

A paired study of prairie carbon stocks, fluxes, and phenology: comparing the world's oldest prairie restoration with an adjacent remnant

CHRISTOPHER J. KUCHARIK*, NATHAN J. FAYRAM† and KIMBERLY NICHOLAS CAHILL‡

*Center for Sustainability and the Global Environment, University of Wisconsin-Madison, 1710 University Avenue, Madison, WI 53726, USA, †Wisconsin Department of Natural Resources, Bureau of Endangered Resources, 3911 Fish Hatchery Road, Madison, WI 53711, USA, ‡Interdisciplinary Program in Environment and Resources, Stanford University, Stanford, CA 94305, USA

Abstract

We measured carbon (C) stocks and fluxes and vegetation phenology in the world's oldest prairie restoration (~ 65 years) and an adjacent prairie remnant in southern Wisconsin from 2001–2004 to quantify structural and functional differences. While the species distributions and frequency differed, the number of species measured per 1 m² quadrat were not significantly different (15.8 ± 4.4 and 14.1 ± 2.1 for remnant and planted [order for all reported values in abstract]; $P = 0.29$), and the annual average aboveground net primary productivity (271 ± 51 and 330 ± 55 g C m⁻²) and peak leaf area index (2.9 – 4.9 m² m⁻²) were comparable under similar fire management. Total root biomass was not significantly different in 2002 (1736 ± 1062 and 1690 ± 459 g dry matter m⁻²) or 2003 (3029 ± 2081 and 2146 ± 898 g m⁻²), but annual average soil respiration (1229 ± 77 and 1428 ± 24 g C m⁻² yr⁻¹) was significantly higher in the restoration ($P < 0.0001$). However, the prairie remnant contained 37% greater soil C ($P < 0.0001$) in the top 25 cm. Soil respiration response to 10 cm soil temperature (Q_{10}) varied with respect to prairie and soil moisture conditions as annual Q_{10} values ranged from 2.5 to 3.6. We calculated a range of net ecosystem production (NEP) values using estimated heterotrophic respiration and three root turnover values. Average NEP varied from -1.4 to 1.9 and -2.3 to 1.3 Mg C ha⁻¹ yr⁻¹ for the remnant and planted prairies, respectively. While these two prairies share similar structural components and functional attributes, the large uncertainty in NEP casts doubt as to whether we can verify these prairies as C sources or sinks without direct measures of heterotrophic respiration and root turnover. We argue that quantitative studies of C exchange in prairies, which differ in restoration methodology, management intensity, and fire frequency, are needed to solidify the relationship between prairie structure and potentially desired functions such as C sequestration.

Keywords: carbon cycling, carbon sequestration, phenology, prairie restoration, soil respiration

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Introduction

The disappearance of the American prairie may be one of the largest ecological and biological disturbances of modern times. European immigrants changed the once-expansive tallgrass prairie and organic matter-rich soils of the US Great Plains via farming dating back to the 1830s. Plowed croplands, cattle pastures, and urban

areas replaced native grasses and forbs, bison, and fire, leading to a loss of plant and animal biodiversity and soil carbon (C) (Mann, 1986; Manies *et al.*, 2001), while potentially impacting regional climate (Chase *et al.*, 2000) and hydrology (Twine *et al.*, 2004), and intensifying nutrient export (Donner *et al.*, 2004). Current land conservation efforts have targeted vulnerable and degraded agricultural land for rehabilitation to help preserve ecosystem services such as water quality, food production, and climate regulation, all of which can be aided through C sequestration (Baer *et al.*, 2002).

Correspondence: Christopher J. Kucharik, tel. +1 608 263 1859, fax +1 608 265 4113, e-mail: kucharik@wisc.edu

Restoration initiatives across the US have targeted the rejuvenation of the tallgrass prairie, an effort that has intensified since 1985 in conjunction with the federal Conservation Reserve Program (CRP). Since 1986, 14 million hectares of agricultural land have been taken out of crop production and rehabilitated to native vegetation, specifically with perennial grasses and forbs (Metting *et al.*, 2001; Baer *et al.*, 2002; Kucharik *et al.*, 2003). Today, the functional benefits of this large-scale program are reduced soil erosion and runoff from farms, improved water quality, enhanced plant biodiversity, and C sequestration (Follett *et al.*, 2001; Baer *et al.*, 2002).

Given the large amount of economic resources devoted to prairie restoration and the important role that these ecosystems play in the global C and water cycles, there is interest in examining the progress of restoration initiatives and their effect on C and water cycling. Measurements of soil organic matter recovery have been widely used for assessing the likelihood that prairie restorations can function as longer-term net C sinks (Gebhart *et al.*, 1994; Reeder *et al.*, 1998; Potter *et al.*, 1999; Brye *et al.*, 2002a; Brye & Kucharik, 2003). Soil organic matter or C is widely used as an indicator of soil recovery, and paired sites (e.g. prairie and row crops) or chronosequences of planted prairies have been used to quantify C accumulation rates (Baer *et al.*, 2002; Brye *et al.*, 2002a; Brye & Kucharik, 2003; Kucharik *et al.*, 2003; Camill *et al.*, 2004). Others have used eddy covariance techniques to quantify seasonal and interannual variations of net ecosystem exchange (NEE) of grassland ecosystems to better understand their role in regional C budgets (Suyker *et al.*, 2003; Verburg *et al.*, 2004).

Unfortunately, there are few studies to date that have examined how efficient restoration efforts have been at returning desired prairie functions to the landscape (e.g. C sequestration) in relation to the aboveground vegetation composition, age, or management intensity (Baer *et al.*, 2002; Brye *et al.*, 2002b; Camill *et al.*, 2004). Often, species diversity and frequency in prairie remnants are used as a measuring stick to judge whether a 'complete' recovery has taken place in restoration efforts (Kindscher & Tieszen, 1998; Allison, 2002; Camill *et al.*, 2004). As Camill *et al.* (2004) discuss, the few reported studies of 'complete' restorations focus on diversity changes through time. These studies have generally failed to quantify how these prairie plant communities are affecting ecosystem processes such as C exchange, using native ecosystems as a comparative reference. Thus, 'structures' are more commonly compared than the resulting 'functions'.

In an effort to address this shortcoming, we studied the world's oldest (~65 years) prairie restoration

(Jordan *et al.*, 1987) and its adjacent remnant counterpart in southern Wisconsin over a 3-year period (2001–2004). Our primary goals were to (1) compare seasonal and inter-annual phenology in response to weather variability and prescribed prairie burns, (2) quantify and compare soil C and N stocks as a function of depth, (3) estimate ANPP and quantify peak root biomass, (4) measure soil surface CO₂ fluxes and generalize soil environmental controls on respiration using exponential (e.g. Q_{10}) functions, and (5) estimate annual net ecosystem production (NEP) and ecosystem carbon balance (ECB) and how they are influenced by weather and fire management.

For the purposes of predicting annual C exchange in ecosystems, soil respiration (R_s) is commonly modeled as a simple exponential function (e.g. Q_{10}) of soil temperature (Davidson *et al.*, 1998; Janssens & Pilegaard, 2003; Yuste *et al.*, 2004). There is growing concern that using a single Q_{10} value for multiple biomes in ecosystem models may no longer be adequate, considering the sensitivity of annual R_s to soil moisture conditions and other factors (Davidson *et al.*, 1998; Lavigne *et al.*, 2004). As a secondary focus, we further investigated whether seasonal and interannual variation in soil moisture conditions at our two prairie sites influenced the determination of Q_{10} values, and used these relationships to calculate annual R_s .

Methods

Site description and experimental design

This study was conducted from October 2001 through October 2004 within the Curtis Prairie at the University of Wisconsin (UW)-Madison Arboretum (43°2'N, 89°26'W). This site has the unique combination of 1.2 ha of previously undisturbed high quality, wet-mesic prairie (~3000 years of age) adjacent to a 28 ha expanse of land previously tilled for row crops from 1836 to 1920 and subsequently planted with native prairie species from 1934 to 1941 (Blewett & Cottam, 1984). This ecosystem rebirth qualifies Curtis Prairie as the world's oldest tallgrass prairie restoration site (Allison, 2002). There has been little published research on biogeochemical cycling at this unique pair of prairies (Nielsen & Hole, 1963). During this study, the remnant prairie was burned in the spring of 2002 and 2003, and the planted portion was burned in the spring of 2002 and 2004.

Each prairie is situated on gentle slopes (1–2%), and the parent material is glacial loess (Table 1). The depth from the soil surface to the underlying water table increases along a northeast to southwest transect from the remnant portion into the planted area. Standing

Table 1 Physiographic, climate and soil characteristics at the UW-Madison Arboretum

Characteristic	Remnant	Restoration
Physiography		
Elevation (m)	264.2	264.5
Slope (%)	1–2	1–2
Aspect	SE	S
Parent Material	Glacial loess	Glacial loess
Climate (1971–2000)*		
Annual mean maximum temperature (°C)		14.2
Annual mean minimum temperature (°C)		0.7
Annual precipitation (mm)		928.4
Soil classification		
Taxonomic description	Fine-silty, mixed, superactive mesic Typic Endoaquoll	
Soil series	Sable silty clay loam	
Soil physical properties		
Sand (%) [†]	34	33
Silt (%) [†]	49	58
Clay (%) [†]	14	9
Bulk density (g cm ⁻³) [‡]	0.87	1.18
Soil chemical properties		
Total soil C (Mg ha ⁻¹) [§]	357 (65.0)	185 (35.0)
Total soil N (Mg ha ⁻¹) [§]	23.8 (7.2)	15.8 (3.0)
C:N [§]	15	11.7
pH [†]	6.65	5.19

Values in parentheses are ± 1 SD ($n = 10$).

