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Impacts of C_4 grass introductions on soil carbon and nitrogen cycling in C_3-dominated successional systems

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Abstract While recent research has focused on the effects of exotic plant species on ecosystem properties, less is known about how restoring individual native plant species, differing in biomass and tissue chemistry, may impact ecosystems. We examined how three native C_4 prairie grasses affected soil C and N cycling 11 years after reintroduction into successional old-field communities dominated by non-native C_3 grasses. The species examined in this study differ in traits that are expected to influence soil C and N cycling (biomass and tissue chemistry). Thus, we hypothesized that cycling rates would decrease, thereby increasing pool sizes in soils under C_4 species compared under C_3 species. As predicted, the C_4 species had greater biomass and more recalcitrant tissue [higher C:N, acid detergent fiber (ADF):N] compared to the dominant C_3 species. The three C_4 species did not differ in tissue C:N, ADF:N, or root biomass, but *Andropogon* had more than twice the shoot biomass of *Schizachyrium* and *Sorghastrum*. Soils under the C_4 species did not differ in inorganic N levels, but levels were lower than in soils under the C_3 species, and soils under *Andropogon* had slightly lower in situ net N mineralization rates compared to those under C_3 species. We found little evidence of larger surface soil C pools under C_4 species versus C_3 species after 11 years and no differences in subsurface soil C or N among species. The C_4 species contributed a significant amount of C to both soil depths after 11 years. Our results demonstrate that C_4 species reintroduction into old-fields can alter C and N cycling on relatively short timescales, and that individual C_4 species differ in the magnitude of these effects. Improving our understanding of how species influence ecosystem properties is essential to predicting the ecosystem-level consequences of plant community alterations due to land use changes, global change, and species introductions.

Keywords Stable carbon isotope ratio · *Andropogon gerardii* · *Bromus inermis* · *Elymus repens* · Old-field

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Introduction

Human activities, such as land use change and the introduction of exotic species, are altering biodiversity on a global scale (Lawton and May 1995; Pimm et al. 1995; Chapin et al. 2000; Hooper et al. 2005). However, the ecological implications of such shifts in plant species distributions and abundances are poorly understood. A number of studies have shown that the introduction of an exotic species can dramatically and rapidly alter ecosystem properties (Vitousek and Walker 1989; Evans et al. 2001; Mack and D'Antonio 2003), but few studies have focused on the reverse: how the reintroduction of native species affects ecosystem properties (sensu Hooper et al. 2005) and whether individual native species differ in their impact on these properties. This study examined how the

reintroduction of individual native prairie grass species into abandoned agricultural fields altered aspects of soil C and N cycling relative to C_3 grasses over the course of 11 years.

Agriculture has substantially reduced and fragmented prairie systems throughout the United States (Mlot 1990; Samson and Knopf 1994), altering plant communities and ecosystem properties (Camill et al. 2004; DeGryze et al. 2004). In southwestern Michigan, agricultural development has restricted once-common, native C_4 grasses (Gotshall 1972) to prairie remnants, and these species are now rarely found in abandoned agricultural fields (old-fields). Old-fields throughout the Midwest are typically colonized by a successional trajectory of C_3 species, many of which are non-native (Inouye and Tilman 1988, 1995; Foster and Gross 1997; Averett et al. 2004; Gross and Emery 2007). While the C_3 and C_4 species examined in this study typically differ in many traits that are expected to influence ecosystem properties such as C and N cycling (e.g., tissue chemistry and biomass production; Craine et al. 2002a, b; Tjoelker et al. 2005), little is known about the ecosystem-level impacts of species composition shifts between C_4- and C_3-dominated communities. Currently, large tracts of former agricultural land are being reverted to C_4-dominated communities (e.g., prairie restorations and the USDA Conservation Reserve Program) and many climate change models predict shifts in C_4 species distribution (Epstein et al. 1997; Collatz et al. 1998; Epstein et al. 2002; Winslow et al. 2003). In addition, the growing interest in biofuels as an alternative energy source is likely to increase the land area planted to native C_4 grass monocultures such as *Panicum virgatum* (Samson et al. 2005; Sanderson et al. 2006; Tilman et al. 2006). Thus, it is important to understand how the re-establishment, or introduction, of species with particular traits likely will influence ecosystem properties compared to species that typically colonize these communities.

There is considerable evidence that species' functional characteristics drive important ecosystem properties (Hooper and Vitousek 1998; Reich et al. 2004; Wardle et al. 2004; Hooper et al. 2005). Two common ways in which plant species influence soil processes is through the quality and quantity of litter inputs (Hobbie 1992; Wardle et al. 1998; Dijkstra et al. 2006). Changes in litter quantity and quality can directly and indirectly influence microbial community activity, abundance, and composition (Zak et al. 2003; Carney and Matson 2005; Hooper et al. 2005; Zavaleta and Hulvey 2007), thereby altering nutrient cycling rates, and potentially feeding back to alter the plant community.

The particular grasses examined in this study provide an opportunity to examine how plant traits are linked to soil properties because they have similar growth forms yet differ in a number of functionally important traits. These three C_4 prairie grasses typically produce more biomass (above- and belowground) and have more recalcitrant tissue (i.e., C:N, lignin:N) than their C_3 grass counterparts (Wedin and Tilman 1990; Baer et al. 2002; Craine et al. 2002b; Camill et al. 2004; Tjoelker et al. 2005), and the magnitude of these trait differences also vary among the individual C_4 species. These traits can directly influence soil processes via changes in the amount and form of substrates available for microbial utilization (Zak et al. 2003; Carney and Matson 2005; Hooper et al. 2005; Zavaleta and Hulvey 2007). Indeed, several grassland studies have found lower net N mineralization and higher C mineralization rates soon after C_4 species become dominant (Baer et al. 2002; Camill et al. 2004). However, these study sites were not dominated by a single C_4 species, and so comparisons of how dominance by an individual species impacts soil properties could not be made.

