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Effects of nitrogen addition on vegetation and ecosystem carbon in a semi-arid grassland

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Abstract To clarify responses of plant and soil carbon (C) and nitrogen (N) pools in grassland ecosystem to N addition, a field experiment was performed in a grassland in Keerqin Sandy Lands, Northeast China. We investigated vegetation composition and C and N pools of plant and soil (0–30 cm) after five consecutive years of N addition at a rate of 20 g N m^{-2} y^{-1}. Vegetation composition and species diversity responded dramatically to N addition, as dominance by C_4 perennials was replaced with C_3 annuals. Carbon in aboveground pool increased significantly (over two-fold), mainly due to the increase of the C in aboveground living plants and surface litter, which increased by 98 and 134%, respectively. Although soil C did not change significantly, the root C pool decreased in response to 5 years of N addition. The total ecosystem C pool was not significantly impacted by N addition because the large soil pool did not respond to N addition, and the increase in aboveground C was offset by the decrease in root C pool. Moreover, N addition significantly increased the aboveground N pool, but had no significant effects on belowground and total ecosystem N pools. Our results suggest that in the mid-term N addition alters the C and N partitioning in above- and belowground pools, but has no significant effects on total ecosystem C and N pools in these N-limited grasslands.

Keywords Carbon partitioning · Carbon pool · Keerqin Sandy Lands · Nitrogen limitation · Sandy grassland · Species composition

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Introduction

Nitrogen (N) is recognized as the primary limiting nutrient for plant growth in many terrestrial ecosystems (Vitousek and Howarth 1991; LeBauer and Treseder 2008). Therefore, N fertilization has been widely used to improve soil N availability and increase plant growth and productivity in terrestrial N-limited ecosystems (Frink et al. 1999). On the other hand, atmospheric N deposition associated with anthropogenic activities is increasingly regarded as a large source of N to many terrestrial ecosystems (Vitousek et al. 1997; Galloway et al. 2004). The alteration of global N cycles has the potential to profoundly change plant growth and net primary production in terrestrial ecosystems, with consequent impacts on global carbon (C) cycles and other ecosystem processes (Vitousek et al. 1997; Gruber and Galloway 2008; Xia and Wan 2008).

Many studies have reported that the increased input of N could affect ecosystem C dynamics. Previous experimental studies of N addition have shown varying responses of ecosystem C storage, including positive (Dijkstra et al. 2005), negative (Mack et al. 2004), and negligible (Nadelhoffer et al. 1999; Bechtold and Inouye 2007). Over the long term, ecosystem C storage depends on the balance between net primary production and decomposition (Hu et al. 2001; Neff et al. 2002; Mack et al. 2004), and the factors that regulate those two processes are different. It has widely been documented that N enrichment usually increases gross primary productivity and net primary productivity by stimulating plant growth and biomass production (Xia and Wan 2008). The response of decomposition and soil organic matter pools is more complex, as increased N often stimulates decay of labile components while inhibits that of more recalcitrant organic matter (Fog 1988). Moreover, N addition may alter plant partitioning of C between above- and belowground tissues (Bardgett et al. 1999) with potential consequent effects on soil C pools. The overall response of terrestrial ecosystem C storage to N addition remains uncertain (Asner et al. 2001) in part because of the limited number of experimental studies in many regions. The present study was designed to provide such information for extensive sandy grasslands in northern China.

Grasslands that are characterized by sandy soils constitute a large percent of natural vegetation in arid and semi-arid regions of northern China, but little information exists on biogeochemical cycling in these sandy grasslands (Zhou et al. 2008; Li et al. 2009a). Moreover, economic development in China is causing increases in the deposition of reactive N throughout the country (Galloway et al. 1996; Lü and Tian 2007; Zhang et al. 2008; Li et al. 2009b). Will N enrichment result in increased C storage in widespread sandy grasslands in China? Knowledge of the responses of community structure and composition, and ecosystem C and N storage under N enrichment is crucial for managing ecosystems for C and other ecosystem services. We hypothesized that N addition would promote plant production and thus total ecosystem C and N storage in sandy grasslands. We measured C and N concentrations and pools in soils and above- and belowground vegetation of a sandy grassland in the southeastern Keerqin Sandy Lands after five consecutive years of N addition. We also examined the response of vegetation composition to N addition. In accord with observations of Wedin and Tilman (1996) and Reich et al. (2001), we hypothesized that N addition would favor plants with the C_3 photosynthetic pathway over C_4 plants and non-N-fixing species over N-fixing plants. Hence, implication of changes in vegetation composition and relative belowground C allocation for ecosystem C and N pools was evaluated.

