, legumes, C_3 grasses, and C_4 grasses are those used in previous functional group classifications in prairie (Kindscher and Wells 1995, Tilman et al. 1997). We separated native and non-native perennials, since the non-native perennials in our study site were most common early in the chronosequence (Table 1) and so were functionally different from the native perennials. We also defined a functional group for perennial native composites (family Asteraceae), because composites made up the large majority (>80%) of the cover of summer/fall forbs (Table 1).

In 2000, all six prairie plantings (95–00) were sampled ($n = 72$), and the same plots were resampled in 2002. Also in 2002 we added plots in the two new

[2] ⟨http://www.co.dakota.mn.us/gis/data/soils.htm⟩
[3] ⟨http://ortho.ftw.nrcs.usda.gov/osd/⟩

TABLE 1. Plant species abundance in 2002 in prairie restorations of different ages in Minnesota, USA, ranked by abundance within functional groups.

Functional group and species (family)	Mean percent cover in restorations of different age (by year of growth)							
	First	Second	Third	Fourth	Fifth	Sixth	Seventh	Eighth
Annuals/biennials								
Setaria spp. (Poaceae)	37.9	3.7	2.6	0.3	0.0	4.8	0.3	3.2
Conyza canadensis (Asteraceae)	0.4	17.5	0.1	0.0	0.0	1.5	0.0	0.0
Ambrosia artemisiifolia (Asteraceae)	9.6	2.8	12.8	0.9	0.0	1.2	0.0	0.0
Chamaecrista fasciculata (Fabaceae)	0.0	0.1	1.8	0.0	2.5	0.0	0.0	0.1
Digitaria spp. (Poaceae)	2.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Chenopodium album (Chenopodiaceae)	2.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Non-native perennials								
Medicago sativa (Fabaceae)†	7.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Silene latifolia (Caryophyllaceae)	2.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Taraxacum officinale (Asteraceae)	1.4	0.2	0.0	0.0	0.0	0.2	0.1	0.0
Native perennial composites								
Solidago rigida (Asteraceae)	0.0	2.8	5.0	18.7	11.6	0.3	1.3	3.6
Solidago canadensis (Asteraceae)	0.0	0.6	7.9	5.3	1.8	0.0	17.2	4.6
Rudbeckia hirta (Asteraceae)‡	0.0	9.0	0.4	0.0	0.1	1.4	0.3	0.0
Solidago gigantea (Asteraceae)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	6.1
Achillea millefolium (Asteraceae)	2.6	4.9	0.8	0.1	2.5	0.7	1.3	0.1
Aster ericoides (Asteraceae)	0.0	0.1	1.7	0.6	4.5	0.1	0.0	0.0
Artemisia ludoviciana (Asteraceae)	0.0	0.1	0.0	0.6	0.6	0.0	2.3	3.8
Ratibida pinnata (Asteraceae)	0.0	2.2	1.1	2.7	0.9	0.6	0.1	0.1
Solidago speciosa (Asteraceae)	0.0	0.0	0.0	2.4	0.0	0.0	0.0	0.0
Silphium laciniatum (Asteraceae)	0.0	0.0	0.0	0.0	0.1	1.9	0.6	0.0
Aster laevis (Asteraceae)	0.0	0.0	0.1	1.6	0.4	0.0	0.0	0.0
Helianthus grosseserratus (Asteraceae)	0.0	0.0	0.0	1.6	1.6	0.0	0.0	0.0
Artemisia campestris (Asteraceae)	0.0	0.0	0.0	0.1	1.4	0.0	0.3	0.0
Aster oolentangiensis (Asteraceae)	0.0	0.9	0.0	1.4	0.3	0.0	0.0	0.0
Native perennial legumes								
Baptisia alba (Fabaceae)	0.0	0.0	0.6	0.0	0.0	0.0	0.6	4.5
Desmodium canadense (Fabaceae)	0.0	0.0	0.0	0.9	0.2	0.0	3.2	0.0
Lespedeza capitata (Fabaceae)	0.0	0.0	0.0	0.0	0.1	0.0	0.0	1.6
Other native perennials								
Monarda fistulosa (Lamiaceae)	0.1	1.4	4.2	3.8	1.2	0.0	2.3	3.6
Asclepias syriaca (Asclepiadaceae)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.3
C_4 grasses								
Sorghastrum nutans (Poaceae)	0.0	2.8	26.9	22.0	50.0	49.1	28.8	18.3
Andropogon gerardii (Poaceae)	0.0	2.6	7.1	9.4	5.3	6.3	3.3	26.5
Panicum virgatum (Poaceae)	0.0	3.7	2.0	2.3	3.4	11.7	2.1	1.9
Schizachyrium scoparium (Poaceae)	0.0	1.0	1.6	3.3	0.0	3.2	6.7	0.0
Muhlenbergia spp. (Poaceae)	0.0	0.0	0.0	2.7	0.0	0.0	0.9	0.0
C_3 grasses								
Elytrigia repens (Poaceae)	0.0	3.3	0.0	0.0	0.0	0.0	0.0	4.2
Elymus canadensis (Poaceae)	0.0	0.5	2.2	0.1	0.0	0.1	0.1	0.0
Bromus latiglumis (Poaceae)	0.0	0.1	1.0	0.4	0.1	0.0	0.0	0.0

Notes: Twelve plots of 2 m^2 were sampled in each age category, when restorations were in their first to their eighth year of growth. All species that had mean cover >1% in any age are listed. Nomenclature follows Kartesz (1994).

† Alfalfa (*Medicago sativa*) had been planted in this area when it was used for agriculture, particularly in the restoration that was in its first growing season in 2002.

‡ *Rudbeckia hirta* can be either a short-lived perennial or a biennial (Barkley 1986, Antonio and Masi 2001).

restorations, 01–02 (n = 96). Our analyses of community composition therefore include the 6- to 8-yr chronosequence as well as two years of longitudinal data for the 95–00 plantings.