Here, we examined the decadal-scale effects of the reintroduction of three C_4 grasses on aspects of soil C and N cycling in two old-fields. Both fields were abandoned from agriculture over 35 years ago and monoculture plots of the three native C_4 grass species were established in 1995 in each field (Foster 1999). Those C_4-dominated plots were still intact in 2006, allowing us to compare plant traits, soil properties, and soil processes across the three C_4 and C_3 grass-dominated communities after 11 years. We predicted that: (1) the individual C_4 species would differ in certain traits and therefore vary in the magnitude of their effect on soil properties; however, we also predicted that all three C_4 species would (2) produce greater biomass (root and shoot), which would cause an increase in surface litter and total soil C pools compared to the C_3-dominated communities; (3) have more recalcitrant tissue, which would result in greater accumulation of total soil C and N pools; and (4) have more recalcitrant tissue, resulting in net immobilization of N and therefore smaller pools of inorganic N.

Materials and methods

Study sites

We compared experimental plots dominated by each of three C_4 species [*Andropogon gerardii* (Vitman) or big bluestem; *Sorghastrum nutans* (L.) or Indian grass; and *Schizachyrium scoparium* (Michx) or little bluestem] to the surrounding C_3-dominated old-field communities at Michigan State University's W.K. Kellogg Biological Station in southwestern Michigan, USA (Kalamzoo County; 42°24′N, 85°24′W, elevation ~280 m). Non-native C_3 grasses dominated both old-fields, though the

dominant species in each field differed. *Bromus inermis* (Leyss; smooth brome) dominated Turkey Meadow while *Elymus repens* (L; quackgrass) dominated McKay Field (Table 1). Nomenclature for all species follows the USDA Plants Database (http://plants.usda.gov). Both fields have sandy loam soils (Foster and Gross 1997) in the Kalamazoo Series; McKay Field has a higher sand fraction and appears more drought-prone than Turkey Meadow. Mean annual precipitation is 890 mm and the mean annual temperature is 9.7°C. Both old-fields were abandoned over 35 years ago following decades of row crop agriculture (Burbank et al. 1992; Foster and Gross 1997). This area of Michigan had extensive prairies and savannas prior to agricultural development, and the C_4 species examined in this experiment were common components of those grasslands (Gotshall 1972; Burbank et al. 1992).

The experimental monocultures were established in 1995 for competition experiments described in Foster (1999). Species were transplanted into clipped plots with minimal soil disturbance, weeded for 1 year, and then abandoned in 1996. After 11 years, the experimental plots in both fields were still dominated by the C_4 species, and the surrounding matrix remained dominated by C_3 grass species (Table 1). By using two overall similar sites with different dominant C_3 species, we hope to increase our ability to generalize about the results.

Field sampling

In 2006, we randomly placed nine plots (0.5 m × 0.5 m) in each area dominated by the C_4 species, *A. gerardii* (*Andropogon* plots), *S. nutans* (*Sorghastrum* plots) and *S. scoparium* (*Schizachyrium* plots) in each old-field. Nine additional plots (0.5 m × 0.5 m) were established in the surrounding C_3 matrix community (C_3 plots), within 10–12 m of the C_4 plots. We determined aboveground net primary production in August 2006 by clipping all vegetation at ground level (0.5 m × 0.5 m plots) and separating individual species. We then collected surface litter from the plots. Two soil cores (0–20 cm deep, 3.8 cm diameter) were collected from each plot for C, N, and isotopic analyses. Both cores were split into two depths (0–10, 10–20 cm), and the soil from each depth within each plot was combined and refrigerated at 4°C until processed in the lab. We determined root biomass by taking a single core (6.35 cm diameter) from a subset of plots ($n = 6$ per species), split into two depths (0–10 and 10–20 cm), and refrigerated at 4°C until roots could be separated from the

Table 1 Plant community characteristics of the plots at harvest in both old-fields, 11 years after the C_4 species were established

Site	Plot	Shoot biomass[a] (g m^{-2})	Dominant species	% Shoot biomass[a]	Species richness[b] (mean, Σ)
McKay	Ag	1,637 ± 162	*Andropogon gerardii* (Vitman) C_4 M	97.5	2, 4
			Elymus repens (L.) C_3 M	1.6	
	Ss	577 ± 68	*Schizachyrium scoparium* (Michx) C_4 M	85.5	3, 9
			Elymus repens C_3 M	9.8	
	Sn	442 ± 49	*Sorghastrum nutans* (L.) C_4 M	76.7	4, 10
			Elymus repens C_3 M	16.3	
	Er	307 ± 18	*Elymus repens* C_3 M	98.7	2, 5
			Achillea millefolium (L.) C_3 F	1.0	
Turkey	Ag	1,570 ± 129	*Andropogon gerardii* C_4 M	95.8	3, 8
			Bromus inermis (Leyss) C_3 M	2.8	
	Ss	577 ± 56	*Schizachyrium scoparium* C_4 M	68.9	8, 22
			Bromus inermis C_3 M	8.7	
			Solidago canadensis (L.) C_3 F	5.0	
	Sn	959 ± 108	*Sorghastrum nutans* C_4 M	84.4	7, 13
			Poa pratensis (L.) C_3 M	5.0	
			Bromus inermis C_3 M	4.7	
	Bi	282 ± 27	*Bromus inermis* C_3 M	74.4	4, 13
			Poa pratensis C_3 M	21.3	

Ag Andropogon, *Ss Schizachyrium*, *Sn Sorghastrum*, *Er Elymus*, *Bi Bromus*, *M* monocot, *F* forb

[a] Shoot biomass (mean ± SE; $n = 9$) and species percentages of the total biomass are based on the average of nine samples for each dominant vegetation plot

[b] Species richness is given as the mean of the plots ($n = 9$; 0.5 m × 0.5 m) and as the total across plots (mean, Σ)

soil. All soil cores were taken immediately after sampling the litter.

Seasonal patterns of N availability in the *Andropogon* and C_3 plots were determined using repeated 28-day in situ net N mineralization incubations from June to November 2006. In situ incubations were done in *Andropogon* and C_3 plots (0–10 cm depth, $n = 5$ each) at both sites. At the onset of each incubation period, two PVC pipes (3.8 cm diameter, sharpened on one end) were pounded into the ground to 10-cm depth. Upon installing PVC cores, one core (t_0) was removed and taken to the lab for soil inorganic N analyses. The second core (t_{final}) was removed, capped on the top and bottom, and placed back into its original hole (modified from Robertson et al. 1999). After 28 days, the t_{final} core was removed from the ground, sealed in a plastic bag, and refrigerated at 4°C until processed in the lab. On this same day, a new set of t_0 and t_{final} cores were collected and installed, respectively. This process was repeated every 28 days from June to November 2006.