Materials and methods

Site description

This study was conducted in a sandy grassland on flat topography at Daqinggou Ecological Station (42°58′ N, 122°21′ E, 260 m above sea level), Institute of Applied Ecology, Chinese Academy of Sciences in the southeastern Keerqin Sandy Lands, Northeast China. The area is within the temperate climatic zone; its mean annual temperature is about 6.4°C, with the lowest mean monthly temperature occurring in January (−12.5°C) and the highest in July (23.8°C); mean annual precipitation is 450 mm, with more than 60% occurring in June–August. Soils have developed from eolian parent material (Typic Ustipsamment) and are characterized by coarse texture and loose structure. The textural composition is 90.9% sand, 5.0% silt, and 4.1% clay (Zeng et al. 2009). The vegetation is dominated by *Pennisetum flaccidum*, *Chenopodium acuminatum*, and *Cleistogenes chinensis*. The growing season lasts approximately 4 months, with leaf budburst occurring in late April and leaf senescence in early September in this area.

Experimental design

In 2003, the experimental grassland was fenced to exclude livestock grazing, and twelve 4 m × 4 m plots were established. Each of the twelve plots was surrounded by a 2 m wide buffer strip. Two N fertilization treatments (N addition and control; six replicate plots per treatment) were assigned to the twelve plots. From 2004 to 2008, N was added at a rate of 20 g N m^{-2} y^{-1} in the form of urea/NH_4NO_3. The fertilizer was applied twice annually, in late April to early May (6 g N m^{-2}) and mid-June (14 g N m^{-2}) of each year, respectively. Fertilizer was weighed, mixed with 16 l water in a sprayer, and applied to each of six randomly selected treatment plots. The control plots received 16 l water without N addition. The amount of N addition applied in this study was comparable with agricultural inputs in the region, and it was chosen to ensure that N was no longer limiting to any biological processes, such as plant or microbial growth (Allison et al. 2008).

Sampling and analyses

Vegetation surveys were conducted in mid-August 2008, the time of peak biomass. In each plot, four random 1 m × 1 m quadrats were assigned to investigate plant community characteristics such as plant density and cover. A total of 24 quadrats were measured in each treatment. Aboveground plant samples were collected from three randomly selected 20 cm × 50 cm quadrats in each plot. Aboveground biomass in these quadrats was clipped at the ground level, and sorted into living plants and standing dead plants. Surface litter (including the duff component) was collected subsequently. Three samples of each component were combined and formed a composite sample for each plot. Root biomass (0–30 cm) was quantified using soil core sampling (10 cm in diameter) in the same locations used for aboveground biomass clipping. Roots, containing both living and dead parts, were separated from soil by hand picking and washing with water. All plant samples (aboveground living plants, standing dead plants, surface litter, and roots) were oven-dried at 70°C for 48 h, weighed to determine the biomass, and then stored in desiccators. A portion of each sample was ground with a mill and passed through a 0.25-mm sieve for determination of organic C and total N concentrations.