*Based on daily weather data collected on site.

[†]Average for 0–50 cm soil depth range.

[‡]0–20 cm average.

[§]Total to 1 m depth.

water is commonly found in springtime to early summer, and is a likely reason why the remnant portion was not used to grow row crops. Mean annual (based on 1971–2000; <http://www.ncdc.noaa.gov>) precipitation for the UW Arboretum is 928 mm, with a mean annual minimum temperature of 0.7 °C and mean annual maximum temperature of 14.2 °C (Table 1). Average annual growing degree days (GDD) accumulated (base 8 °C) are 1633 °C.

We delineated a representative 0.5 ha area in each prairie section (100 m apart) where measurements could be collected on the same soil series (sable silty clay loam; fine-silty, mixed, superactive, mesic Typic Endoaquoll, poorly drained). A centralized 15 m \times 15 m plot in the center of each 0.5 ha study area was used to continuously monitor soil environmental conditions and soil CO₂ respiration. Two 150 m transects were used within each 0.5 ha section to collect other data including leaf area index (LAI), aboveground and belowground biomass, and soil C and nitrogen (N). Because the experimental design was unable to be replicated, conclusions drawn from this research are limited to this particular site (Hurlbert, 1984).

Vegetation characteristics

Ten 1 m² quadrats in each prairie were sampled during summer 2002 to determine the presence-absence for all vascular flora (Snyder, 2004). A frequency of occurrence for each species was quantified as the number of quadrats with a particular species divided by the total number of quadrats. The small subset of data reported here from Snyder (2004) is for a total of 10 quadrats each in the planted and remnant portions of Curtis prairie in close proximity to the study areas, and should not be assumed applicable to the entire Curtis prairie. A two-sample *t*-test was used to test for significant differences of species diversity (per quadrat) between the two prairie sections.

Soil environmental conditions

Within each 15 m \times 15 m plot, data loggers (Campbell Scientific, Pullman, WA) were installed in October 2001 in conjunction with laboratory-calibrated copper-constantan thermocouples and Campbell Scientific CS615 water content reflectometers (Campbell Scientific). Four

replicates of thermocouples installed at 2, 10, 30, 70, and 120 cm soil depths were used in each plot. Two CS615 sensors in each plot measured volumetric soil moisture in the 0–15 and 15–30 cm soil layers. Instantaneous soil temperature and volumetric soil moisture readings were collected every 60 s to form hourly and daily plot averages. Daily rainfall measurements were made on-site by Arboretum staff.

Soil carbon stocks and other chemical properties

In October 2001, 10 replicates of three soil cores (2 cm diameter) spaced 10 m apart were taken in cross-transsects across each 0.5 ha study area. Soil cores were stratified into 0–10, 10–25, 25–50, and 50–100 cm depth increments. At each sampling location, the three cores were combined and well mixed to form a single composite sample for each depth interval. Total soil N and C, textural composition, and pH were determined on subsamples that were previously oven dried and hand ground by mortar and pestle to pass through a 100 mesh (0.15 mm) sieve. Total soil N and C were determined by high-temperature catalytic combustion using a Carlo-Erba Model NA 1500 C and N analyzer (CE Instruments, Milan, Italy). Soil textural analysis was performed on 50 g of soil using the hydrometer method (Ashworth *et al.*, 2001), and soil pH was determined using a 1:1 soil:deionized water mixture after equilibrating for 30 min. Five surface (0–20 cm) soil bulk density cores were collected randomly in each study area using a 184 cm³ cylinder (4.8 cm diameter) inserted within a gravity driven hammer attachment (Elliott *et al.*, 1999).

Soil surface CO₂ fluxes

Soil surface CO₂ efflux was measured approximately weekly between April and December of each year, and periodically during the remainder of each year, using a portable infrared CO₂ gas analyzer (Li-Cor, Inc., model 6400, Lincoln, NE, USA) equipped with a 1 L soil respiration chamber (Li-Cor LI-6009; Norman *et al.*, 1997). Ten circular polyvinyl chloride (PVC) collars (10 cm diameter, 5 cm height) were randomly distributed within each 15 m × 15 m plot and were repositioned every 4–6 weeks. The measurement protocol produced 30 daily R_s observations in each prairie between 08:00 and 16:00 hours local time on 77 days during the 3-year study. Instantaneous, 10 cm soil temperature measurements were obtained using a soil temperature probe inserted within 30 cm of each PVC collar. One to two measurements of surface (0–6 cm) volumetric soil water content (m³m⁻³) were collected concurrently with R_s

measurements using a Dynamax theta probe (Dynamax Inc., model TH20, Houston, TX, USA).

We calculated the relationship between soil temperature and R_s using a standard Q_{10} function (Yuste *et al.*, 2004):

$$R_s = R_{s,10} Q_{10}^{((T-10)/10)},$$

where $R_{s,10}$ is the soil respiration value at 10 °C, T is 10 cm soil temperature, and Q_{10} is a factor quantifying the increase in respiration for every 10 °C increase in temperature. This relationship was used to derive a daily R_s value in each prairie (using the continuous observations of soil environmental conditions) for each year so that annual R_s could be estimated.

Fine root biomass (FRB)

FRB was determined by collecting eight 6.67 cm diameter soil cores to a depth of 50 cm (partitioned into 10 cm increments) within each 0.5 ha study area on 26 June 2002 and 20 August 2003. Samples were not collected during the 2004 season. Samples were immediately frozen at –5 °C and later thawed at room temperature and sorted into live and dead components by a combination of hand-sorting and wet sieving. Live root fractions were used to estimate belowground NPP (BNPP). Roots were subsequently oven dried and then dry ashed for 24 h at 450 °C to correct for mineral contamination and weighed to quantify mass (Steele *et al.*, 1997).

LAI measurements

LAI (m² leaf area per m² ground area) was measured approximately every 10 to 14 days during the growing season each year (April through October) at 15 locations spaced 10 m apart along transects within each 0.5 ha study area using a Li-Cor (Li-Cor, Lincoln) LAI-2000 plant canopy analyzer (Welles & Norman, 1991). All measurements were collected either under overcast (uniform, diffusely-lit) sky conditions or at sunrise or sunset.

Aboveground vegetation biomass measurements

In 2002, aboveground vegetation and surface litter in each prairie was collected on 26 September. In 2003, aboveground vegetation was collected on 9 May, 18 June, 15 August, and 24 September from the prairie restoration study area, and on the latter three dates from the prairie remnant. In 2004, biomass was sampled at the end of the growing season (late September) in both prairies. Eight to ten random locations in each 0.5 ha study area had all vegetation removed inside of a

0.5 m × 0.5 m sampling frame, and vegetation was subsequently dried and weighed. During years in which a prairie section was not burned, biomass was sorted in the field into live, standing dead, and thatch fractions to facilitate aboveground NPP (ANPP) calculations. Vegetation C and N concentrations were determined on finely ground subsamples (~10 g) of dried plant material for the 2002 and 2003 field seasons using a Carlo Erba Model NA 1500 C and N analyzer (CE Instruments) and high-temperature catalytic combustion.

Calculation of aboveground NPP, belowground NPP, NEP, and ECB

Because each prairie section was burned in April 2002 before significant plant growth occurred, we used measurements of the total aboveground vegetation collected in September as an estimate of ANPP for 2002. The same methodology was applied to the remnant prairie in 2003 and the restoration in 2004 because both were burned in spring. Vegetation C content was used to convert dry matter m⁻² to g C m⁻² for 2002 and 2003, and the average of those years (~43%) was used to convert 2004 data. Due to the lack of burning and presence of dead biomass from the previous growing season, ANPP was calculated differently within the restored prairie for 2003 and prairie remnant in 2004. ANPP was estimated as the peak live biomass, plus statistically significant ($P < .05$) increases from the previous sample date in either dead or thatch pools while total biomass was increasing in 2003 for the restoration (Scurlock *et al.*, 2002). The peak live biomass value was used from the remnant prairie in 2004 to estimate ANPP (Scurlock *et al.*, 2002).

We calculated a range of annual BNPP values using belowground biomass (BGB) estimates and three root turnover constants (e.g. proportion of roots that are produced or die annually), which were taken to be a constant (0.65 yr⁻¹), a linear function of ANPP (0.0009 ANPP g m⁻² yr⁻¹ + 0.25 g m⁻² yr⁻¹), or an exponential function of mean annual temperature (MAT) (0.2884e^{0.046MAT}) (Gill *et al.*, 2002). The equation used to calculate BNPP was

$$\text{BNPP} = \text{LRF} \cdot \text{BGB} \cdot \tau \cdot C_{\text{frac}},$$

where LRF is live root fraction, BGB is belowground FRB (g dry matter m⁻²), τ is annual root turnover, and root carbon fraction (C_{frac}) is 0.40 (Brye *et al.*, 2002a). Because we were unable to sample root growth in 2004, the average BGB for 2002–2003 was used to estimate 2004 BNPP.

Subsequently, three estimates of NEP were calculated by summing ANPP and BNPP and subtracting annual heterotrophic soil respiration. We partitioned root and

microbial contributions to annual R_s using the approach of Bond-Lamberty *et al.* (2004), which quantified the root contribution (RC) to R_s in forest and grassland systems by

$$\text{RC} = -0.66 + 0.16 \ln(R_s),$$

where R_s is total annual soil respiration in g C m⁻² yr⁻¹. Estimates of total ECB were derived by considering the amount of C that was removed from each prairie ecosystem as a result of prescribed burning (Suyker & Verma, 2001; Brye *et al.*, 2002a). These values were based on pre-burn biomass sampling and fractional C content values.