Laboratory analyses

Aboveground biomass (separated by species) and surface litter were dried for at least 72 h at 65°C and weighed (±0.01 g). Tissue samples were taken from a subset of the harvested biomass ($n = 5$ per species) for each dominant species—*Andropogon*, *Schizachyrium*, *Sorghastrum*, *Bromus* (in Turkey Meadow), *Elymus* (in McKay Field)—to determine nutrient concentrations. The dried tissue was coarse ground in a Wiley Mill, then ground to <1.0 mm on a Tecator Cyclotech sample mill (Foss North America, Eden Prairie, Minn.), and re-dried for 48 h at 65°C. Oven-dried tissue (2–3 mg) was then packed in tin capsules for C, N and isotope analyses (analyzed at the UC Davis Stable Isotope Facility). Acid detergent fiber (ADF; recalcitrant compounds, primarily lignin and hemicellulose) analyses of ground tissue (~0.5 g) were performed on an Ankom 2000 fiber analyzer (Macedon, N.Y.) at Michigan State University.

Root cores were washed in tap water and roots were floated in a pan, removed with tweezers, and rewashed to remove any remaining soil. Root material was then dried for 48 h at 65°C, and weighed (±0.0001 g). Root tissue for each depth interval was finely ground using a Precellys 24 homogenizer (Bertin Technologies, France), dried for 48 h at 65°C, and analyzed for C and N (5–10 mg samples) on an elemental analyzer (Costech Analytical, Ventura, Calif.). Total plant N was estimated as biomass multiplied by the average N content of the dominant species for each of the following components: shoots, surface (0–10 cm) roots, and subsurface (10–20 cm) roots.

Soil cores collected for chemical analyses were sieved through a 2-mm soil sieve to homogenize and remove large debris. Inorganic N was extracted from a 20-g sub-sample of soil using 50 ml of 1 M KCl, within 24 h of sample collection. Extracts were placed in the freezer until analysis on an O.I. Analytical Flow Solution IV analyzer (O.I. Analytical, College Station, Tex.). Gravimetric soil moisture was determined on another sub-sample of soil (~25 g fresh weight) by drying soils at 105°C for 48 h. The remaining soil was air-dried and stored in the laboratory. For C, N and isotope analyses, ~50 g air-dried soil was ground to a flour-like texture using a roller mill and dried at 65°C for 48 h. C and N was determined on 10–20 mg subsamples using an elemental analyzer (Costech Analytical). Subsamples (20–50 mg) were then packed into tin capsules and sent to the UC Davis Stable Isotope Facility for determinations of stable C isotope ratio ($\delta^{13}C$) (relative to PeeDee Belemnite) and $\delta^{15}N$ (relative to air). Because C_3 and C_4 species differ markedly in $\delta^{13}C$, the percentage of soil C contributed by C_4 species could be calculated for each plot using a simple end-member mixing model (using the $\delta^{13}C$ of the dominant C_4 species in each plot):

$$\%C_4 \text{ carbon} = (C_4 \text{ soil } \delta^{13}C - C_3 \text{ soil } \delta^{13}C)/(C_4 \text{ plant } \delta^{13}C - C_3 \text{ soil } \delta^{13}C) \times 100.$$

The use of C_3 soil $\delta^{13}C$ in this model eliminated any historical C_4 $\delta^{13}C$ signal from our calculation as well as any bias with soil depth. Soil bulk density was determined at each site using an Eijkelkamp root corer (8 cm diameter × 10 cm deep). Bulk density was calculated as oven-dried mass/volume (g cm^{-3}). Bulk density was used to convert surface soil C and N to a mass basis. We calculated C accumulation rate (g C m^{-2} $year^{-1}$) in the C_4-dominated plots as soil C (g m^{-2}) × $\%C_4$ − C over a period of 11 years.

For each in situ net N mineralization incubation, t_0 and t_{final} samples were taken back to the lab and processed according to the inorganic N extraction procedure described above. Net N-mineralization and nitrification rates were calculated as the change in total inorganic N (NH_4–N and NO_3–N) and NO_3–N (in μg N g^{-1} dry soil), respectively, over the incubation period. Bulk density was used to convert values from micrograms N per gram of dry soil to area-based (in g N m^{-2} day^{-1}) values for the depth interval.

Statistical analyses

All data were checked for normality and equal variance, and appropriate transformations were performed prior to analysis. Plant and soil variables were compared among plots (C_3, *Andropogon*, *Schizachyrium*, and *Sorghastrum*) using PROC Mixed in SAS (Statistical Analysis Systems, Cary, N.C.), with site as a random effect and species as a

fixed effect. Tukey–Kramer contrasts were performed when a significant species effect was found. Pearson correlations were performed to determine whether plant traits were correlated with soil variables. In addition, in situ N mineralization and nitrification rates were compared between *Andropogon* and C_3 plots using PROC Mixed with repeated measures in SAS, with site as a random effect and species as a fixed effect.

Results

Species traits: biomass and tissue characteristics

Differences among the dominant species in shoot biomass and surface litter were evident, with both typically greater in plots dominated by a C_4 prairie species than by a non-native C_3 species (Table 2, Fig. 1). Surface root biomass (0–10 cm) was higher for *Andropogon* versus C_3 species, and subsurface root biomass (10–20 cm) was higher for all three C_4 species plots compared to the C_3 plots (Table 2, Fig. 1). Analyses of tissue chemistry for the dominant species separated C_3 from C_4 species. Shoot and surface root N content and C:N did not differ among the three C_4 species, but C:N was higher than for the C_3 species and N was lower for the C_4 species than the C_3 species (Table 3; root data not shown). Isotope analyses demonstrated that all three C_4 species had a higher shoot $\delta^{13}C$ compared to the C_3 species, indicating a greater discrimination by C_3 species against ^{13}C, and *Andropogon*'s $\delta^{13}C$ was also higher than *Schizachyrium*'s (Table 3). All C_4 species had higher shoot ADF content and almost double the ADF:N than the C_3 species, and *Schizachyrium* had a higher ADF content than both *Andropogon* and *Sorghastrum* (Table 3). Estimates of total plant N stocks were greater for *Andropogon* compared to all other species (Fig. 2).