C and N pools and soil texture

Soils were sampled for texture, bulk density, litter mass, and pools of C and N between 25 August and 7 September 2000 using 8.125 cm diameter bucket augers. Three soil samples were collected at depths of 0–10, 10–20, 20–35, 35–50, and 50–65 cm and composited into a single soil sample for each depth for all 12 permanent plots in all 13 sites (n = 780). A temporary catwalk was constructed while sampling soils to prevent vegetation damage in the permanent plots. Three composite litter samples were collected from a known area in each permanent plot and oven dried at 70°C for 24 h. Soil samples were passed through a 2-mm sieve and oven dried at 70°C for 24 h. The volume of pebbles >2 mm diameter was calculated using vol-

umetric displacement in water. Bulk density was calculated using the <2-mm oven-dried soil mass, and auger volumes were corrected by subtracting the volume of >2-mm pebbles. Dried soils for total C and N analyses were ground to analytical fineness in a ball mill (8000-D, Spex Certiprep, Metuchen, New Jersey, USA), and percentage of C and N were determined using elemental combustion with a CN analyzer (Costech, Valencia, California, USA). Bulk density was used to convert C and N from concentration (in grams per gram of soil) to area-based values (in grams per square meter) for each depth interval.

Because soils in the study site were relatively sandy, we measured soil texture using a combination of direct measurement of the sand fraction and the hydrometer method (Sheldrick and Wang 1993) to characterize the clay and silt fractions. For each of the 780 samples, 40 g of oven-dried, <2-mm sieved soil was soaked in a 5% sodium hexametaphosphate solution for 24 h and then agitated for 5 min in a malt mixer. Samples were passed through a 53-μm sieve to manually collect and wash the sand fraction, which was dried and massed. The remaining soil solution was collected in hydrometer cylinders and analyzed for clay after 24 h.

C and N mineralization rates

We determined potential net C and N mineralizations using laboratory incubations of soils held at constant moisture (approximate field capacity) and temperature (25° ± 1°C) to eliminate field variability in these factors (Mielnick and Dugas 2000). Soils collected from the permanent plots were placed immediately on ice and processed within 4–6 h. Field capacity was estimated by determining the mass of water retained in a subsample of each soil allowed to drain excess gravitational water. We limited C and N mineralization determinations to a subset of sites (95, 96, 98, and 00 prairies and 01, 03, and 04 agriculture) and soil depths (0–10, 10–20, and 50–65 cm; $n = 252$).

Carbon mineralization rates were determined using direct measurements of CO_2 respired in laboratory incubations of 20 g of soil (Nadelhoffer et al. 1991, Pastor et al. 1993, Hobbie et al. 2002, Weintraub and Schimel 2003). Fresh soil was added to 100-mL polypropylene specimen cups. The predetermined masses of distilled water were added to raise moisture content to field capacity, and the specimen cups were placed in 1-L mason jars and covered with polyethylene film permeable to air. Separate subsamples of fresh soil were weighed and dried at 70°C for 24 h to estimate the oven-dried mass of the incubated samples. Soil respiration was measured after 1, 3, 7, 14, 28, 60, 90, 120, 150, and 180 d. At each of these sample periods, the polyethylene film was removed, jars were capped with a septum-permeated lid, and initial gas samples (5 mL) were withdrawn with a syringe and analyzed immediately with thermal conductivity detector (TCD) gas chromatography (Schimadzu Model 8, Columbia, Maryland, USA). Respiration rate was calculated by the change in headspace CO_2 in capped jars measured over time, and samples were allowed to incubate for 24 h in a climate-controlled (25° ± 1°C) walk-in growth chamber. Cumulative C mineralization rates (in grams of carbon per square meter per year) were determined using the mean respiration rate during the incubation, multiplying by the time interval between sampling periods, and summing the intervals (Pastor et al. 1993, Hobbie 2002), and we report these data as an area-based daily flux (in grams of carbon per square meter per day) to be consistent with our presentation of N mineralization rates (see below). Between headspace sampling periods, jar lids were removed and replaced with polyethylene plastic wrap. Specimen cup masses were measured every 2 d over the six-month period, and water was added whenever needed.

Potential net N mineralization was determined using 30-d laboratory incubations of 20-g soil samples in 250-mL polypropylene bottles covered with punctured aluminum foil to maintain ambient O_2 and held at constant temperature (25° ± 1°C) and darkness in a growth chamber. A set of initial samples was processed at the same time as the C mineralization samples. Incubated soils were measured every 2 d, and soil moisture was maintained at field capacity over the 30-d incubation period. Initial and incubated soils were extracted with 2 mol/L KCl and analyzed for NH_4 and NO_3/NO_2-N using alkaline phenate and Cd reduction methods for autoanalysis (Lachat FIA 8000, Milwaukee, Wisconsin, USA). Net mineralization rate was calculated as the quantity of NH_4-N and NO_3/NO_2-N in incubated samples minus the quantity in initial samples. Bulk density and soil solution ratio were used to convert values from concentration (in milligrams of N per liter per day) to area-based (in grams of N per square meter per day) values for each depth interval.

Above- and belowground primary productivity

During the growing season in 2001, we measured above- and belowground net primary productivity (ANPP and BNPP) in fertilized, watered, and control plots located ~2 m adjacent to each of the permanent plots. Measurements were made during an average, non-drought year in Rice County, Minnesota, with annual precipitation at our sites totaling 76.7 cm compared to the long-term (1931–1995) mean of 75.4 cm. Over the growing season, fertilized plots were amended with a NH_4NO_3 solution, delivering a total N mass per area approximately equal the natural rate of N mineralization in this region (10 g $N \cdot m^{-2} \cdot yr^{-1}$). Watered plots were amended with distilled water at the same volume applied to fertilized plots (1 L). Plots were fertilized and watered at the beginning of each month from April to September. Because the total water addition (6 L per plot) amounted to <1% of annual precipitation at this site, we intended the watered treatment to serve as a moisture control for the fertilized treatment instead of

as treatment with which to assess water limitation on NPP. Control plots were not supplemented with fertilizer or water.