Statistical analysis

All statistical analyses were conducted using the SAS-JMP statistical discovery software (SAS Institute Inc., 2002). One-way analysis of variance (ANOVA) was used to detect significant differences ($P < 0.05$) between prairies for ANPP, daily and annual soil R_s , FRB, LAI, soil C and N, bulk density, and soil environmental conditions. All calculations and statistical analyses assumed each prairie site was the experimental unit and the replicated measurements of each quantity were used to generate an average value. Nonlinear regression analysis was used to develop exponential models describing the effect of soil temperature on R_s . When average values for observations are reported, they are followed by ± 1 SD where applicable.

Results and discussion

Vegetation characteristics

The average number of species per quadrat (1 m²) was 15.8 ± 4.4 in the prairie remnant with 50 total species sampled, and 14.1 ± 2.1 in the restoration with 47 total species encountered (Table 2); these differences were not statistically significant. However, the actual species distribution was markedly different. The five most common species in the prairie restoration were big bluestem (*Andropogon gerardii*), Kentucky bluegrass (*Poa pratensis*), grass-leaved goldenrod (*Euthamia graminifolia*), gray dogwood (*Cornus racemosa*), and wild bergamot (*Monarda fistulosa*). In the prairie remnant, the five most frequent species encountered were woolly sedge (*Carex pellita*), big bluestem (*Andropogon gerardii*), Kentucky bluegrass (*Poa pratensis*), sawtooth sunflower (*Helianthus grosseserratus*), and common mountain mint (*Pycnanthemum virginianum*). Some species that existed in the prairie restoration area but were not found in the prairie remnant were grass-leaved goldenrod, redbud (*Agrostis gigantea*), and alsike clover (*Trifolium hybri-*

Table 2 Vegetation characteristics at the UW-Madison Arboretum

Characteristic	Remnant	Restoration
Average species diversity*	15.8 (4.4)	14.1 (2.1)
Total species sampled [†]	50	47
Legume species	3	2
Legume frequency (%)	10 (all three)	40, 50
Average frequency of sedges (%)	43	20
Non-native species	2	7
C3 grass species	3	4
Average C3 frequency (%)	43	43
C4 grass species	3	3
Average C4 frequency (%)	60	40
Most common species [‡]	Woolly sedge Big bluestem Kentucky bluegrass Saw-tooth sunflower Common mountain mint	Big bluestem Kentucky bluegrass Lance-leaved goldenrod Gray dogwood Bergamot
Years burned	2002, 2003	2002, 2004

Values in parentheses are ± 1 SD ($n = 10$).

*Species per 1 m² quadrat; based on data collected by Snyder (2004).

[†]Species sampled from 10 quadrats, 1 m²; from Snyder (2004).

[‡]Five most common species (presence/absence); from Snyder (2004).

dum). Species that were present in the prairie remnant but not in the restoration were flat-stemmed spike rush (*Eleocharis compressa*), leafy satin grass (*Muhlenbergia mexicana*), and culver's root (*Veronicastrum virginicum*).

Two species of nitrogen-fixing legumes (*Fabaceae*) were found in 40% and 50% of plots sampled within the planted prairie, while three species of legumes were each found in only 10% of remnant plots. Additionally, sedges (*Cyperaceae*) were found over twice as frequently in the remnant than in the planted prairie. Seven non-native species were found in the restoration, comprising 15% of the total species in the prairie, compared to only two (4% of the species) in the remnant prairie. The two prairies were similar in frequency and number of both C₃ and C₄ grass species. Kentucky bluegrass (C₃) and big bluestem (C₄) were each found in 90% of plots sampled in the remnant, and 100% of the restoration plots (Table 2).

Weather and soil environmental conditions

Growing season precipitation (Fig. 1a) and GDD (Fig. 1b) deviated significantly from 30-year averages during the 3-year study. The June through September period in 2002 and 2003 had positive GDD anomalies of 275 and 120 GDD, respectively. However, 2002 had warmer than average trend commencing in late April, while 2003 saw above average temperatures from late July through August (Fig. 1b). In 2002, a precipitation surplus in June became a 106 mm deficit (–19%) by July 21, and re-

mained 50–100 mm below average through the growing season (Fig. 1a). In 2003, precipitation was near normal through early July, but from July 15 through September 12, drought conditions led to a 163 mm (–82%) deficit (Fig. 1a). In 2004, a warmer than average spring (+100 GDD through June) was followed by cooler than average temperatures for the remainder of the growing season. The 2004 growing season also saw record May rainfall, which led to a precipitation surplus of 182 mm (56%) by the end of May and a 268 mm surplus (49%) by the end of July.

Figure 2a illustrates the soil temperature data collected in the remnant plot. Maximum 2 cm soil temperatures of 23 °C were typically observed in mid-July and 70 and 120 cm temperatures peaked around 17 °C in mid-August. Daily average soil temperatures at all sampled depths were significantly different ($P < 0.0001$) between the two prairies over the aggregated 3-year period; daily average temperatures in the remnant prairie were 0.20 °C, 0.17 °C, 0.26 °C, 0.39 °C, and 0.39 °C cooler than the restoration at 2, 10, 30, 70, and 120 cm, respectively. Daily average soil temperatures were 0.7 °C (at 2 cm) to 2.0 °C (at 70 cm) cooler in the remnant prairie during summer (Jun–Aug), but were 0.2 °C (at 10 cm) to 1.0 °C (at 70 cm) warmer during winter (Dec–Feb) ($P < 0.0001$) (Fig. 2b).

Over the entire study period, the 0–6, 0–15, and 15–30 cm daily average volumetric water contents (VWC; Fig. 3) were all significantly greater in the remnant prairie ($P < 0.0001$). This was attributed to a combination

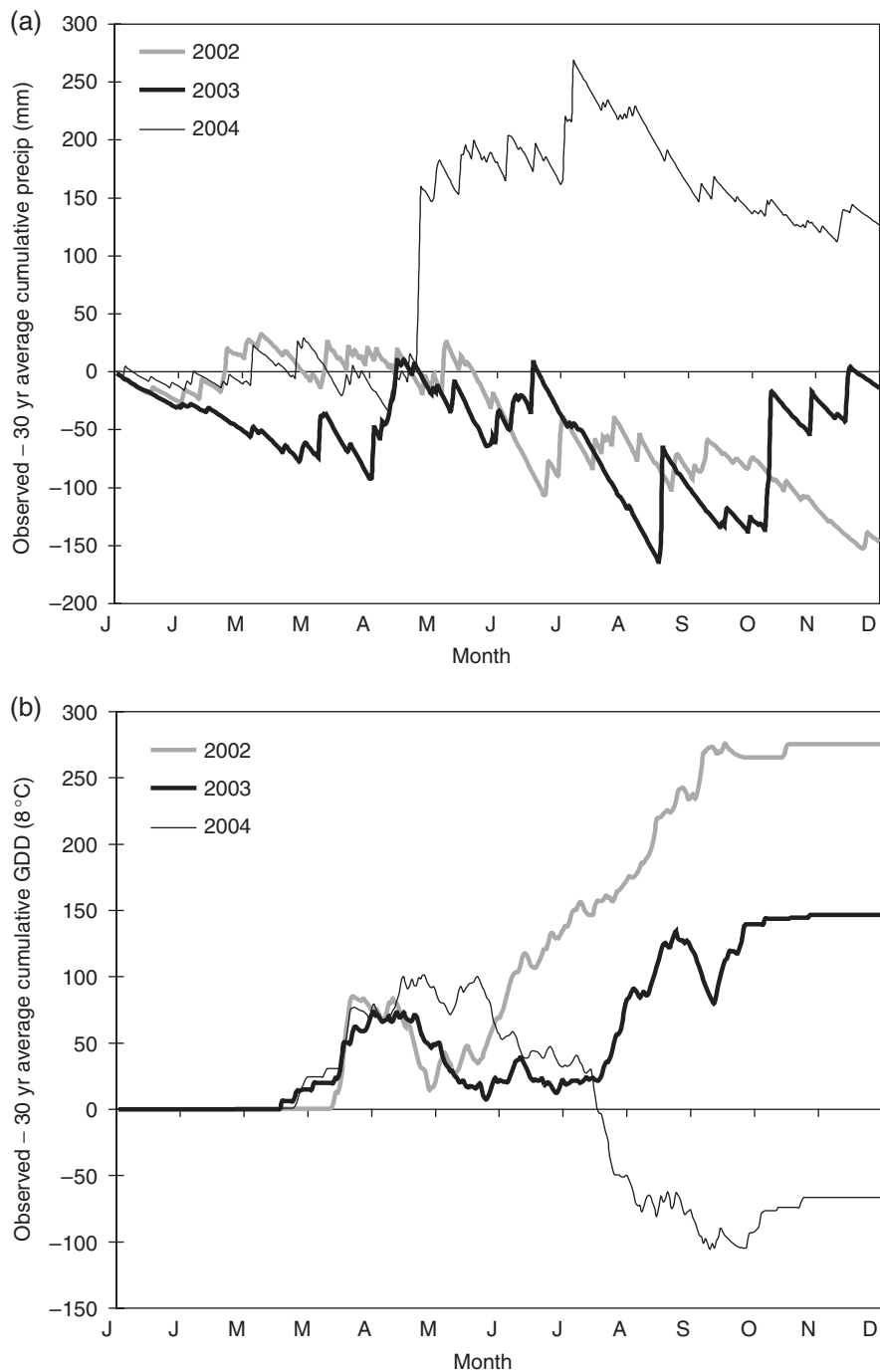


Fig. 1 Accumulated (from January 1) daily (a) precipitation (mm) and (b) growing degree day (GDD, base 8 °C) departures from the 30-year average (1971–2000) at the University of Wisconsin Arboretum.