Soil properties

Surface (0–10 cm) soil C was greater in soils under *Andropogon* than in soils under *Sorghastrum* and *Schizachyrium* (Table 4). Subsurface (10–20 cm) soils sampled from under the different species did not differ in total soil C content (Table 5). However, both surface and subsurface soil $\delta^{13}C$ values were enriched under C_4 compared to C_3 species, indicating that the C_4 species have contributed significant amounts of soil C after 11 years (Tables 4, 5). However, there were also differences in soil $\delta^{13}C$ values among the C_4 species (Tables 4, 5). C_4 species contributed 9–26% of the soil C in the surface and 6–16% in the subsurface pools (Fig. 3), and this contribution was correlated with total biomass of the C_4 species (surface soil, $n = 25$, $P = 0.031$, $r = 0.43$; subsurface soil, $n = 21$, $P = 0.046$, $r = 0.44$). C accumulation rates in surface soils (0–10 cm) of C_4-dominated plots averaged 13.4–49.2 g C m^{-2} $year^{-1}$ in McKay Field and 28.3–63.9 g C m^{-2} $year^{-1}$ in Turkey Meadow, and again corresponded to total plant biomass differences (highest accumulation in *Andropogon* plots and lowest in *Schizachyrium* plots).

Soil inorganic N was lower in both surface and subsurface soils under C_4 species than under C_3 species (Tables 4, 5).

Table 2 Model results for various measures of plant production, using site as a random effect and dominant species (plot) as a fixed effect

Variable	*F*	*df*	*P*-value
Shoot biomass	81.63	3, 67	<0.001
Surface litter	35.17	3, 67	<0.001
Root biomass (0–10 cm)	3.10	3, 43	0.037
Root biomass (10–20 cm)	10.45	3, 43	<0.001

Natural log transformations were used to normalize the data for all variables except surface biomass, which was $1/x$ transformed

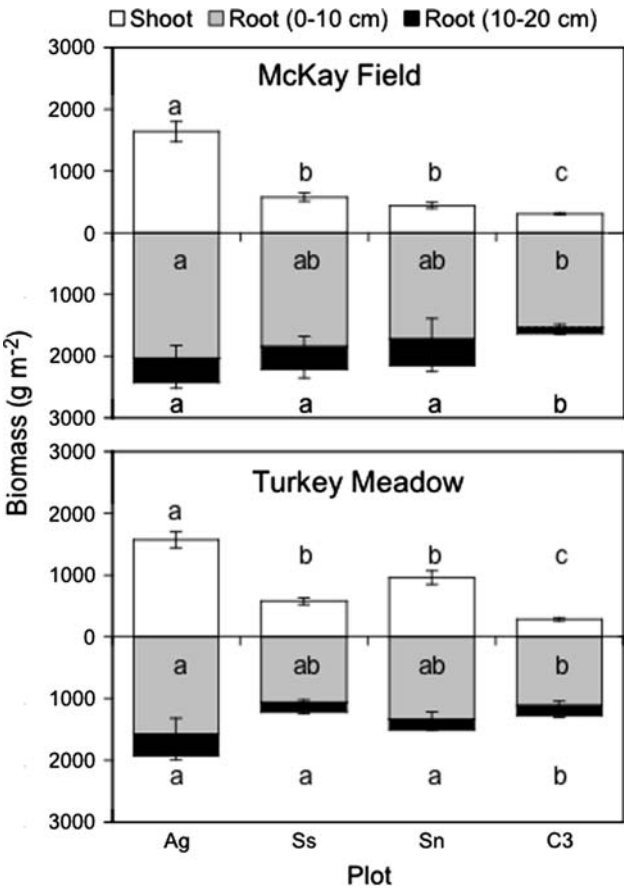

Fig. 1 Root and shoot biomass (mean ± SE, g m^{-2}) at both old-fields, 11 years after C_4 species were established. *Different lowercase letters* denote significant differences (Tukey–Kramer, $P < 0.05$) between plots for shoot ($n = 9$), surface root, and subsurface root ($n = 6$) biomass. *Ag Andropogon*; *Ss Schizachyrium*; *Sn Sorghastrum*; *C_3 Elymus* (McKay Field), *Bromus* (Turkey Meadow)

Table 3 Model results for plant tissue chemistry variables, using site as a random effect and species (dominant vegetation) as a fixed effect

Site Model	Species	N^a (%) $F_{3,27} = 21.34$, $P < 0.001$	C^a (%) $F_{3,27} = 11.67$, $P < 0.001$	$C:N^a$ $F_{3,27} = 12.76$, $P < 0.001$	ADF^b (%) $F_{3,35} = 26.46$, $P < 0.001$	$ADF:N^a$ $F_{3,27} = 14.33$, $P < 0.001$	$\delta^{13}C^a$ $F_{3,27} = 1{,}233$, $P < 0.001$
McKay	Ag	0.80 ± 0.08 a	45.5 ± 0.2 bc	58.5 ± 6.3 a	79.0 ± 1.3 b	100.4 ± 10.9 a	−12.7 ± 0.1 a
	Ss	0.90 ± 0.08 a	45.3 ± 0.3 ab	51.0 ± 4.4 a	81.1 ± 0.4 a	91.3 ± 7.7 a	−13.5 ± 0.5 b
	Sn	1.01 ± 0.09 a	44.7 ± 0.5 a	45.2 ± 4.7 a	77.5 ± 1.1 b	77.3 ± 7.5 a	−14.0 ± 0.5 ab
	Er	1.26 ± 0.03 b	45.7 ± 0.4 c	36.5 ± 0.6 b	74.6 ± 0.8 c	59.7 ± 1.9 b	−28.7 ± 0.1 c
Turkey	Ag	0.74 ± 0.06 a	49.4 ± 0.5 bc	67.7 ± 5.1 a	74.3 ± 0.5 b	101.9 ± 8.2 a	−12.5 ± 0.1 a
	Ss	0.67 ± 0.04 a	46.2 ± 0.8 ab	69.5 ± 4.5 a	79.1 ± 1.4 a	118.8 ± 7.5 a	−13.9 ± 0.4 b
	Sn	0.64 ± 0.05 a	43.6 ± 0.3 a	69.3 ± 4.6 a	75.9 ± 1.0 b	121.8 ± 8.8 a	−12.8 ± 0.4 ab
	Bi	1.21 ± 0.10 b	51.9 ± 0.2 c	43.5 ± 3.4 b	68.3 ± 1.1 c	57.9 ± 4.9 b	−28.1 ± 0.2 c