For each treatment, biomass and surface litter were removed from 1.5 × 1 m plots using hand-clipping and collection immediately following snowmelt in April 2001. Aboveground NPP was measured in a 1 × 1 m subsection of each plot clipped at the end of the growing season (1–7 October). Biomass was oven dried at 70°C for 72 h and weighed. Belowground NPP was measured in the remaining 0.5 × 1 m vegetated section of fertilized, watered, and control plots at a depth of 0–20 cm using the root ingrowth method (Robertson et al. 1999). In April 2001, soil was removed from one core in each plot using 3.75 cm diameter, schedule 40 PVC pipes cut to length. Holes were lined with steel mesh with openings 0.625 mm in diameter. Soil was sieved free of roots and returned to the core hole. In October 2001, root biomass was sampled from core holes, washed using a 500-μm sieve, and oven dried at 70°C for 24 h.

Statistical analyses

We recognize that our use of a prairie chronosequence is subject to the limitations of pseudoreplication and space-for-time substitutions (Hurlbert 1984). Given the large size of each prairie planting (~3 ha) and the overall size of the restoration (~40 ha), it was not practical to establish replicate plantings of the same age that were sufficiently large to minimize edge effects. Although site-specific factors, such as soil texture, bulk density, and seed composition, can confound processes that change over time, we addressed this issue by undertaking a detailed assessment of texture and bulk density to characterize site-to-site variability and to incorporate differences into our analyses and interpretations. We examined mass-based measurements of soil C and N data in addition to area-based measurements to consider the effects of bulk density on carbon accumulation. Finally, we examined changes in vegetation dynamics over two separate growing seasons (2000, 2002), giving us repeated measures of community composition. The chronosequence approach has been a valuable method for understanding changes occurring in managed grassland systems (Barker et al. 1995, Burke et al. 1995, Reeder et al. 1998, Bruce et al. 1999, Karlen et al. 1999, Baer et al. 2000, 2002), and tests of the power of the chronosequence approach indicate that successional changes are reliably described (Foster and Tilman 2000).

We eliminated the effects of pseudoreplication by using site, rather than the 12 permanent plots within each site, as our experimental unit for all analyses with the exception of the vegetation analyses (see below). Changes in vegetation and ecosystem processes were examined with regression, using the 12 permanent plots as subreplicates to generate mean values for each site. The seven agricultural sites were averaged together to generate a single mean value for each ecosystem property. For the productivity experiment, we assessed the effects of prairie age, fertilization/water treatments, and potential interactions on ANPP and BNPP, using two-way ANOVA with Type III sums of squares (Sokal and Rohlf 1994). For prairie age, we divided sites into those that were <3 yr old (00 and 01 restorations) and those ≥3 yr old (95–99 restorations), which become dominated by warm-season C_4 grasses. We used contrasts to test for differences among control, watered, and fertilized treatments.

We analyzed plant community traits using two approaches. To compare sites across the chronosequence, we averaged permanent plot data into site means. However, we did not use regression analysis because vegetation changes were highly nonlinear. To test for significant changes in vegetation through time in each restoration, we used 2000 and 2002 census data from permanent plots to calculate paired *t* tests (permanent plot is the experimental unit, $n = 12$ per restoration). This is valid statistical use of the 12 replicate plots because we are comparing changes *within* a site through time, rather than comparing vegetation changes *across* sites, which, as described above, would be more appropriately addressed using regression with site means. Because we calculated six multiple tests per data set, we used Bonferroni adjustments of Type I error (α) from 0.05 to 0.008. This approach allows us to describe vegetation changes across time and to verify these changes with repeated measures.

RESULTS

Changes in community composition

Overall species richness in 2000 and 2002 varied across plantings (Fig. 2A), and species richness per plot varied between 10 and 17 species/2 m^2. Most restorations had no change in species richness between 2000 and 2002, though the oldest restoration (95) had a significant decline. Comparison among restorations shows that there was an increase in the proportion of native species after the first growing season (Fig. 2B). There was a significant increase in proportion of native species between 2000 and 2002 in the 00 restoration (age 1 in 2000 vs. age 3 in 2002), the 99 restoration (age 2 vs. age 4), the 98 restoration (age 3 vs. age 5), and the 96 restoration (age 5 vs. age 7).

In the first season of growth, restorations were composed mainly of annuals and biennials, many of which are weedy, non-native species (Fig. 2C, Table 1). Comparisons among restorations show that annuals/biennials declined after the first growing season (Fig. 2C), and there was a significant decline between 2000 and 2002 surveys in the 00 restoration (age 1 in 2000 vs. age 3 in 2002), the 99 restoration (age 2 vs. age 4), and the 97 restoration (age 4 vs. age 6).

Perennial native composites were common in the restorations after the second growing season (Fig. 2D),