In mid-August 2008, mineral soils were collected with a soil core sampler (2.5 cm in diameter) in the same quadrats where above- and belowground samples were collected. The samples were separately collected from two layers at the depth of 0–15 cm and 15–30 cm in each sampling point. For each layer, the samples from three quadrats were mixed completely to form a composite in each plot. After roots and organic debris were removed by hand, the soil samples were air-dried, passed through a 2-mm sieve, and ground to pass through a 0.25-mm sieve for analyses of soil organic C (SOC), total N (TN) and total P (TP) concentrations. Organic C in the samples of aboveground living plants, litter, standing dead plant material, roots and soils was determined by the Walkley–Black wet oxidation method following removal of carbonates by acid pretreatment (Lu 1999). TN concentrations of plant and soil samples were determined by the Kjeldahl method and soil TP was determined by molybdenum-stibium colorimetry method with a continuous-flow autoanalyzer (AutoAnalyzer III, Bran + Luebbe GmbH, Germany) after the samples were digested with H_2SO_4. Soil bulk density was measured in each plot using the soil cores obtained from the two layers. Air-dried soil samples that have passed through a 2-mm sieve were used to determine soil pH (soil:water ratio 1:2.5) with a PHS-3C pH Meter (Shanghai Lida Instrument Factory, China).

Data processing and analysis

As an overall measure of vegetation change, species diversity was measured by the Shannon-Wiener index, Simpson index and species richness (Wang et al. 2006). The relative importance (dominance) of species was calculated using the importance value which is the mean of relative cover, relative frequency and relative density. Shannon–Wiener index and Simpson index were calculated based on the importance value of species. Species richness based on searches in the plots was expressed as species number per square meter.

Biomass C pools for aboveground parts (aboveground living plants, standing dead plants and surface litter) and roots for each plot were estimated by multiplying sample biomass by the organic C concentration for each component. Soil C pools were calculated by multiplying SOC concentration by soil bulk density and soil thickness. We summed all biomass C pools in aboveground living plants, standing dead plants, and surface litter to calculate total aboveground C pool, and added soil C pool to 30 cm depth to root C pool to estimate total belowground C pool. Total ecosystem C pool was estimated by summing all above- and belowground pools. Total ecosystem N storage was similarly calculated.

All statistical analyses were performed using the software program SPSS 13.0 for Windows. All data were expressed as mean ± 1 standard error (SE). Statistical significance of the differences in any of the variables between the N addition treatment and the control was tested by the Student's *t*-test of the SPSS package.

Results

Soil pH was significantly lower ($P < 0.05$) in the N added plots than the control plots in 0–15 cm layer of the soil (Table 1). Bulk density, SOC, TN and TP concentrations, and C:N ratio were not significantly impacted by N addition in both 0–15 cm and 15–30 cm soil layers ($P > 0.05$; Table 1).

The addition of N dramatically changed plant species composition (Table 2). After addition of N, dominant species in the plots shifted from perennial C_4 grasses (*Pennisetum flaccidum*, *Cleistogenes chinensis*) to C_3 plants (*Cannabis sativa*, *Phragmites communis*). The addition of N also reduced the dominance of some legume species (*Lespedeza davurica*), and resulted in the disappearance of others (*Lespedeza hedysaroides*). The dominance of annual plants was greatly increased by N addition (Table 2). There were pronounced differences in the species diversity (Shannon–Wiener index, Simpson index, and species richness) between the N added and the

Table 1 Effects of N addition on soil pH, bulk density, soil organic C (SOC), total N (TN), total P (TP) and C:N in grassland at Keerqin Sandy Lands, Northeast China

Soil depth (cm)	Treatment	pH	Bulk density (g cm^{-3})	SOC (g kg^{-1})	TN (g kg^{-1})	TP (g kg^{-1})	C:N
0–15	Control	6.61 (0.03) a	1.47 (0.04) a	4.79 (0.36) a	0.36 (0.02) a	0.11 (0.01) a	13.4 (0.3) a
	N added	5.31 (0.05) b	1.49 (0.04) a	4.71 (0.23) a	0.34 (0.01) a	0.10 (0.01) a	13.9 (0.6) a
15–30	Control	6.52 (0.07) a	1.50 (0.03) a	3.94 (0.35) a	0.25 (0.01) a	0.13 (0.01) a	16.0 (0.3) a
	N added	6.16 (0.15) a	1.56 (0.01) a	3.44 (0.39) a	0.23 (0.02) a	0.12 (0.01) a	14.8 (0.6) a