Mean (±SE) values are shown for the dominant species at each site below the model. *Different lowercase letters* indicate significant species differences ($P < 0.05$). For abbreviations, see Table 1

[a] $n = 4$

[b] $n = 6$

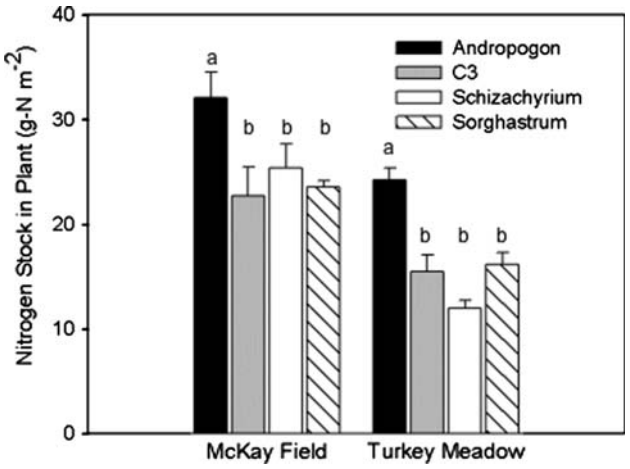

Fig. 2 Total plant N stocks (mean ± SE, g N m^{-2}) for each dominant species at both sites. *Different lowercase letters* denote significant differences (Tukey–Kramer, $P < 0.05$) between plots. C_3 *Elymus* (McKay Field), *Bromus* (Turkey Meadow)

Both surface and subsurface soil NH_4^+ was higher for C_3 plots versus all three C_4 species plots ($F_{3,67} = 9.27$, $P < 0.0001$; $F_{3,67} = 4.94$, $P = 0.004$, respectively); surface soil NO_3^- was lower for *Andropogon* than all other species ($F_{3,67} = 6.42$, $P = 0.001$) and subsurface NO_3^- was higher for C_3 than for *Andropogon* and *Sorghastrum* ($F_{3,67} = 3.92$, $P = 0.012$). In situ net nitrification and N mineralization rates (performed in C_3 and *Andropogon* plots only) varied over the growing season ($F_{4,32} = 10.19$, $P < 0.001$ and $F_{4,36} = 13.48$, $P < 0.001$, respectively), and were negligibly higher in soils under C_3 species than under *Andropogon* ($F_{1,12} = 2.37$, $P = 0.151$ and $F_{1,21} = 1.62$, $P = 0.217$, respectively; Fig. 4) due to high variability among replicates.

Total subsurface soil N pools did not differ among species, but surface N pools were lower under *Schizachyrium* compared to *Andropogon* and the C_3 species (Tables 4, 5). Surface soil $\delta^{15}N$ was higher for C_3 species and *Sorghastrum* than for *Andropogon* ($F_{3,43} = 8.07$, $P < 0.001$), but did not differ for subsurface soils. Surface soil C:N was higher under *Andropogon* and *Sorghastrum* compared to C_3 species. C accumulation was strongly positively correlated with surface soil N (soil, $n = 36$, $P < 0.001$, $r = 0.59$) and C:N ($n = 36$, $P < 0.001$, $r = 0.56$), indicating a strong influence of plant species root and litter biomass on soils. Surface soil C:N was correlated with surface soil $\delta^{13}C$ ($n = 48$, $P < 0.001$, $r = 0.60$), suggesting that soil C:N increases with greater C_4 species contribution to surface soil C pools.

Several plant traits were highly correlated with particular soil variables. Total plant biomass was correlated with soil $\delta^{13}C$ (surface soil, $n = 48$, $P < 0.001$, $r = 0.59$; subsurface, $n = 40$, $P = 0.001$, $r = 0.57$) and surface soil C:N ($n = 72$, $P < 0.001$, $r = 0.44$). There was no relationship between total plant N stocks and either soil N pool size or inorganic N pool size (surface and deep, $P > 0.05$). Shoot tissue C:N was positively correlated with soil $\delta^{13}C$ (surface soil, $n = 48$, $P < 0.001$, $r = 0.57$; subsurface, $n = 40$, $P < 0.001$, $r = 0.57$), suggestive of a strong influence of plant species biomass on soil C.

Discussion

Eleven years after the establishment of native C_4 species, there were detectable differences in soil C and N cycling in C_4-dominated areas compared to the surrounding C_3-dominated matrix community, as well as differences in how individual C_4 species affected these cycles. Changes in soil C and N pools and cycling rates corresponded to species differences in biomass production and tissue chemistry.

Table 4 Model results for surface soil (0–10 cm) C and N variables, using site as a random effect and plot (dominant vegetation) as a fixed effect