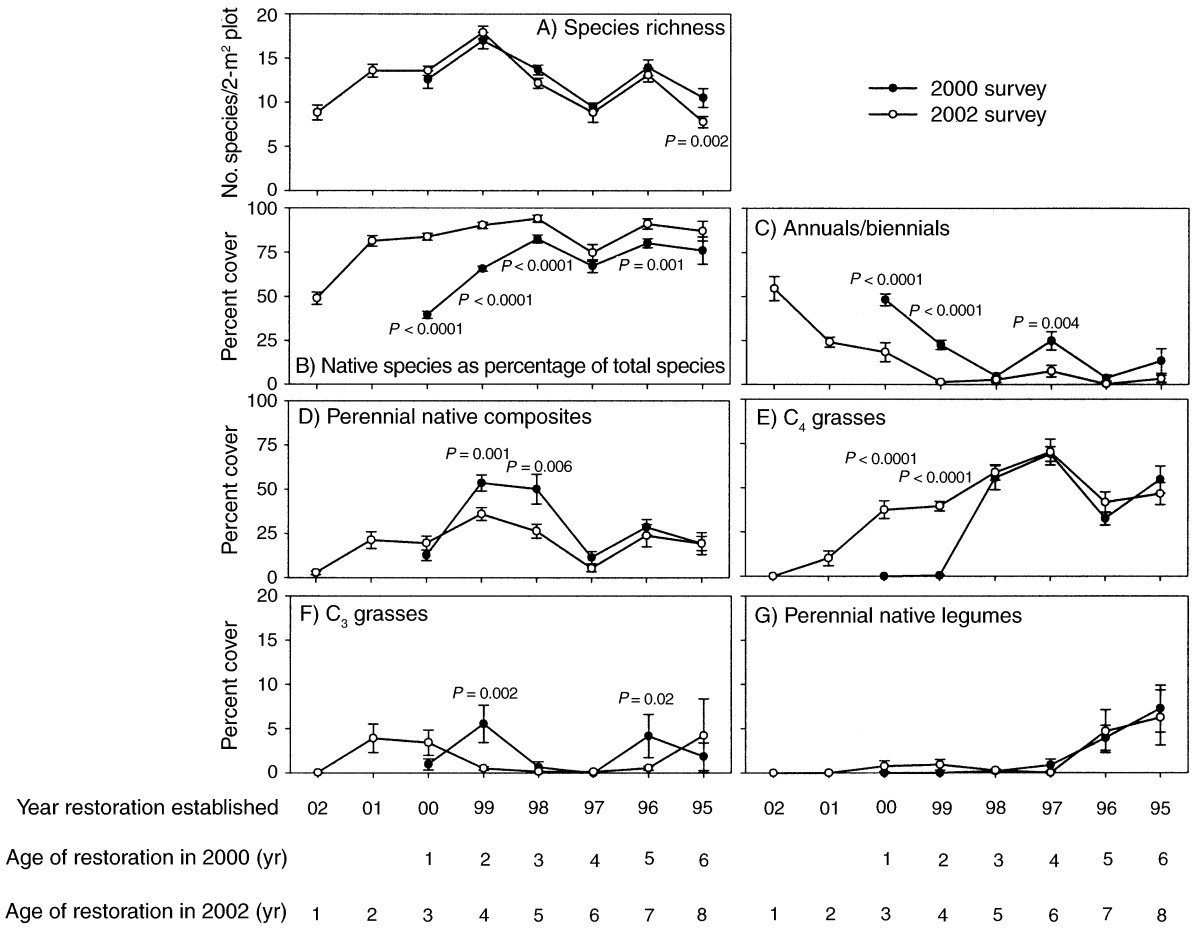

FIG. 2. Plant community changes as a function of number of growing seasons from the 2000 and 2002 surveys. The year of first growing season (site name) is also shown for both surveys. Mean differences in cover between the 2000 and 2002 surveys with P values <0.05 are shown; the Bonferroni-adjusted critical probability is $\alpha = 0.008$. Standard error bars accompany the mean from the 12 sampling plots in each site and are used to assess variability in means between surveys rather than across the chronosequence. The year when restoration began is indicated by two digits: 00 = 2000, 99 = 1999, etc.

but declined significantly from 2000 to 2002 in the 99 restoration (age 2 in 2000 vs. age 4 in 2002) and the 98 restoration (age 3 vs. age 5). Restorations that were >3 yr old in 2000 did not show a significant change in composite cover between 2000 and 2002.

By the third growing season, a significant fraction of vegetative cover (38–57%) became dominated by warm-season C_4 prairie grasses (Table 1, Fig. 2E), which, once established, remained the most dominant functional group in the community in growing seasons 3–8 (Fig. 2C–G). There were significant increases in C_4 grass cover between 2000 and 2002 in the 00 restoration (age 1 in 2000 vs. age 3 in 2002) and the 99 restoration (age 2 vs. age 4), but not in older restorations.

C_3 grasses had low cover and did not have a consistent pattern among restorations of different age (Fig. 2F), though there was a significant decrease in cover between 2000 and 2002 in the 99 restoration (age 2 in 2000 vs. age 4 in 2002). The decline in the 96 restoration (age 5 vs. age 7) was not significant ($P = 0.02$, Bonferroni-adjusted $\alpha = 0.008$). Perennial native legumes were uncommon except in the two oldest restorations (95 and 96; Fig. 2G). There was no significant change in legume cover between 2000 and 2002 in any restoration.

There was some evidence for site-specific effects on species richness and functional group composition in the first 6–8 yr of prairie establishment (Fig. 2). Collectively, these results suggest that consistent changes in annuals/biennials, perennial native composites, and C_4 grasses occur in the initial years of prairie establishment but that site-specific patterns can be maintained through time, especially for total species richness and perennial native legumes.

Site differences in soil texture and bulk density

Soil texture was more homogeneous than bulk density across prairie and agricultural sites (Fig. 3A, B).