of significantly lower soil bulk density (Table 3) and a higher water table level in the remnant prairie, the latter of which is due to increased runoff from hydrologic flow patterns. On a seasonal basis, the average 0–15 cm VWC ranged from $0.44 \text{ m}^3 \text{ m}^{-3}$ during fall to $0.52 \text{ m}^3 \text{ m}^{-3}$ in spring within the remnant prairie, and from $0.39 \text{ m}^3 \text{ m}^{-3}$ in winter to $0.47 \text{ m}^3 \text{ m}^{-3}$ in spring within the restora-

tion. Seasonally averaged 15–30 cm VWC ranged from $0.61 \text{ m}^3 \text{ m}^{-3}$ in fall to $0.71 \text{ m}^3 \text{ m}^{-3}$ in spring for the remnant prairie, and from $0.37 \text{ m}^3 \text{ m}^{-3}$ in fall to $0.47 \text{ m}^3 \text{ m}^{-3}$ in spring within the restoration (Fig. 3). Point measurements of surface (0–6 cm) VWC averaged 0.41 and $0.35 \text{ m}^3 \text{ m}^{-3}$ for the remnant prairie and restoration over the study period, respectively. Minimum 0–6 cm VWC

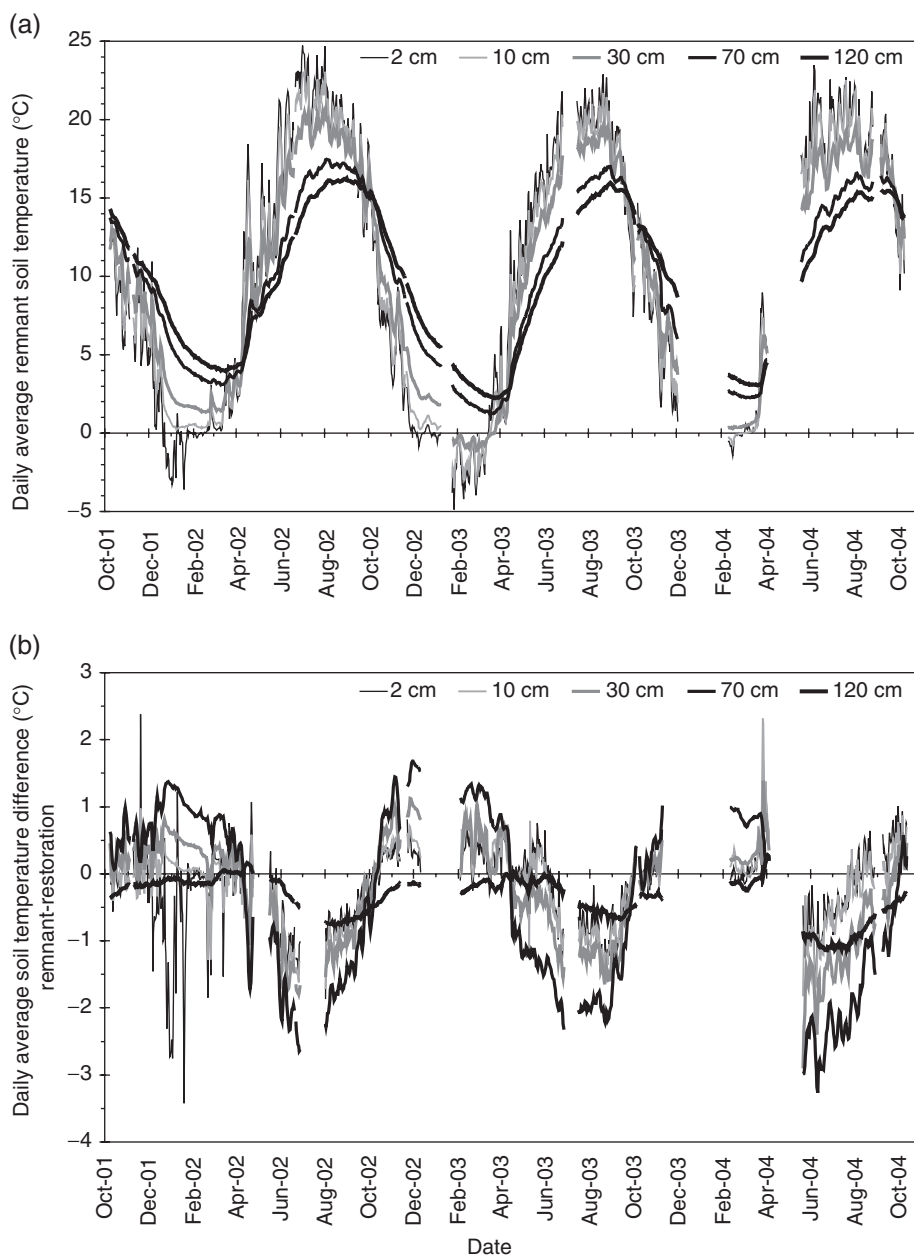


Fig. 2 (a) Daily average soil temperature at 2, 10, 30, 70, and 120 cm for the remnant prairie, (b) daily average temperature differences between the two studied prairies (remnant–restoration).

values of $0.15\text{--}0.20\text{ m}^3\text{ m}^{-3}$ were recorded during the late summer in both 2002 and 2003 (Fig. 3).

Soil physical and chemical properties

Soil bulk density (0–20 cm) was 36% lower ($P = 0.0002$) in the remnant prairie ($0.87 \pm 0.10\text{ g cm}^{-3}$) than the planted prairie ($1.18 \pm 0.06\text{ g cm}^{-3}$) (Table 3). The percent soil C was generally 50% higher in the remnant site, and was statistically significant at each depth

interval sampled (Table 3; $P < 0.00001$). The total organic soil C storage to 1 m depth was 357 Mg ha^{-1} in the remnant site, and 48% less in the prairie restoration (184 Mg ha^{-1}). Soil C storage differences between the two prairies were greatest below 25 cm (55%) and less (37%) in the 0–25 cm region. We hypothesize that previous agricultural land use has contributed to a loss of soil organic matter (Kucharik *et al.*, 2003), although the actual loss could have been greater because soil C accumulation in the planted prairie may have occurred

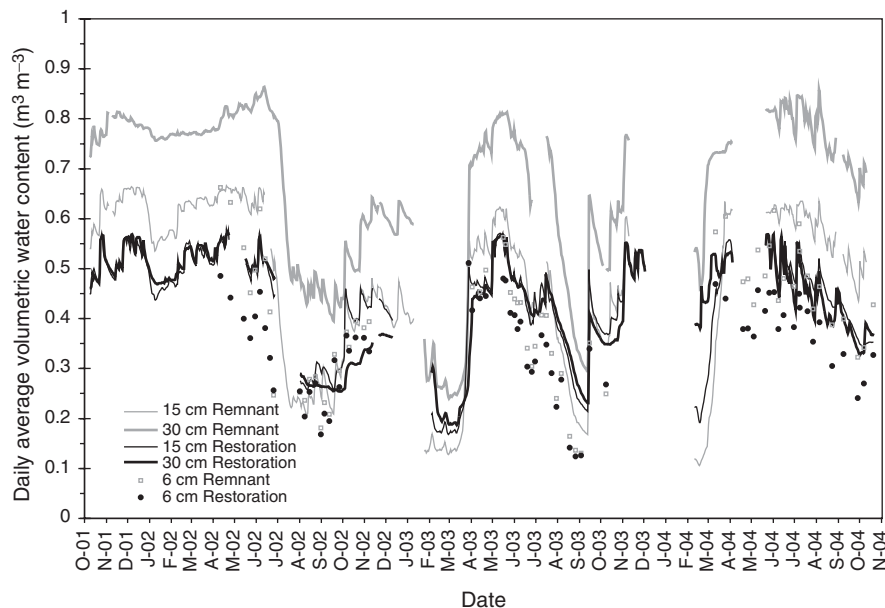


Fig. 3 Daily average volumetric water content for the two prairies in the 0–6, 0–15, and 15–30 cm soil depth layers.

during the past 65 years. However, given that average soil moisture is significantly higher in the remnant prairie, and average soil temperatures are also cooler there during the growing season, these factors have likely enhanced the ability of the prairie relic to store larger amounts of soil C compared to the prairie restoration region, which was previously used for agricultural production. The observed soil moisture conditions in the remnant prairie, if representative of historical conditions, likely deterred the previous landowners from planting row crops in the 1800s.

Soil N differences were also statistically significant at all depths, but the relative difference between prairies below 50 cm (25–41%) was less than differences in corresponding soil C stocks (Table 3). The overall C:N for the top 1 m of soil was 15.0 in the remnant site, and 11.7 in the restored prairie. Soil pH was significantly higher ($P < 0.00001$) in the remnant site at all soil depth intervals (Table 3). Values ranged from 6.4–7.1 in the remnant site, compared to 5.1–5.6 in the planted prairie.

We found that coefficients of variation (CV) for the majority of soil physical and chemical properties sampled were consistently higher in the remnant prairie (Table 3). Thus, evidence of agricultural disturbance (e.g. tillage, mixing of soil, and possible erosion) not only exists 65 years later in terms of decreased soil C amounts and a higher bulk density in the upper 25 cm of the soil profile, but is also supported by a higher level of within site homogeneity of observed soil properties, potentially due to previous mechanical mixing of the plow layer.

FRB

Total (live plus dead) FRB (0–50 cm) was 1736 ± 1062 and $1690 \pm 459 \text{ g m}^{-2}$ for remnant and planted prairies (Table 4), respectively, on 26 June 2002, but these differences were not statistically significant ($P = 0.92$). Soil cores obtained on 20 August 2003 yielded 3029 ± 2081 and $2146 \pm 898 \text{ g m}^{-2}$ in the remnant and planted prairies, respectively (Table 4), but the differences were again not statistically significant ($P = 0.29$). These root values are on the higher end of reported values for other grassland sites around the world (Rice *et al.*, 1998; Gill *et al.*, 2002).