Values in parentheses are SE ($n = 6$). Different letters within a column indicate the significant difference of mean values ($P < 0.05$) in a given soil layer

Table 2 Species composition and their importance value (IV) of control and N treated plots in Keerqin Sandy Lands, Northeast China

Species	Functional group	IV (%)		
		Control	N added	Change
Pennisetum flaccidum	C_4-perennial	20.3 (1.8)	1.4 (1.0)	−18.9**
Cleistogenes chinensis	C_4-perennial	9.3 (1.7)	0.9 (0.4)	−8.4**
Phragmites communis	C_3-perennial	8.0 (0.4)	17.5 (4.2)	9.5*
Lespedeza davurica	Legume-perennial	7.4 (1.1)	1.1 (0.7)	−6.3**
Cannabis sativa	C_3-annual	6.4 (0.7)	32.3 (5.8)	25.9**
Corispermum flexuosum	C_3-annual	6.4 (0.8)	0.7 (0.5)	−5.7**
Lespedeza hedysaroides	Legume-perennial	5.1 (1.4)	0	−5.1*
Chenopodium acuminatum	C_4-annual	9.9 (1.1)	16.8 (4.4)	6.9
Artemisia scoparia	C_3-biennial	8.0 (1.8)	4.3 (1.0)	−3.7
Erodium stephanianum	C_3-annual	5.9 (0.8)	3.7 (1.4)	−2.2
Setaria viridis	C_4-annual	3.9 (0.9)	8.6 (2.5)	4.7
Others		9.4	12.7	3.3

The importance value (IV) is the mean of relative cover, relative frequency and relative density. Values in parentheses are SE ($n = 6$). Significant differences between treatments indicated by * $P < 0.05$, ** $P < 0.01$

Table 3 Effects of N addition on species diversity in grassland at Keerqin Sandy Lands, Northeast China

Treatment	Species number (m^{-2})	Shannon–Wiener index	Simpson index
Control	10.3 (0.4) a	2.22 (0.04) a	0.88 (0.01) a
N added	5.2 (0.8) b	1.47 (0.17) b	0.73 (0.04) b

Values in parentheses are SE ($n = 6$). Different letters within a column indicate the significant differences of mean values ($P < 0.05$)

control plots ($P < 0.05$; Table 3). The addition of N decreased species richness by 50% ($P < 0.05$; Table 3).

The C pool of the aboveground living plants (shoots) and litter in the N fertilized plots was increased by 98 and 134%, respectively (Fig. 1a). For the standing dead plants, the C pool was not different between the N added and the control plots. The C pool in roots was significantly lower ($P < 0.01$) in the N added plots than the control plots (Fig. 1a), and the root:shoot ratio of the vegetation declined in half in response to the N addition. Changes in aboveground C pool were observed with a 105% increase in the N fertilized plots (Fig. 1b). However, the soil C pool did not significantly differ between control and N treatment plots in both 0–15 cm and 15–30 cm soil layers (Fig. 1a). The total belowground C pool (which is the sum of C in roots and mineral soil of top 30 cm) was not significantly impacted by the addition of N (Fig. 1b). The total ecosystem C pool, the sum of above- and belowground pools, did not respond significantly to N addition despite the dramatic increase in the aboveground C pool (Fig. 1b).

The addition of N increased the amount of total N stored in living plants and litter ($P < 0.05$ and