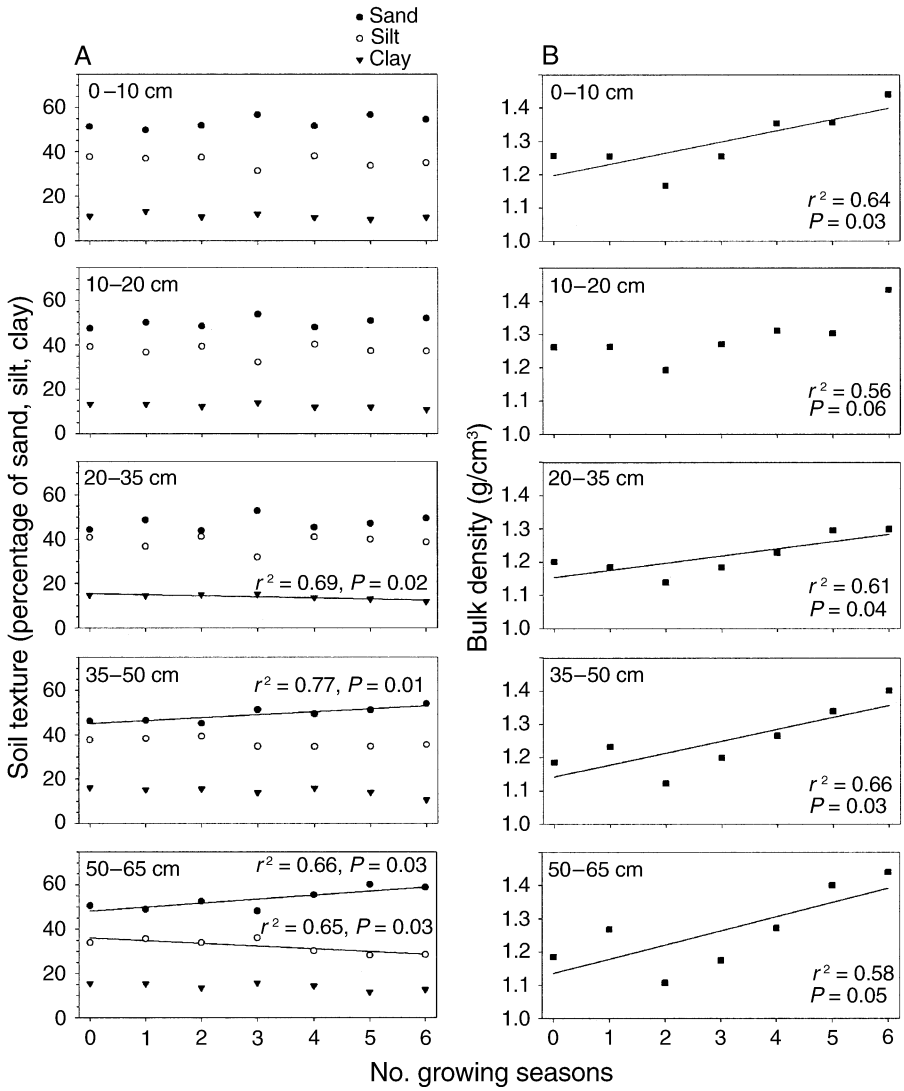

FIG. 3. (A) Soil texture and (B) bulk density as a function of depth across the prairie restoration chronosequence. No. growing seasons = 0 corresponds to sites currently in agriculture.

Mean soil texture consisted of loams and sandy loams, reflecting relatively uniform texture over the entire restoration site, and there were few significant differences in percentage of sand, silt, and clay among prairie and agricultural sites for all five depths (Fig. 3A). Sand fraction in the 35–50 and 50–65 cm depths was highest in older prairie sites (95 and 96), probably reflecting the shallower depths to sandy substratum in the Kanazari and Wadena soils (see *Study site* above). The clay fraction in the 20–35 cm depth was slightly (<3%), but significantly, lower in older restoration sites. The silt fraction changed significantly only in the 50–65 cm depth, where it was higher in older restoration sites. Bulk density exhibited highest values (>1.3 g/cm^3) in the 95 and 96 prairie restorations, causing marginally significant differences across the chronosequence (Fig. 3B).

Changes in soil C and N pools and litter mass

We found little change in total C and N over the first 6 yr of the chronosequence (Fig. 4A, B). There were no significant differences in total C and N across the agricultural or restoration sites for each of the five depths (Fig. 4A, B), and both total C and N declined with depth at most sites.

Litter mass increased significantly with the establishment of prairies and the shift to C_4 grasses after the third growing season (Fig. 5). We omitted the 3-yr-old (98) prairie restoration because a prescribed burn in 2000 significantly reduced surface litter at that site.

Changes in C and N mineralization

Potential C mineralization rates were significantly higher in older prairies dominated by C_4 grasses com-

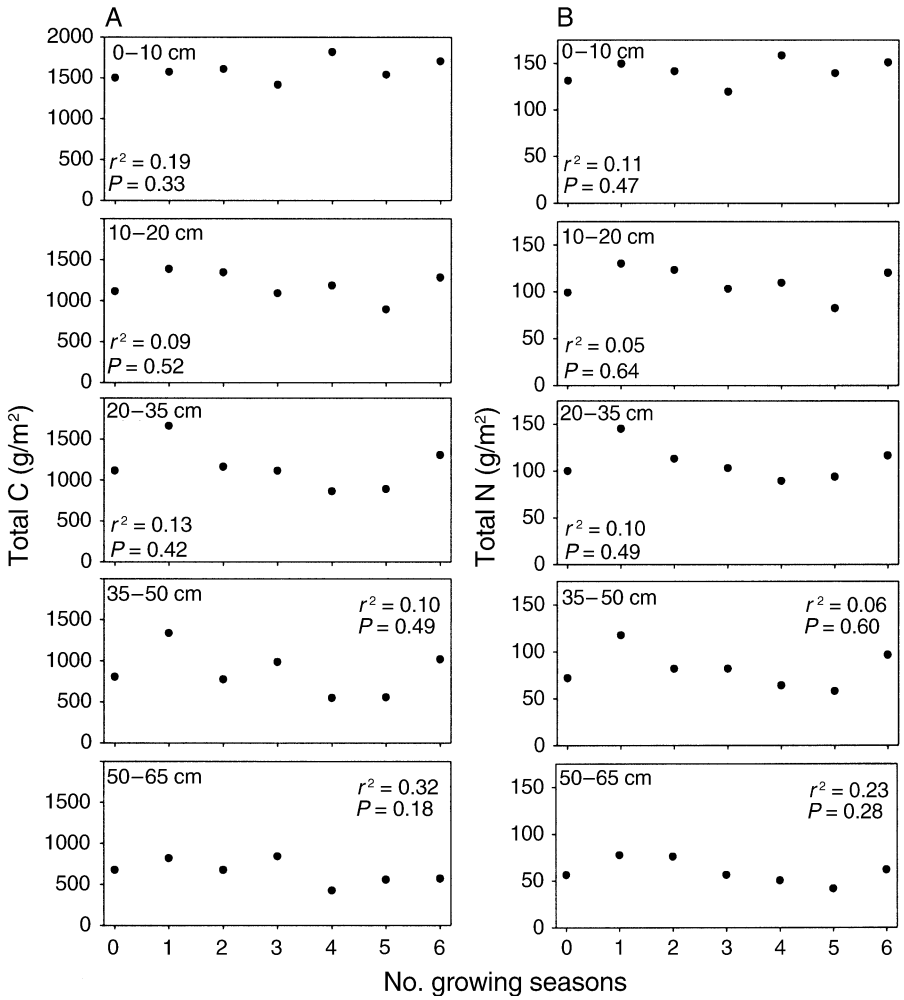

FIG. 4. Total (A) carbon and (B) nitrogen as a function of depth across the prairie restoration chronosequence. No. growing seasons = 0 corresponds to sites currently in agriculture.

pared to agricultural sites in the 0–10 cm depth (Fig. 6A). This trend was not observed for deeper soil profiles. Significant differences are probably not an artifact of site differences in bulk density used to convert mass-based C fluxes into area-based estimates because the mass-based C fluxes also showed similar differences in C mineralization rates across sites. In contrast, potential net N mineralization rates declined in older prairie restorations compared to agricultural sites and young prairies for all three depths (Fig. 6B), although the trends were not statistically significant.