The percentage of FRB as a function of depth was consistent for each prairie; 54–61% of the total FRB to 50 cm was contained in the 0–10 cm layer in each prairie, 77–83% in the top 20 cm, and 88–92% in the top 30 cm (Table 4). These averages closely approximate other reported values (Cahill *et al.*, submitted; Rice *et al.*, 1998). Only 8–12% of the FRB in the top 50 cm was found below 30 cm. The fraction of FRB that was living in 2002 was 0.60 ± 0.14 and 0.61 ± 0.15 for the planted and remnant prairies, respectively, and in 2003, these values were 0.59 ± 0.10 (planted) and 0.67 ± 0.12 (remnant). These live values are within the reported typical ranges for temperate grasslands (Jackson *et al.*, 1997; Gill *et al.*, 2002). The within-site variability among individual cores in the remnant prairie produced a CV (0–50 cm FRB) of 61% and 69% for 2002 and 2003, respectively. In contrast, the variation among core samples (0–50 cm FRB) in the planted prairie was 27% and 42% in 2002 and 2003, respectively.

Table 3 Summary of soil physical and chemical properties

Quantity	Remnant		Restoration		P
	Mean	CV	Mean	CV	
Bulk density (g cm ⁻³)* (n = 5)	0.87	11	1.18	5	0.0002
Percent soil C (n = 10)					
0–10 cm	5.4	24	2.7	13	< 0.00001
10–25 cm	4.2	27	1.8	15	< 0.00001
25–50 cm	3.4	23	1.7	26	< 0.00001
50–100 cm	1.9	48	0.9	34	< 0.00001
Soil C (Mg ha ⁻¹) [†]					
0–10 cm	46.7		31.5		
10–25 cm	54.6		32.5		
25–50 cm	111.6		55.4		
50–100 cm	144.3		65.4		
0–100 cm total	357.2		184.8		
Percent soil N (n = 10)					
0–10 cm	0.46	31	0.23	19	0.0001
10–25 cm	0.35	48	0.16	16	0.003
25–50 cm	0.25	45	0.15	27	0.014
50–100 cm	0.1	22	0.07	37	0.039
Soil N (Mg ha ⁻¹) [†]					
0–10 cm	4.0		2.7		
10–25 cm	4.5		2.9		
25–50 cm	8.0		4.7		
50–100 cm	7.3		5.5		
0–100 cm total	23.8		15.8		
0–100 cm C:N	15.0		11.7		
Soil pH (n = 10)					
0–10 cm	6.4	7	5.2	3	< 0.00001
10–25 cm	6.5	10	5.1	5	< 0.00001
25–50 cm	6.8	8	5.2	4	< 0.00001
50–100 cm	7.1	6	5.6	8	< 0.00001

CV is the coefficient of variation, expressed as percent. The *P*-value denotes the significance level of differences (*t*-test) between the remnant prairie and restoration.

Each quantity is based on 10 plot replicates, with the exception of bulk density in which data are based on 5 subplots in each prairie.

*0–20 cm average.

[†]Used measured bulk density for 0–25 cm, and 1.3 for 25–50, and 1.5 for 50–100 cm based on data from Hole (1976).

Soil CO₂ respiration

Figure 4a shows periodic soil surface CO₂ efflux measurements between April 12 2002 and October 20 2004. These values represent the average quantity for the 10 PVC soil collars measured in each prairie plot. The general response of *R_s* follows seasonal soil temperature changes, with summer soil drying imparting a secondary control in 2002 and 2003. Soil respiration was

greater (*P* < 0.0001) in the planted prairie over the 77 measurement days, with the most significant daily differences occurring in early spring. During late spring through summer, the differences were generally less between prairies with the exception of 2004, which had adequate soil moisture during the entire the growing season (Fig. 4a). The maximum soil respiration rates in 2002 and 2003 occurred in early to mid-summer before drought conditions persisted. The peak flux rates for 2002 (July 1) were $10.5 \pm 1.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the remnant prairie, and $12.9 \pm 3.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ in the restored prairie. In 2003, the peak flux rate in the restored prairie (June 25) was $12.1 \pm 3.5 \mu\text{mol m}^{-2} \text{s}^{-1}$, while in the remnant prairie the peak flux rate was $11.3 \pm 2.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ (August 6). In 2004, the higher soil moisture conditions caused *R_s* to be lower in the remnant prairie compared to the previous 2 years, while the restoration saw similar to slightly higher peak rates ($\sim 15 \mu\text{mol m}^{-2} \text{s}^{-1}$). Wintertime *R_s* was approximately $0.10 \mu\text{mol m}^{-2} \text{s}^{-1}$ in each prairie from late January through early March. Our maximum respiration rates are slightly higher than those reported by Brye *et al.* (2002a, b) for a 24-year-old restored prairie 30 km to the north of our site ($7.9\text{--}8.5 \mu\text{mol m}^{-2} \text{s}^{-1}$), and by Cahill *et al.* (submitted) for a 16-year-old restored prairie 50 km west of our site ($7.6 \mu\text{mol m}^{-2} \text{s}^{-1}$).

Figure 4b illustrates all *R_s* data plotted against 10 cm soil temperature for all years. The exponential fit to the planted prairie soil respiration data yielded a *Q*₁₀ of 2.62, and captured 61% of the observed respiration variation with temperature (Table 5; *P* < 0.0001). The planted prairie *R_s* at 10 °C was $2.97 \mu\text{mol m}^{-2} \text{s}^{-1}$. The exponential fit to the remnant prairie *R_s* data yielded a *Q*₁₀ of 2.9 and explained 66% of the observed respiration variation with temperature (Table 5; *P* < 0.0001). The mean *R_s* at 10 °C was $2.55 \mu\text{mol m}^{-2} \text{s}^{-1}$, which is 14% lower than in the planted prairie because of the typically higher soil moisture content during springtime when 10 cm soil temperature is near 10 °C. The exponential model fit to the data had a consistent bias of being higher than *R_s* rates when soil temperature was below 5 °C (Fig. 4b).

We compared the results of the aforementioned exponential models developed with respiration data aggregated for all 3 years with models for each year (and prairie), individually. Lavigne *et al.* (2004) suggested that interannual variability in soil respiration would lead to erroneous *Q*₁₀ values based on aggregated multiyear data. The *Q*₁₀ values for each year ranged from 2.49 (2002) to 3.46 (2004) in the planted prairie, and 2.64 (2003) to 3.27 (2004) in the remnant prairie (Table 5). The calculated *Q*₁₀ values were dependent on the variability of soil moisture conditions from early spring to late summer. During 2002 and 2003, when adequate

Table 4 Fine root biomass (g m^{-2}) and percentage of the total to a depth of 50 cm

Soil depth (cm)	Remnant				Restoration			
	2002		2003		2002		2003	
	FRB	% of total	FRB	% of total	FRB	% of total	FRB	% of total
0–10	929 (834)	53.5 (19.9)	1743 (1251)	57.5 (4.8)	1031 (610)	61.0 (22.1)	1227 (519)	57.2 (5.4)
10–20	497 (556)	28.6 (18.7)	768 (666)	25.3 (4.9)	312 (164)	18.4 (11.8)	404 (230)	18.8 (3.6)
20–30	149 (95)	8.6 (6.9)	265 (133)	8.7 (3.6)	209 (152)	12.4 (9.0)	239 (112)	11.2 (3.1)
30–40	114 (83)	6.6 (5.7)	154 (65)	5.1 (2.0)	80 (56)	4.7 (3.9)	160 (67)	7.4 (1.8)
40–50	47 (43)	2.3 (6.4)	100 (37)	3.3 (2.2)	58 (42)	3.4 (2.4)	116 (58)	5.4 (4.9)
Total	1736 (1062)		3029 (2081)		1690 (459)		2146 (898)	

Values in parentheses are ± 1 SD ($n = 8$).

FRB, fine root biomass.

but not saturated spring soil moisture was followed by extended drought periods in June through August, the Q_{10} values were lowest and the soil respiration value at 10°C was highest. Conversely, in 2004 when record rainfall in May was followed by adequate to optimal soil moisture for the entire growing season, the Q_{10} values for each prairie were the highest, and the R_s value at 10°C was the lowest (Table 5).

Therefore, in 2002 and 2003 when soil VWC was as low as 0.13 to $0.17 \text{ m}^3 \text{ m}^{-3}$ during summer and 10 cm soil temperature was at a maximum, the response of R_s to temperature appeared to be decreased, but the underlying reason was extremely low soil moisture. In 2004, the very wet April through May yielded a decreased soil respiration value at 10°C compared to the previous 2 years, and the lack of a mid to late summer dry period kept VWC above $0.30 \text{ m}^3 \text{ m}^{-3}$ all season (Fig. 3). This allowed R_s to have an apparently larger response across a similar temperature range compared to the previous 2 years. Davidson *et al.* (1998) suggested that wet sites that dry out sufficiently could have elevated soil respiration at intermediate soil water content. In 2002 and 2003 it appeared that soil moisture decreased to a point that impeded higher respiration when soil temperatures were at a maximum for the season. However, when we investigated the relationship between soil moisture and R_s over each season, they were inversely ($r^2 = -0.05$ to -0.10), but not significantly ($P > 0.6$) correlated in either prairie. Future work will continue to investigate how these temperature-respiration models can be improved by incorporating soil moisture conditions that likely reduce microbial respiration during very wet or dry conditions and impede root respiration during drought periods (Davidson *et al.*, 1998). The interannual variability in growing season precipitation made it difficult to isolate what effect, if any, prescribed prairie burns had on R_s .