Site	Plot	Inorganic N ($\mu g\ N\ g^{-1}$ dry soil)	C:N	C ($kg\ m^{-2}$)	N ($kg\ m^{-2}$)	$\delta^{13}C$
Model		$F_{3,67} = 9.01$, $P < 0.0001$	$F_{3,67} = 6.61$, $P = 0.0005$	$F_{3,67} = 6.68$, $P = 0.0005$	$F_{3,67} = 5.32$, $P = 0.0024$	$F_{3,43} = 20.44$, $P < 0.0001$
McKay Field	Ag	3.91 ± 0.43 a	12.2 ± 0.2 a	2.91 ± 0.40 a	0.24 ± 0.02 a	−24.6 ± 0.6 a
	Ss	3.55 ± 0.47 a	12.0 ± 0.2 ab	1.78 ± 0.16 b	0.15 ± 0.02 b	−25.8 ± 0.5 b
	Sn	4.11 ± 0.43 a	12.1 ± 0.1 a	2.05 ± 0.15 b	0.17 ± 0.01 ab	−25.7 ± 0.3 b
	Er	7.08 ± 0.60 b	11.7 ± 0.1 b	2.52 ± 0.21 ab	0.22 ± 0.02 a	−27.1 ± 0.1 c
Turkey Meadow	Ag	3.12 ± 0.37 a	12.4 ± 0.3 a	3.06 ± 0.21 a	0.25 ± 0.01 a	−23.3 ± 0.8 a
	Ss	3.95 ± 0.81 a	11.9 ± 0.2 ab	2.43 ± 0.13 b	0.21 ± 0.01 b	−25.5 ± 0.3 b
	Sn	4.17 ± 0.39 a	12.0 ± 0.2 a	2.64 ± 0.14 b	0.22 ± 0.01 ab	−24.9 ± 0.4 b
	Bi	4.83 ± 0.55 b	11.5 ± 0.2 b	2.49 ± 0.18 ab	0.22 ± 0.01 a	−27.1 ± 0.1 c

Mean (±SE) values are shown below the model. *Different lowercase letters* indicate species differences ($P < 0.05$). The data shown are untransformed values, but inorganic N, total soil N, and C:N were ln transformed prior to analysis. For abbreviations, see Table 1

Table 5 Model results for subsurface soil (10–20 cm) C and N variables, using site as a random effect and plot (dominant vegetation) as a fixed effect

Site	Plot	Inorganic N ($\mu g\ N\ g^{-1}$ dry soil)	C:N	C ($g\ kg^{-1}$)	N ($g\ kg^{-1}$)	$\delta^{13}C$
Model		$F_{3,67} = 5.87$, $P = 0.001$	$F_{3,55} = 0.26$, $P = 0.855$	$F_{3,55} = 1.35$, $P = 0.268$	$F_{3,55} = 1.46$, $P = 0.236$	$F_{3,35} = 16.78$, $P < 0.0001$
McKay Field	Ag	1.15 ± 0.25 a	11.8 ± 0.1	10.60 ± 0.63	0.91 ± 0.06	-24.5 ± 0.3 a
	Ss	0.92 ± 0.10 a	12.0 ± 0.1	8.54 ± 0.73	0.71 ± 0.06	-25.1 ± 0.2 b
	Sn	0.86 ± 0.08 a	11.9 ± 0.1	8.47 ± 0.79	0.71 ± 0.06	-24.8 ± 0.3 ab
	Er	1.82 ± 0.22 b	11.6 ± 0.1	9.28 ± 0.83	0.80 ± 0.07	-25.7 ± 0.1 c
Turkey Meadow	Ag	0.83 ± 0.19 a	10.4 ± 0.1	9.14 ± 0.82	0.88 ± 0.08	-23.7 ± 0.5 a
	Ss	1.07 ± 0.27 a	10.4 ± 0.2	8.83 ± 0.49	0.85 ± 0.04	-24.9 ± 0.1 b
	Sn	0.93 ± 0.22 a	10.4 ± 0.2	8.86 ± 0.42	0.85 ± 0.05	-24.5 ± 0.2 ab
	Bi	1.29 ± 0.19 b	10.4 ± 0.1	9.31 ± 0.52	0.89 ± 0.04	-25.8 ± 0.2 c

Mean (±SE) values are shown below the model. *Different lowercase letters* indicate species differences ($P < 0.05$). The data shown are untransformed means, but the following variables were transformed prior to analysis: inorganic N (ln), C:N (ln) and $\delta^{13}C$ (square root). For abbreviations, see Table 1

Further, although the focus of this study was species differences and not functional group characteristics, the three C_4 species were generally more similar to one another than to the C_3 grasses for both plant characteristics and impacts on soil properties. For example, tissue chemistry (C:N and ADF:N) did not differ among the C_4 species but was significantly higher than for the C_3 species. Craine et al. (2002a, 2005) found similar results when examining grassland species in the Midwest US and internationally (but see Craine et al. 2002b).

Consistent with our expectations, the C_3 and C_4 species differed in both the quantity and quality (C:N, ADF:N) of biomass produced. Total shoot biomass was 0.5– to 8-fold higher in C_4-dominated compared to C_3-dominated plots, and C_4 plots tended to have larger total root biomass and more investment in deeper root systems than C_3 plots (Fig. 1). Many studies (e.g., Baer et al. 2002; Camill et al. 2004) have found higher biomass (root and shoot) and surface litter accumulation in grasslands as C_4 grass dominance increases, and our results show that C_4 species identity influences the magnitude of that increase in biomass and litter accumulation relative to the C_3-dominated successional community. Overall, the predicted increase in tissue quantity with C_4 species reintroduction was supported by our results, as was the prediction that C_4 species have more recalcitrant tissue (higher C:N and ADF:N) than C_3 species. These results were not surprising, given the extensive examination of these particular species at Cedar Creek (Wedin and Tilman 1990; Craine et al. 2002a, b; Tjoelker et al. 2005; Dijkstra et al. 2006). However, studies attempting to understand how these particular grass species, common to prairies and old-fields, impact soil processes in old-fields and prairie restorations are less common.

Despite differences in tissue quality and quantity between the C_3 and C_4 species in this study, we did not find

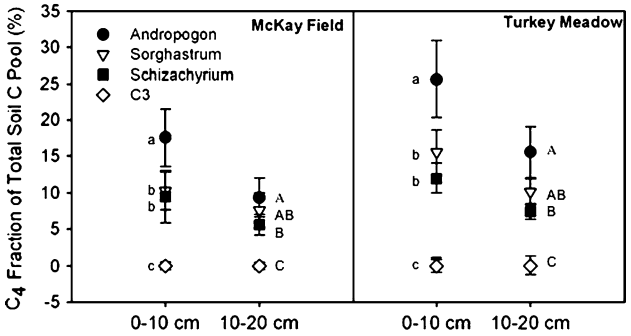

Fig. 3 Percentage of total soil C (mean ± SE) contributed by C_4 species at both surface (0–10 cm; $n = 6$) and subsurface (10–20 cm; $n = 5$) soil depths at both sites. *Different letters* denote significant differences (Tukey–Kramer, $P < 0.05$) between plots separately for each depth. *C_3 Elymus* (McKay Field), *Bromus* (Turkey Meadow)