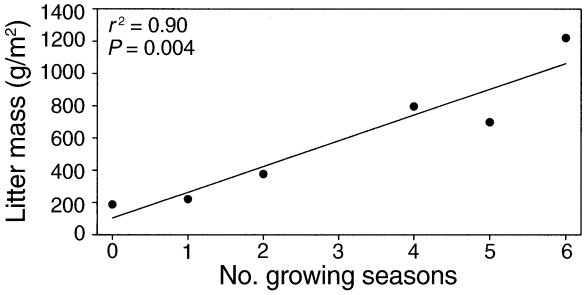

FIG. 5. Changes in litter mass across the prairie restoration chronosequence. No. growing seasons = 0 corresponds to sites currently in agriculture.

Changes in above- and belowground NPP

ANPP and BNPP showed significantly different responses with respect to prairie age. There were no significant differences in ANPP between prairies <3 yr old compared to prairies ≥3 yr in control, fertilized, and watered plots (Fig. 7, Table 2), despite large shifts in functional dominance from annuals/biennials and perennial native composites to C_4 grasses (Fig. 2C–E). In contrast, BNPP responded strongly to prairie age, increasing significantly by the third growing season coincident with the rise of C_4 grasses (Fig. 7, Table 2). BNPP was significantly higher for >3-yr-old sites than for <3-yr-old sites.

ANPP and BNPP also showed significantly different responses to N amendments (Fig. 7). Relative to the

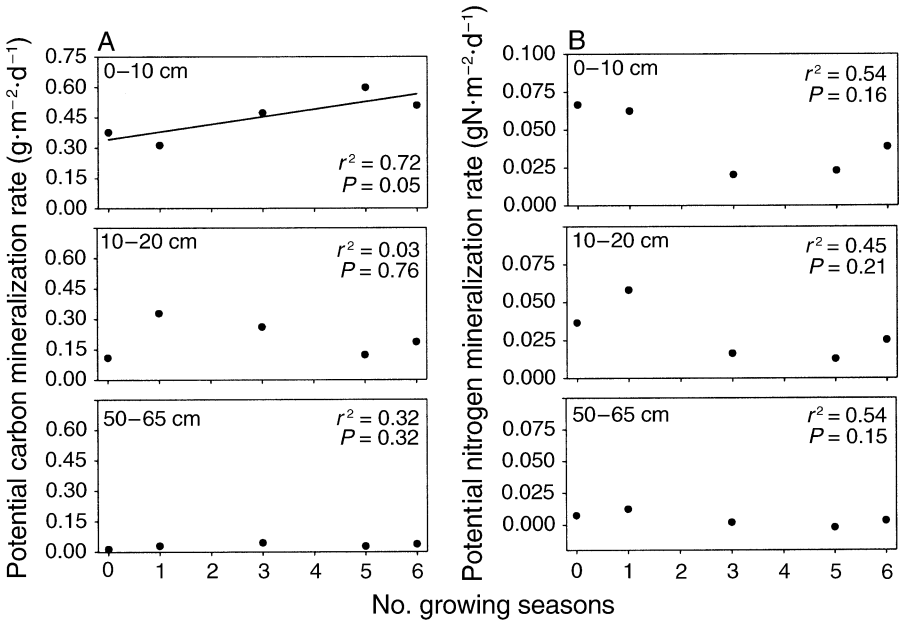

FIG. 6. (A) Potential carbon mineralization rate and (B) potential net nitrogen mineralization rate as a function of depth across selected sites in the prairie restoration chronosequence. No. growing seasons = 0 corresponds to sites currently in agriculture.

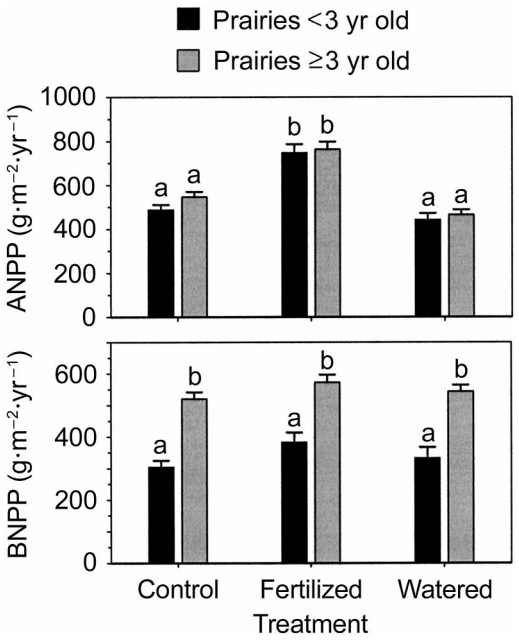

FIG. 7. Changes in restored prairie aboveground net primary productivity (ANPP) and belowground net primary productivity (BNPP) as a function of treatment and number of prairie growing seasons (means + 1 SE). Letters denote significant differences in mean productivity within each panel at the $\alpha = 0.05$ level.

control and watered plots, the fertilizer treatment significantly enhanced ANPP (Fig. 7, Table 2). Because there were significant differences between fertilized and control plots and no statistical difference between control and watered plots (Fig. 7, Table 2), the enhanced ANPP in fertilized plots was caused by the additional N rather than water in the fertilizer solution. In contrast, there were no differences in BNPP among the treatments (Fig. 7, Table 2).

DISCUSSION

Results from this study support several emerging community- and ecosystem-level patterns from managed grassland ecosystems, including species-rich restorations, CRP lands, and old-field successional sites.