Using the exponential models of daily R_s based on 10 cm soil temperature, the annual average R_s was 14% lower in the cooler and wetter remnant prairie, averaging $1229 \pm 77 \text{ g C m}^{-2} \text{ yr}^{-1}$ compared to $1428 \pm 24 \text{ g C m}^{-2} \text{ yr}^{-1}$ for the planted prairie (Table 6). During the prolonged summer drought of 2003, annual R_s in the prairie remnant was only 4% lower (-54 g C m^{-2}) than the planted prairie, suggesting that low soil moisture conditions were limiting root and microbial respiration similarly in each prairie. Conversely, in 2004, when excessive spring and early summer rainfall occurred (Fig. 1a), predicted annual R_s was 22% lower (-337 g C m^{-2}) in the remnant prairie (Table 6). This could be attributed to saturated soil moisture conditions that contributed to a less than optimal (e.g. anaerobic) environment for microbial decomposition of organic matter in spring and early summer.

Plant phenology and LAI

Rapid green-up of the prairies took place after May 24 in 2002, after May 19 in 2003, and after May 15 in 2004 (Fig. 5). In 2002, the LAI was not significantly different between prairies ($P = 0.42$), both of which were burned earlier in the spring. The prairies reached a maximum LAI of $4.4 \pm 0.28 \text{ m}^2 \text{ m}^{-2}$ (remnant) and $4.5 \pm 0.38 \text{ m}^2 \text{ m}^{-2}$ (planted) during the first week of August in 2002. In 2003, the remnant prairie was burned in spring, and reached a maximum LAI of $4.9 \pm 0.88 \text{ m}^2 \text{ m}^{-2}$ on August 6, compared to a maximum of $2.9 \pm 0.29 \text{ m}^2 \text{ m}^{-2}$ for the unburned prairie restoration on August 6 (Fig. 5). The difference in LAI in 2003 between prairies was statistically significant after July 1 ($P = 0.006$). Dead vegetation leftover from the previous growing season (2002) was equal to an LAI of $0.9 \pm 0.07 \text{ m}^2 \text{ m}^{-2}$ in the planted prairie. In early spring of 2004, dead vegetative cover was equal to an LAI of

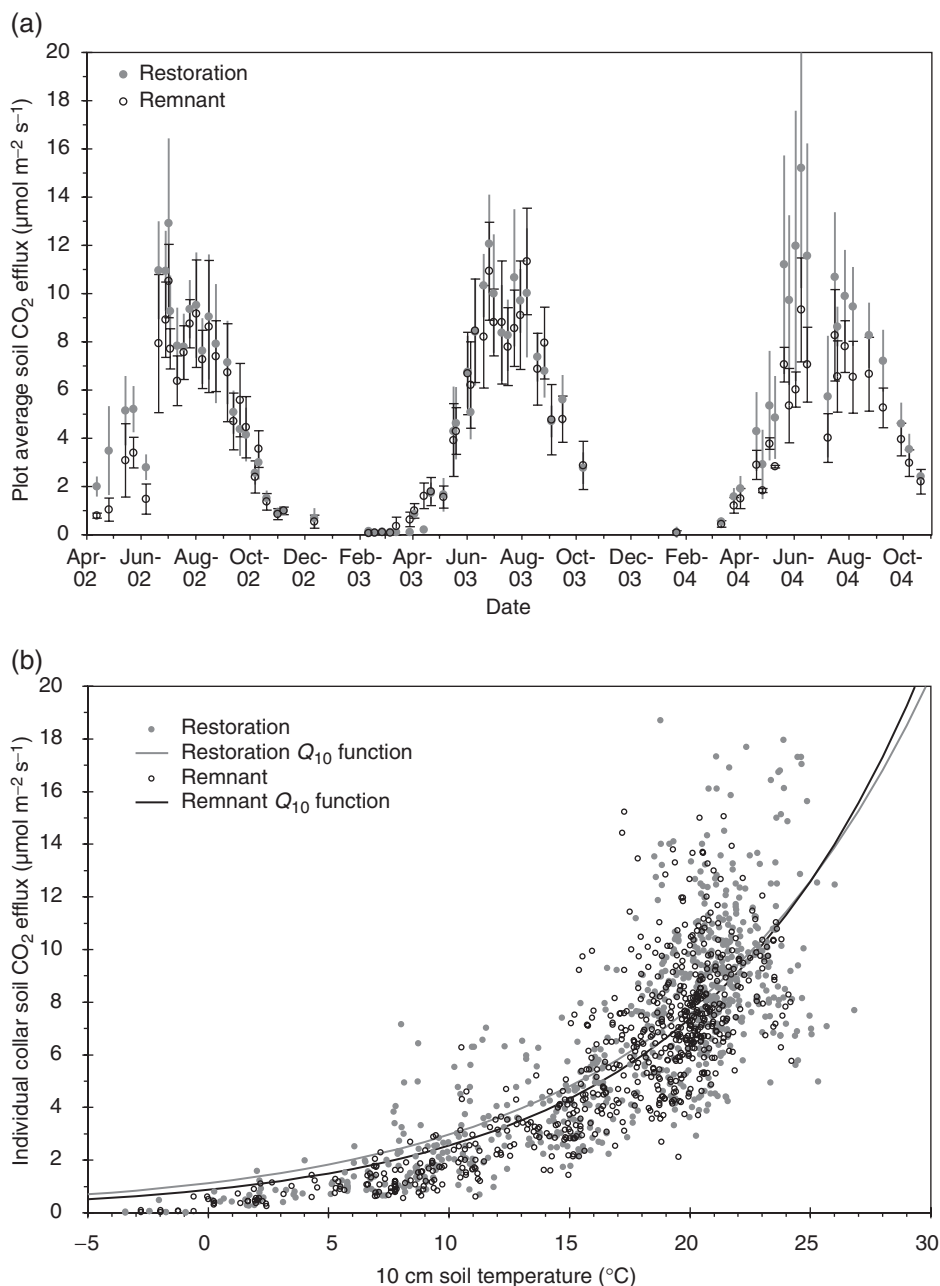


Fig. 4 (a) Daily average soil CO₂ efflux for the two prairies, based on the average of 10 replicate measurement collars in each study area. Error bars denote ± 1 SD; (b) individual collar measurements of soil CO₂ efflux in each prairie on 77 measurement days from 2001–2004 and fitted exponential models.

$0.6 \pm 0.26 \text{ m}^2 \text{ m}^{-2}$ in each prairie, and the planted prairie was burned in May. The peak LAI for the burned (spring 2004) planted prairie of $4.6 \pm 0.59 \text{ m}^2 \text{ m}^{-2}$ occurred on August 24, whereas the unburned remnant reached a maximum of $3.9 \pm 0.74 \text{ m}^2 \text{ m}^{-2}$ near July 20 (Fig. 5). The planted prairie LAI was significantly higher ($P < 0.001$) than the remnant prairie for the measurement period after the burn to the end of the growing season. These data suggest the significant differences

that occurred in 2003 and 2004 were largely driven by burn management differences.

Aboveground biomass and NPP

Aboveground NPP for 2002 and 2003 was not significantly different between prairies ($P = 0.81$ and 0.88 , respectively), but differences were significant in 2004 ($P < 0.01$). In 2002, when both prairies were burned in

Table 5 Fitted exponential relationships between 10 cm soil temperature and soil surface CO₂ flux denoted by the equation $\text{Flux} = R_{\text{soil}} Q_{10}^{[(T-10)/10]}$ where the quantity R_{soil} is the surface CO₂ flux ($\mu\text{mol m}^{-2} \text{s}^{-1}$) at 10 °C, and T is the 10 cm daily average soil temperature

Plot	Year	R_{soil}	Q_{10}	r^2	P	Obs	RMSE
Restoration	2002	3.02	2.49	0.66	<0.0001	301	2.14
Remnant	2002	2.49	2.96	0.70	<0.0001	264	1.79
Restoration	2003	2.81	2.58	0.63	<0.0001	226	2.33
Remnant	2003	2.90	2.64	0.61	<0.0001	223	2.26
Restoration	2004	2.62	3.46	0.74	<0.0001	192	2.77
Remnant	2004	2.17	3.27	0.69	<0.0001	168	1.50
Restoration	All years*	2.97	2.62	0.61	<0.0001	719	2.50
Remnant	All years*	2.55	2.90	0.66	<0.0001	655	1.91

*The values in these rows are not a bulk mean of the results of the other years, but are derived from aggregating all observations together (for each prairie, respectively) and fitting a single exponential function. RMSE, root mean square error.

the spring and growing season precipitation deficits existed for a 4-week period in early summer, the total aboveground production was $839 \pm 164 \text{ g dry matter m}^{-2}$ in the planted prairie and $809 \pm 317 \text{ g dry matter m}^{-2}$ in the prairie remnant (Fig. 6). In 2003, aboveground production appeared to be significantly limited by soil moisture stress to the extent that the spring burning of the remnant prairie did not lead to higher production compared to the unburned restoration; ANPP was $590 \pm 110 \text{ g m}^{-2}$ in the restoration and $580 \pm 144 \text{ g m}^{-2}$ in the remnant prairie. In 2004, when the restoration was burned in spring and a precipitation surplus of greater than 150 mm was maintained for the entire growing season (Fig. 1a), the ANPP was $901 \pm 63 \text{ g m}^{-2}$, compared to only $508 \pm 32 \text{ g m}^{-2}$ for the unburned remnant (Fig. 6). The within-site variability (CV) for total dry matter sampled at the end of the growing season over the 3 years was 7–21% in the planted portion of Curtis prairie, and 28–40% in the remnant portion.