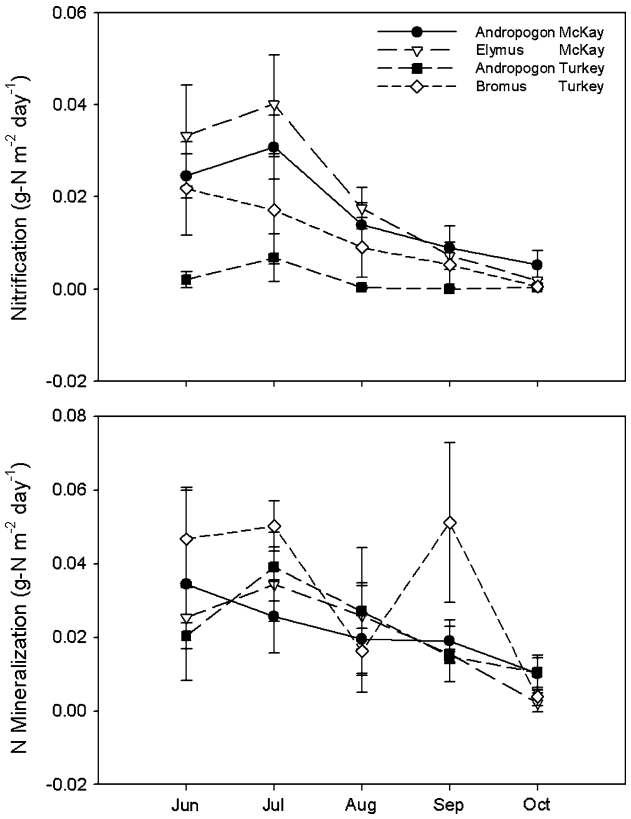

Fig. 4 In situ net nitrification and N mineralization rates (mean ± SE; $n = 5$) for *Andropogon* plots (*solid symbols*) and C_3 plots (*open symbols*) at both Turkey Meadow (Turkey) and McKay Field (McKay). Rates are calculated from 28-day in situ incubations performed consecutively from June to November 2006

higher total soil C in the C_4 plots compared to the C_3 plots. Camill et al. (2004) saw a similar lack of soil C accumulation in the surface soils (0–10 cm) after 6–8 years of C_4 species dominance in restored prairies in Minnesota. In contrast, McLauchlan et al. (2006) found increased soil C (0–10 cm) in grasslands on decadal timescales after agricultural abandonment, regardless of whether they were planted as C_3- or C_4-dominated communities. Conventionally tilled agricultural fields in close proximity to our sites have much lower soil C (~690 g m^{-2} in 0–5 cm depth; Grandy et al. 2006) than in the old-fields in our study (~2,660 g m^{-2} in 0–10 cm depth), even if the unrealistic assumption is made that the soil C pool from 5 to 10 cm is equal in size to the 0–5 cm pool. This suggests that soil C pools are increasing under both C_3 and C_4 species in our sites, potentially making it more difficult to detect species effects on total pool sizes after just 11 years.

Based on the fraction of C_4-soil C after 11 years, we determined that soil C in the top 10 cm has accumulated at a rate of between 13 g C m^{-2} $year^{-1}$ for *Schizachyrium* and 64 g C m^{-2} $year^{-1}$ for *Andropogon*. While we were unable to estimate C accumulation under the C_3 species, our values for the C_4 species are within the range (~65 g C m^{-2} $year^{-1}$ in the top 10 cm) found by others in the Midwest (Lal et al. 1999; McLauchlan et al. 2006). Knops and Tilman (2000) calculated an average of 19.7 g C m^{-2} $year^{-1}$ in old-field soils (0–10 cm) and found higher accumulation rates for C_4 species than for C_3 species, which they attributed to the higher C:N ratio in C_4 species. The larger C accumulation rates for *Andropogon* relative to the other C_4 species correspond to the larger total (root and shoot) biomass (Pearson's correlation: surface, $r = 0.43$; subsurface, $r = 0.45$). This difference, combined with the 398–565 g C m^{-2} larger surface soil C pool size under *Andropogon* compared to the C_3 species, suggests that soil C under *Andropogon* may be increasing at a faster rate relative to under the C_3 species. C_4 species are contributing 9–26% of the total surface soil C pool and 6–16% of the total subsurface soil C pool after just 11 years. Wedin et al. (1995) found that monocultures of C_4 species contributed 14% of the total soil C after 4 years. While this estimate suggests faster rates than reported here, our results still suggest a relatively rapid turnover of the soil C pools. This fast turnover of C suggests that any increases in total soil C by the C_4 species are likely to become apparent relatively quickly. Assuming a linear C contribution rate by the C_4 species, complete turnover of surface soil C could happen in 50–100 years, and any increase in total soil C under C_4 species should become measurable prior to complete turnover.

One potential explanation for the lack of soil C increases found in so many of the studies mentioned above is that the interactive effect of litter quality and quantity differences on soil processes in this study confounds our ability to independently examine the individual influence of each factor on C cycling, and thus how C pools may change. While the increase in tissue quantity, and therefore potential contributions to the soil C pool, associated with the C_4 species would be expected to stimulate microbial

activity, the greater recalcitrance of this tissue may suppress C mineralization rates. Several studies have shown that decomposition is strongly, inversely correlated with tissue C:N and lignin:N (Wardle et al. 1997; Vinton and Goergen 2006). While there were no significant differences in tissue C:N and ADF:N among the three C_4 species in this study, these species differed in their root and shoot biomass. Thus, if tissue chemistry was the main factor determining soil C cycling then the three C_4 species should have similar soil C pool sizes and C accumulation rates, and if biomass was the main factor determining soil C cycling then *Andropogon* should have larger C pools, followed by *Sorghastrum* and *Schizachyrium*, and then the C_3 species. While the C_4–C contribution corresponded strongly to biomass differences, soil total C pool sizes did not follow either chemistry or biomass differences between species, with the exception of *Andropogon*. In fact, *Sorghastrum* and *Schizachyrium* both had slightly smaller C pools than the C_3 species, despite having greater biomass and more recalcitrant tissue than the C_3 species. One explanation for this apparent contradiction is that the larger rooting system of these C_4 species may release greater quantities of labile material to the microbial community (e.g., fine root turnover and exudation), stimulating C mineralization in the rooting zone (Baer et al. 2002). Indeed, recent work in restored prairies found higher C mineralization rates in sites that have high levels of C_4 species dominance (Baer et al. 2002; Camill et al. 2004). Thus, changes in soil C may reflect a balance between increased C mineralization in the rhizosphere and slowed decomposition in bulk soil, and this balance may differ across the three C_4 species in this study.