Establishment of C_4 grass dominance

Despite large differences in initial floristic composition, restored prairie community composition shifts towards C_4 grass dominance (Kindscher and Tieszen 1998, Sluis 2002, Baer et al. 2003). Our results indicate that large changes in functional diversity and increases in C_4 grass cover occur within 3 yr of prairie restoration (Fig. 2). Prairies in Illinois showed a 50% decline in species richness within 15 yr of restoration concurrent with the rise in dominance of *Andropogon gerardii* (Sluis 2002). In a study of 5- and 35-yr-old restored prairies, Kindscher and Tieszen (1998) observed a significant rise in C_4 cover for the 35-yr-old restoration (71–92%) relative to an adjacent prairie remnant (59%). The cover of C_4 grasses was also large in the 5-yr-old restoration (81%), which was comparable to

TABLE 2. Two-way ANOVA test for the effects of prairie age (<3 yr old vs. ≥3 yr old) and fertilizer/water treatment on above- and belowground net primary productivity (ANPP and BNPP, respectively).

Test	*F*	df	*P*
ANPP			
Overall model	5.81	5, 15	0.004
Prairie age (<3 yr old vs. ≥3 yr old)	0.38	1, 15	0.55
Fertilizer/water treatment	11.98	2, 15	0.001
Contrast 1: control vs. fertilized			<0.0001
Contrast 2: control vs. watered			0.35
Contrast 3: fertilized vs. watered			<0.0001
Prairie age × fertilizer/water treatment	0.07	2, 15	0.94
BNPP			
Overall model	5.86	5, 15	0.003
Prairie age (<3 yr old vs. ≥3 yr old)	27.31	1, 15	<0.0001
Fertilizer/water treatment	0.93	2, 15	0.41
Prairie age × fertilizer/water treatment	0.043	2, 15	0.96

Note: Contrasts are presented to show significant differences among fertilizer/water/control treatments.

C_4 grass cover in an adjacent prairie remnant (79%). In an old-field chronosequence at the Cedar Creek LTER site in Minnesota, Tilman et al. (1997) described successional shifts to C_4 species (*A. gerardii*, *Schizachyrium scorparium*) that occurred over several decades because of recruitment limitation (Inouye et al. 1987). These results suggest that the dynamics of the plant community are potentially an order of magnitude faster in restored grasslands than in sites undergoing natural succession.

Species richness in long-term restored prairies generally persists at levels lower than native remnants (Curtis 1959, Weaver 1968, Collins and Glenn 1990), largely as a result of C_4 grass dominance (Kindscher and Tieszen 1998, Sluis 2002). As noted by Sluis (2002), there is currently no explanation for why dominant species exclude other species to a greater extent in restorations than in remnants. Fire is often promoted to maximize species richness in prairies (Leach and Givnish 1996, Collins et al. 1998), and fire has been regularly applied to all of the prairies in the Carleton Arboretum and other restorations (Curtis and Partch 1948, Sluis 2002), but not those described by Kindscher and Tieszen (1998). Frequent burning may exacerbate the shift to C_4 grasses at the expense of forbs (Howe 1994, Collins et al. 1998, Copeland et al. 2002).

Competition for soil resources may be a potential mechanism for the rise in C_4 grasses because ANPP was limited by N in our study (Fig. 7, Table 2), and our restoration fields have been degraded by more than a century of agriculture. The C_4 grass species in our sites (Table 1) have been shown to tolerate lower levels of available inorganic N than those required by early successional species (Tilman 1982, Tilman and Wedin 1991*a*, *b*, Wedin and Tilman 1993). However, N competition was probably not a dominant mechanism of competition in our sites because total N concentration across all agricultural and prairie soils 0–20 cm deep in this study was >1000 mg/kg (Fig. 4B)—approximately the same N concentration in Tilman and Wedin's (1991*a*) highest N treatment, where competition for light was deemed a greater factor than competition for N. Moreover, available inorganic N in our restored prairie soils (1–2 mg/kg, data not shown) was well above critical (*R**) levels for survival of all species (Tilman and Wedin 1991*b*), suggesting that light limitation may facilitate competitive exclusion.

Plant–mycorrhizal interactions may also facilitate C_4 grass dominance and contribute to reduced community diversity (Smith et al. 1998, Wilson and Hartnett 1998, Hartnett and Wilson 1999). Many C_4 grasses, including *A. gerardii*, are obligate mycotrophs (Brejda et al. 1993, Anderson et al. 1994, Wilson and Hartnett 1998), and mycorrhizal symbioses may disproportionately favor clonal species and hasten succession to C_4 dominance. In an extensive assessment of responses by 36 species of warm- and cool-season prairie grasses and 59 prairie forbs to arbuscular mycorrhizal (AM) fungal colonization, Wilson and Hartnett (1998) showed that biomass was enhanced by mycorrhizae in C_4 grasses and forbs, but not C_3 grasses or annuals. However, several other studies suggest that mycorrhizae may also benefit competitive subdominants (Walter et al. 1996, Marler et al. 1999).

Since most prairie restorations involve only the introduction of native plants, the absence of other members of the community could allow C_4 grasses to achieve competitive dominance that would not occur in a more trophically complex prairie. Selective grazing by bison (*Bison bison*) can reduce the competitive dominance of grasses and increase forb diversity (Coppedge et al. 1998, Howe 1999), and many restorations do not include regular grazing by bison or other large ungulates. More subtly, species-specific pathogens and insect herbivores could also reduce the ability of potentially dominant species to maintain monospecific stands

(Janzen 1970, Connell 1971, Holah and Alexander 1999, Kliromonos 2002). Such native pathogens and herbivores may not immediately colonize new prairie restorations in sites that are isolated from remnant prairie communities.