The end of the growing season plant tissue C content was similar between the prairies in both years (Fig. 7a). In 2002, the remnant prairie vegetation averaged 42.3% C compared to 42.4% C in the restoration ($P = 0.96$). Similarly, in 2003 the remnant had 43.3% C, while the restored prairie had 42.6% C ($P = 0.28$). The plant tissue N content was higher in the remnant prairie in 2002 ($P < 0.1$) and 2003 ($P = 0.30$), with average values of 0.79% and 1.10%, respectively, compared to 0.59% and 0.98% (Fig. 7b). Plant tissue carbon to nitrogen ratio (C:N) was significantly higher ($P < 0.05$) in 2002 in the restored prairie (75.6) compared to the remnant (54.3). Differences were not significant ($P = 0.34$) in 2003, presumably because of the effects of comparable soil moisture stress on vegetative growth, with a C:N of 46.0 in the planted prairie and 41.2 in the remnant (Fig. 7c).

Estimated NEP and ECB

Following the approach developed in Cahill *et al.* (submitted), we used direct observations of ANPP, live fine root biomass, total soil respiration, and C loss from prescribed burns in conjunction with an estimated heterotrophic soil respiration fraction (Bond-Lamberty *et al.*, 2004) and root turnover values for grasslands (Gill *et al.*, 2002) to estimate a range of NEP and ECB values. Ecosystem C balance was equal to NEP minus estimated C combustion loss due to prescribed burns; this C release to the atmosphere was based on pre-burn biomass sampling and conclusions from previous studies (Brye *et al.*, 2002a; Suyker *et al.*, 2003). We assumed that leached C loss through the soil profile was negligible. Roots were assumed to have a constant C fraction of 0.4 (Brye *et al.*, 2002a).

Table 6 reports all components for each prairie's annual C budget, with the three estimates of BNPP, total NPP (TNPP), NEP, ECB, and BNPP:TNPP based on the three methods of estimating root turnover values. Annual average root turnover based on MAT was 0.43 yr^{-1} for each prairie, and using the relationship to ANPP yielded 0.95 yr^{-1} for the planted prairie and 0.82 yr^{-1} for the remnant prairie. These three approaches yielded an annual average range in BNPP from 196 to 429 g C m^{-2} for the planted prairie and 263– 488 g C m^{-2} for the remnant. Annual average TNPP was comparable between prairies, ranging from approximately 530 g C m^{-2} using the exponential relationship for root turnover to 759 g C m^{-2} for the direct function calculations. The annual average ratio of BNPP to TNPP was between 0.37 and 0.57 for the planted prairie, and 0.49–0.64 for the remnant prairie. These values are comparable to data presented by Gower *et al.* (1999), which suggested a typical range of 0.35–0.75 and average of 0.58 for grasslands. Root to shoot ratios were

Table 6 Estimated annual carbon budgets for prairie ecosystems

Year	ANPP (g C m ⁻²)	BCB _{50cm} (g C m ⁻²)	R : S*	LRF	R _s (g C m ⁻²)	R _H [†] (g C m ⁻²)	C loss [‡] (g C m ⁻²)	RT method	RT _{Cons} (yr ⁻¹)	BNPP (g C m ⁻²)	TNPP (g C m ⁻²)	NEP (g C m ⁻²)	ECB (g C m ⁻²)	BNPP : TNPP
Restoration														
2002	356 ± 65	676 ± 184	2.01	0.60 ± 0.14	1387	697	329.8	Direct	1.005	408	764	67.1	-262.7	0.53
	-	-	-	-	-	-	-	Constant	0.65	264	620	-76.9	-406.7	0.43
	-	-	-	-	-	-	-	Exponential	0.43	174	531	-166.1	-495.9	0.33
2003	251 [§]	858 ± 359	2.64	0.59 ± 0.10	1386	696	0.00	Direct	0.781	396	646	-50.2	-50.2	0.61
	-	-	-	-	-	-	-	Constant	0.65	329	580	-116.5	-116.5	0.57
	-	-	-	-	-	-	-	Exponential	0.43	218	468	-227.9	-227.9	0.46
2004	383 ± 63	767 [¶]	-	-	1510	738	253.7	Direct	1.061	484	867	128.7	-125.0	0.56
	-	-	-	-	-	-	-	Constant	0.65	297	679	-58.9	-312.6	0.44
	-	-	-	-	-	-	-	Exponential	0.43	196	579	-159.4	-413.1	0.34
Average	330 ± 55	767 ± 322	2.33 ± 0.45	0.595 ± 0.01	1428 ± 24	711 ± 8	195 ± 166	Direct	0.95 ± 0.12	429 ± 17	759 ± 67	49 ± 63	-146 ± 106	0.57 ± 0.04
	-	-	-	-	-	-	-	Constant	0.65 ± 0.00	297 ± 33	627 ± 25	-84 ± 21	-279 ± 145	0.47 ± 0.07
	-	-	-	-	-	-	-	Exponential	0.43 ± 0.00	196 ± 22	526 ± 35	-184 ± 32	-379 ± 134	0.37 ± 0.07
Remnant														
2002	346 ± 136	694 ± 424	2.14	0.61 ± 0.15	1181	624	348	Direct	0.979	415	761	137.3	-210.7	0.54
	-	-	-	-	-	-	-	Constant	0.65	275	622	-2.0	-350.1	0.44
	-	-	-	-	-	-	-	Exponential	0.43	182	529	-95.2	-443.3	0.34
2003	248 ± 17	1211 ± 832	5.22	0.67 ± 0.12	1331	678	348	Direct	0.772	624	872	194.3	-153.7	0.72
	-	-	-	-	-	-	-	Constant	0.65	525	773	95.8	-252.2	0.68
	-	-	-	-	-	-	-	Exponential	0.43	347	596	-81.9	-429.9	0.58
2004	217 ± 13	952 [¶]	-	-	1174	621	0	Direct	0.707	426	644	22.8	22.8	0.66
	-	-	-	-	-	-	-	Constant	0.65	392	609	-11.5	-11.5	0.64
	-	-	-	-	-	-	-	Exponential	0.43	259	477	-144.3	-144.3	0.54
Average	271 ± 51	952 ± 366	3.68 ± 2.18	0.64 ± 0.04	1229 ± 77	641 ± 27	232 ± 67	Direct	0.819 ± 0.11	488 ± 106	759 ± 65	118 ± 40	-114 ± 49	0.64 ± 0.09
	-	-	-	-	-	-	-	Constant	0.65 ± 0.00	397 ± 125	668 ± 78	27 ± 50	-205 ± 74	0.60 ± 0.12
	-	-	-	-	-	-	-	Exponential	0.43 ± 0.00	263 ± 83	534 ± 37	-107 ± 13	-339 ± 57	0.49 ± 0.12

Values following ± denote 1 SD.

*R : S is root to shoot ratio based on peak aboveground and belowground measurements.

†Heterotrophic soil respiration fraction estimated by equation 1.0 - [-0.66 + 0.16 ln(R_s)] from Bond-Lamberty *et al.* (2004).

‡Ecosystem C loss is estimated from aboveground biomass removed due to prescribed burns.

§SD not available from statistically significant positive increments in biomass.

¶Value is average of previous 2 years data.

ANPP, aboveground annual net primary production; BCB_{50cm}, peak belowground fine root biomass to 50 cm depth; R : S, root : shoot ratio; LRF, live root fraction; R_s, total soil respiration; R_H, heterotrophic soil respiration; C loss, ecosystem C loss due to prescribed burning; RT, root turnover estimate based on Gill *et al.* (2002); RT_{cons_{yr}}, annual root turnover constant; BNPP, total belowground NPP; TNPP, total NPP (ANPP + BNPP); NEP, net ecosystem production; ECB, ecosystem carbon balance (NEP - C loss).

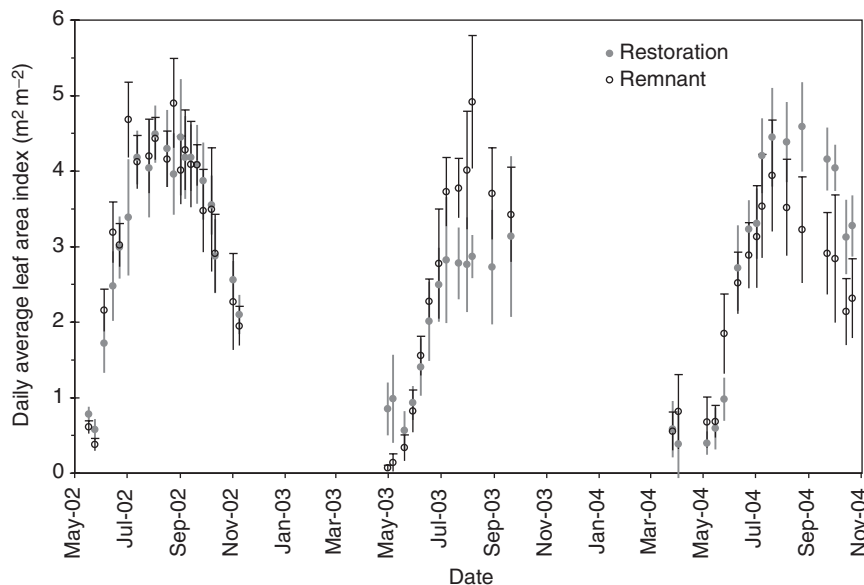


Fig. 5 Daily average leaf area index for the two prairies based on the average of 10–15 replicate measurement points in each study area. Error bars denote ± 1 SD.