As predicted, the re-introduction of C_4 grass species into these old-fields altered N cycling. Our measurements of significantly lower total inorganic N availability in plots dominated by all three C_4 species compared to C_3 plots are consistent with patterns found in several studies from a broad range of temperate grasslands and in data collected at our study sites throughout the 2006 growing season (for *Andropogon* and the C_3 species only, data not shown). Wedin and Tilman (1990) found that after only 3 years, inorganic N levels sampled under monocultures of C_4 species were significantly lower than under monocultures of C_3 species. Evans et al. (2001) found that establishment of an invasive C_3 grass (*Bromus tectorum*) with greater biomass and more recalcitrant tissue compared to the native C_3 species (*Bromus tectorum* is the analog to the C_4 species in our study) significantly altered N cycling within 2 years in an arid grassland in Utah. Decreased potential net N mineralization rates in that study were linked to changes in litter quality and quantity, which resulted in increased microbial N immobilization (Evans et al. 2001). The reduced levels of inorganic N in our C_4 plots compared to the C_3 plots could be a result of slower N mineralization rates and more microbial N immobilization, greater N uptake and storage by C_4 species, or a combination of both factors.

In our study, total plant N stocks in *Schizachyrium* and *Sorghastrum* were not larger than in the C_3 species, suggesting that N uptake differences do not explain the lower inorganic N levels in their soil relative to the C_3 species. In contrast, the total plant N stocks of *Andropogon* were greater than for the other three species, making it difficult to determine if higher inorganic N levels under *Andropogon* are primarily the result of greater uptake or slower mineralization rates. However, we found no significant correlation between plant N stocks and either inorganic N pools or total soil N pools ($P > 0.05$), suggesting that differences in inorganic N are the result of differences in N cycling rates. In situ net N mineralization and nitrification rates, which tended to be higher in C_3 plots compared to *Andropogon* plots despite the high variability, support this assertion. We found significant positive correlations between shoot N concentration and inorganic N levels, suggesting that the species with the highest shoot N (the C_3 species) may have faster N cycling rates, leading to increased inorganic N availability. Studies in forested systems in the Great Smoky Mountains National Park (Garten 1993; Garten and Vanmiegroet 1994) have shown a positive relationship between foliar N and net N mineralization or nitrification rates. Vinton and Goergen 2006 suggested that the lower C:N of *Bromus inermis* may encourage rapid and efficient N cycling, which in turn increases inorganic N availability in the soil. Even though *Andropogon* was the only C_4 species examined for N mineralization and nitrification in our study, one might expect similar results for the other C_4 species because the three species did not differ in tissue C:N or ADF:N.

Soil $\delta^{15}N$ may also be used to indicate qualitative differences in N cycling rates. In a temperate forest in New York, Templer et al. (2007) found that soil $\delta^{15}N$ was positively related to higher rates of net N mineralization ($R^2 = 0.49$) and net nitrification ($R^2 = 0.72$), likely a result of greater microbial discrimination against ^{15}N. Evidence from surface soil $\delta^{15}N$ in our study suggests that N cycling is slower in soils under *Andropogon* compared to under the dominant C_3 species, but under *Schizachyrium* and *Sorghastrum* did not differ from under the C_3 species. Other studies have found faster N cycling under C_3 species relative to C_4-dominated plots (e.g., Wedin and Tilman 1990; Baer et al. 2002; Dijkstra et al. 2006), supporting the hypothesis that the three C_4 species alter inorganic N availability by slowing mineralization rates and/or increasing microbial immobilization.

Total soil N was not significantly different in soils under C_4 or C_3 species, and a lag in pool responses to rate

changes would be expected given the large size of the soil N pool. Kucharik (2007) found no increase in soil C or N after 4–16 years since conversion to a Conservation Reserve Program, although that study examined the 0–25 cm soil depth. Total soil N accumulation in the surface 10 cm was 22–29 g N m^{-2} $year^{-1}$ higher under *Andropogon* than under C_3 species. This provides some evidence to support the prediction that total N pools are increasing under *Andropogon* relative to C_3 species, but that it will take longer than a decade for these differences to become statistically significant. In contrast, *Schizachyrium* plots actually had lower surface soil N than the C_3 plots, suggesting that individual C_4 species have varied effects on N cycling.

Net N mineralization and nitrification rates varied seasonally for both *Andropogon* and C_3 plots and typically were highest in the early summer. Mineralization rates are often high in spring and early summer as a consequence of litter inputs from the previous fall that are available for microbial utilization, as well as warmer soil temperatures and adequate moisture to stimulate microbial activity (Eviner et al. 2006). Net nitrification and mineralization rates were slow by October for all plots; however, the *Andropogon* plots continued to process N later into the fall than the C_3 plots. The higher surface litter in the *Andropogon* plots may insulate the soil in these plots and thereby sustain microbial activity later into the fall. Our results suggest that *Andropogon* has altered the timing and rate of N transformations, but more detailed studies are needed to examine the community- and ecosystem-level importance of such changes, as well as the generality of these results to other C_4 species.

Overall, this study demonstrated that the introduction of a species with different functional traits than the surrounding community alters soil properties. We provide evidence that tissue quantity and quality differences between C_3 and C_4 species influence soil C and N cycling over relatively short timescales, and that differences among individual C_4 species traits correspond to differences in soil properties among C_4 species. Improving our understanding of how plant species impact ecosystem properties and what species traits are driving these changes is imperative for predicting ecosystem-level consequences of changes in species distribution or composition that occur as a consequence of changes in agricultural and land use practices, global change, and species introductions.

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