Changes in C and N cycling

Our study supports the rapid increase in active pools of C and N but slow changes in total C and N over time as documented in several successional grasslands (Burke et al. 1995) and restored grasslands (Karlen et al. 1999, Potter et al. 1999, Baer et al. 2000, 2002, Kucharik et al. 2001). The rise in warm-season C_4 grasses by the third growing season (Fig. 2E) correlated with increased litter mass (Fig. 5), C mineralization rates (Fig. 6A), and BNPP (Fig. 7) and decreased N mineralization rates (Fig. 6B). Compared to other functional groups in our study, C_4 grasses allocate greater biomass belowground (Tilman and Wedin 1991*a*, Craine et al. 2002). Greater BNPP in prairie sites dominated by C_4 grasses (Fig. 7) probably increased fine root turnover and labile C sources in the rooting zone (Burke et al. 1995, Baer et al. 2002), leading to significantly greater C mineralization in the 0–10 cm depth (Fig. 6A), which has been observed elsewhere within the first decade of restoration (Reeder et al. 1998, Baer et al. 2000, 2002). Similar to the results of Karlen et al. (1999) and Baer et al. (2002), we found a decline in N mineralization, rather than the increase reported by others (Burke et al. 1995, Reeder et al. 1998). It is possible that this pattern results from increasing microbial demand for N with increasing labile C inputs from developing root systems (Burke et al. 1995, Barrett and Burke 2000, Baer et al. 2002)—a process that may take 50 years before net nutrient availability increases (Burke et al. 1995).

Prairie NPP revealed an interesting mix of interactions between community and system-level processes. Aboveground NPP was statistically similar across all prairie sites (Fig. 7), suggesting that large changes in functional diversity (Fig. 2) have relatively little effect on ANPP. However, ANPP was significantly enhanced with the addition of N, suggesting that nutrient amendments alleviated N immobilization in the soil (Turner et al. 1997, Baer et al. 2003). In contrast, BNPP increased following the shift to C_4 grasses in older sites (Fig. 7). To the extent that BNPP and root turnover provide C to the soil in grassland systems (Jobbágy and Jackson 2000, Gill et al. 2002), these results suggest that plant species composition and succession may play a significant role in SOC sequestration in managed prairies. It is also interesting to note that ANPP in the first few decades of prairie restoration may ultimately be limited by microbial N immobilization as a result of greater BNPP.

In contrast to the relatively rapid shift to C_4 grasses and changes in BNPP, belowground C mineralization, and N mineralization rates, total soil C and N pools did not differ among restored prairies and agricultural sites for any depth (Fig. 4). This result is consistent with several studies of CRP and other restored grasslands, which report no significant C and N mass change in the first 10 yr since planting (Barker et al. 1995, Bruce et al. 1999, Karlen et al. 1999, Potter et al. 1999, Baer et al. 2000). It is inconsistent, however, with other studies reporting increased SOC in the first decade following agricultural abandonment. Some authors examining higher-resolution depth intervals (generally 0–5 cm deep) have argued that increased SOC in restored grassland soils occurs primarily in shallow depths as a result of above- and belowground litter inputs (Burke et al. 1995, Reeder et al. 1998, Baer et al. 2002), but one study reported increased SOC to a depth of 40 cm 5 yr following the conversion of agriculture to CRP grassland (Gebhart et al. 1994). There are several possible explanations for these discrepancies. Increases in SOC may be easier to detect when background pools are low, perhaps as a result of site-specific differences in agricultural C loss or soils with low initial amounts of SOC (Reeder et al. 1998). Studies of root mass distributions (Craine et al. 2002) indicate that shortgrasses have shallower root mass profiles than tallgrasses (but see Gill et al. [1999]), possibly explaining increases in shallow SOC in semiarid regions dominated by shortgrasses (Burke et al. 1995, Reeder et al. 1998, Baer et al. 2002). Site-specific differences in water availability caused by climatic variability and soil texture could have large impacts on SOC accumulation. Gill et al. (1999) found that soil decomposition rates in a shortgrass prairie soil varied twofold with depth, with greatest decomposition in the 10–15 cm layer and lowest decomposition at 75–100 cm—a pattern they attribute to high water availability in the 10–15 cm zone. A growing body of evidence suggests that achieving SOC levels of total soil C and N contents similar to native grasslands may require centuries, with durations between 180 and 230 years for old field sites that are dispersal limited (Knops and Tilman 2000) and between 100 and 170 years for CRP lands and prairie restorations (Potter et al. 1999, Kucharik et al. 2001).

The extent to which species and functional diversity affect accumulation rates of SOC remains controversial. Field and simulation studies of grassland restorations suggest that grass monocultures in CRP lands have higher potential for rapid accumulation of SOC compared to species-rich prairies. The simulation models developed by Kucharik et al. (2001) indicate that grass-dominated systems maximize SOC accumulation because of greater productivity and allocation to fine root biomass. They reported that species-rich prairie restorations sequestered lower amounts of SOC compared to high-productivity, C_4 grass-dominated systems and even no-till agricultural systems. Similarly, in an old-field chronosequence in Minnesota, Knops and Tilman (2000) found an inverse relationship between C_3 grass and forb cover and SOC accumulation. These

results are consistent with those presented here showing that BNPP increases significantly following the shift to C_4 grasses (Figs. 2E, 7), but the 8-yr duration of our chronosequence was insufficient for detecting a significant difference in total soil C between agricultural and restored prairies (Fig. 4A). However, these results from prairie restorations and natural grassland successional sites contrast with manipulations of species richness in experimental prairie communities, which showed that species-rich plots are capable of overyielding ANPP and total biomass (above and below ground) relative to C_4 grass monocultures (Tilman et al. 2001). To the extent that prairie restorations are less effective than CRP sites for soil C storage, maintaining species diversity and high rates of SOM accumulation may be conflicting management objectives in grassland systems.

Acknowledgments

This work was supported by a National Science Foundation CCLAI award, a small FDE grant from Carleton College, grants to Carleton College from the Howard Hughes Medical Institute, support from the Rosenow Endowment, and fellowships (Bush, Class of '49, and FDE) from Carleton College. Special thanks go to M. Bakke for logistical and planning support in the Carleton Arboretum. We thank M. Bakke, the Arboretum crews from 1995–2002, and Prairie Restorations, Inc., for assistance with prairie planting. We thank M. Peterson for access to agricultural lands and H. Whitesides, M. Buckman, and A. Forche for assistance with fieldwork. Thanks to C. Umbanhowar, Jr., and two anonymous reviewers for comments on this manuscript.

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