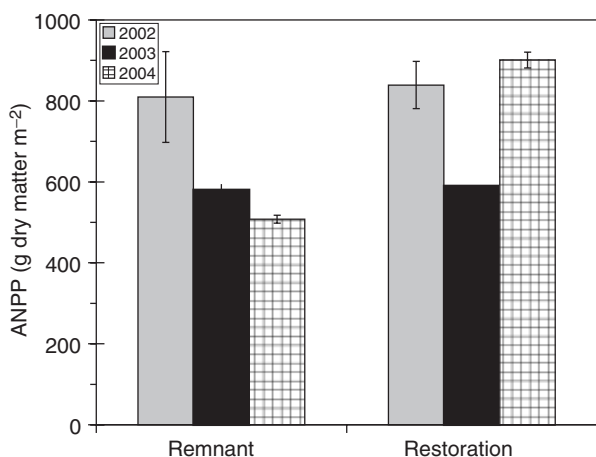


Fig. 6 Annual average aboveground net primary production (in units of $\text{g dry matter m}^{-2}$). Error bars denote ± 1 SD. Both sites were burned in early spring 2002, while the remnant was burned again in spring 2003, and the restoration in spring 2004.

2.01 and 2.64 in 2002 and 2003 for the planted prairie, respectively, and 2.14 and 5.22 in the remnant prairie for 2002 and 2003, respectively (Table 6).

Accounting for C losses from the ecosystems attributed to heterotrophic respiration produced annual average NEP values in the remnant prairie from -107 g C m^{-2} (source) assuming the exponential model of root turnover, to 118 g C m^{-2} (sink) using the direct function (Table 6). The planted prairie annual average NEP calculations had a range of -184 g C m^{-2} (expo-

ponential model) to 49 g C m^{-2} (direct function). In 2004, when the planted prairie was burned in spring and adequate soil moisture existed for the entire growing season, NEP was the highest (129 g C m^{-2} , direct function) and was lowest in 2003 (50 g C m^{-2} , direct function) when it was not burned and severe moisture stress persisted during the mid to late growing season. The NEP calculations for the remnant prairie indicated that 2003 was the most likely year of the three studied to have been a sink of C (194 g C^{-2} , direct function). When C combustion losses from spring burns were accounted for, the annual average ECB for the two prairies had a potential range from -110 to -380 g C m^{-2} , dependent on which root turnover constant was used.

Conclusions

Several quantitative observations in this paired ecosystem study suggested that varied aboveground structures, found in a 65-year-old prairie restoration and an adjacent remnant, are functioning similarly. However, because the experiment was not able to be replicated, conclusions drawn here should not be applied to other paired remnant-planted prairie sites with high confidence. The planted and remnant prairies responded similarly to weather variability, particularly mid to late summer soil moisture stress and fire management. In 2003, soil moisture stress appeared to be the most limiting factor to growth and R_s in both prairies even though burning management differed. We observed that ANPP ($\sim 508\text{--}901 \text{ g biomass m}^{-2} \text{ yr}^{-1}$), the aver-

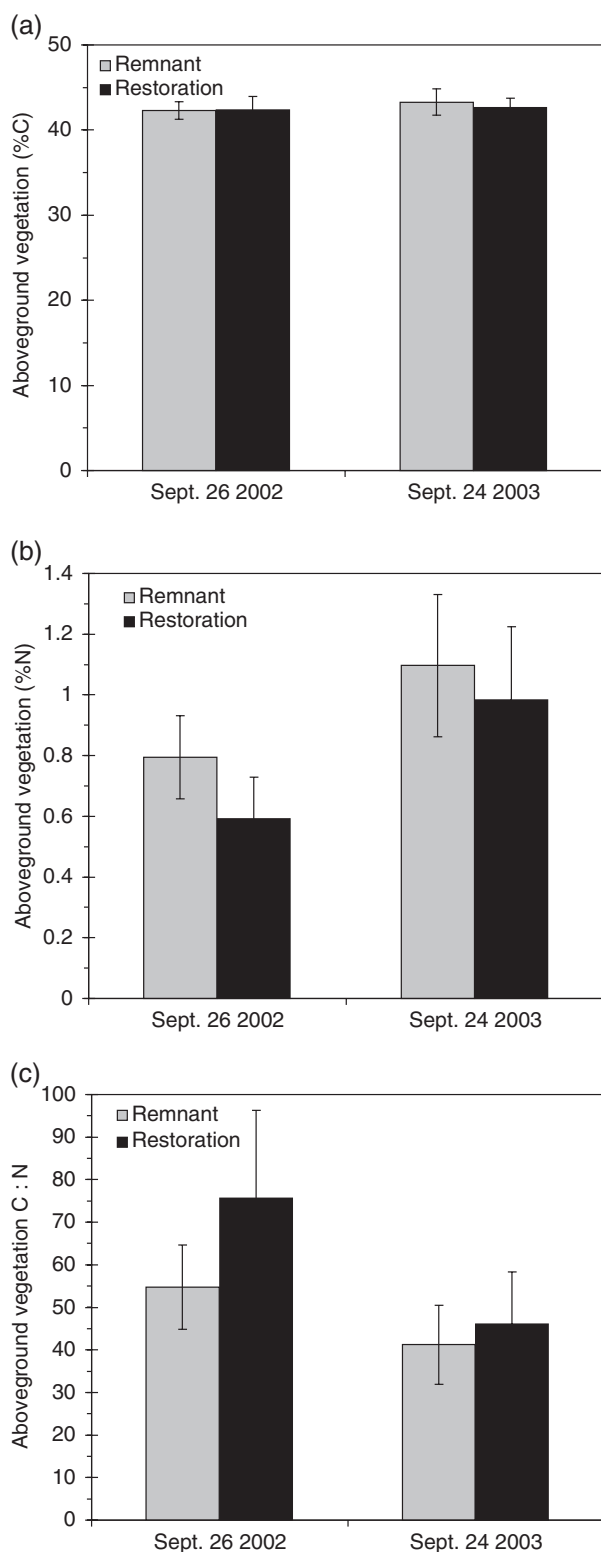


Fig. 7 End of growing season aboveground plant tissue (a) %C, (b) %N, and (c) C:N. Error bars denote ± 1 SD.

age date of spring green-up (\sim May 19), and peak LAI ($\sim 2.9\text{--}4.9\text{ m}^2\text{ m}^{-2}$) were similar even though (1) the species compositions were dissimilar (although the total biodiversity was similar), and (2) the remnant prairie was cooler and wetter during the growing season. Statistically significant differences in ANPP and peak LAI only occurred when burning management differed between prairies. The ANPP values were also similar to productivity data reported for 1959–1961; Nielsen & Hole (1963) reported that annual aboveground vegetation growth was $640\text{--}810\text{ g biomass m}^{-2}$.

Despite the similarity in aboveground productivity and phenology and their response to changing environmental conditions, there still appear to be subtle differences in belowground C stocks and annual R_s . We cannot determine with high confidence whether the belowground differences are attributable to varied land-use history, microbial populations, or long-term differences in mean soil moisture and temperature. The remnant prairie currently stores 37% more soil C in the top 25 cm, has a significantly lower bulk density, and a significantly lower annual average R_s . The spatial variability of sampled variables both above- and below-ground was consistently twice as high in the remnant prairie, suggesting the effects of tillage in the planted prairie in mixing the surface soils and decreasing spatial heterogeneity are still detectable after nearly 70 years.

We observed that R_s response to soil temperature was dependent on seasonal changes in soil moisture. The Q_{10} values varied with respect to prairie and year and the exponential model used to relate R_s and temperature had difficulty in capturing wintertime R_s ($0.1\ \mu\text{mol m}^{-2}\text{ s}^{-1}$) when 10 cm soil temperature was less than 5°C . These findings support the conclusion that ecosystem models that rely on a single Q_{10} relationship to parameterize ecosystem respiration response to temperature are likely to be erroneous, particularly when used to simulate C exchange in ecosystems that have large seasonal variations of soil temperature and moisture.

The results of NEP and ECB were inconclusive as to whether the prairies are functioning as a net source or sink of C to the atmosphere. An exploration of methodological uncertainties suggests the largest uncertainty in NEP calculations were (1) the changing (seasonal) proportion of soil respiration attributed to roots vs. microbial activity, and (2) the annual root turnover constant. These two quantities may not be easily generalized to prairie ecosystems using previously published quantities from other locations. For example, the study of Brye *et al.* (2002a) suggested using a $R_H:R_s$ of 0.25 and an observed root turnover constant of 2.5 yr^{-1} (using minirhizotrons). Conversely, Herman (1977)

estimated that a $R_H:R_s$ of 0.70 was adequate for a tallgrass prairie with 1500 g m^{-2} of belowground biomass. These are in stark contrast to the study of Bond-Lamberty *et al.* (2004) for partitioning of R_s , and Gill *et al.* (2002) for root turnover constant determination, which produced values between 0.43 and $\sim 1.0 \text{ yr}^{-1}$ in this study. While it may be argued that eddy covariance systems could help reduce the uncertainty in net C exchange, the small size (footprint) of many prairie restorations rules out using such an approach.

The Curtis prairie restoration may represent the high-end end of the spectrum in terms of total resources and effort devoted to rehabilitate a prairie ecosystem. While it may be expected that 65 years would be a sufficient length of time to allow for a good representation of native prairie structure to establish, until recently, the means of expressing the *success* of the Curtis Prairie restoration has been through repeated diversity sampling (Snyder, 2004). Clearly, this determination – in a qualitative sense – has been extremely valuable to the science of restoration ecology and habitat restoration, as well as detecting changing species distribution through time. However, in response to the desire to re-establish specific ecosystem functions such as C sequestration to agricultural landscapes, it is necessary to include more quantitative measures of restoration effects, which can be used to assess the effectiveness with which we are creating the desired functions. While it is conceivable that desired ecosystem functioning can be attained with varied structure or biodiversity, as demonstrated in this study, there are likely thresholds in management intensity and species diversity that need to be met (Piper & Pimm, 2002). Likewise, recreating native species diversity may not necessarily lead to the development of some desired functions if the belowground structure and processes do not recover in unison.

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