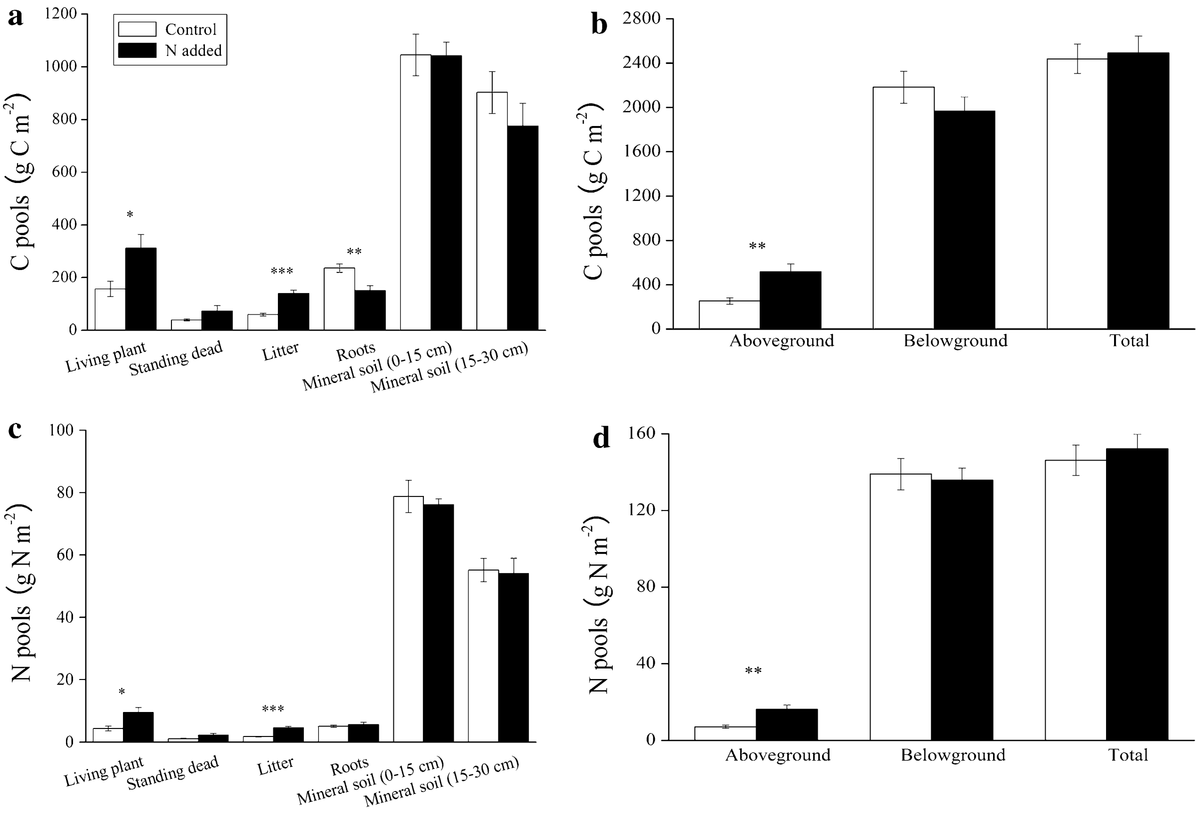

Fig. 1 Effects of nitrogen addition on grassland ecosystem carbon and nitrogen pools (mean ± SE) in Keerqin Sandy Lands, Northeast China. **a** Carbon pools in plant and soil compartments. **b** Above-, belowground and total carbon pools. **c** Nitrogen pools in plant and soil compartments. **d** Above-, belowground and total nitrogen pools. Aboveground pools include aboveground living plants, standing dead plants, and surface litter. Belowground pools include roots and mineral soil (0–15 cm and 15–30 cm). Pool treatment means were compared with *t*-test ($n = 6$). Means that are significantly different are indicated with asterisks: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

$P < 0.001$, respectively) by 119 and 160%, respectively. Nitrogen addition had a negligible effect on the N pool in standing dead plants (Fig. 1c). Nitrogen in total aboveground pools was increased ($P < 0.01$) by 127% due to the increase in the N stored in living plants and litter (Fig. 1d). The amount of N stored in the roots and mineral soil (0–15 cm and 15–30 cm) were not significantly impacted by N addition (Fig. 1c). Thus, the belowground N pool was not significantly impacted by N addition; total ecosystem N pool was also not significantly impacted by N addition (Fig. 1d).

Discussion

The present study confirmed earlier observation that productivity of semi-arid, sandy grasslands in China is limited primarily by N (Chen et al. 2006; Yu et al. 2009). This study is the first to measure the effects of N addition on vegetation dynamics and below- and aboveground C pools in these grasslands. Although the vegetation of this region has been profoundly modified by human activity, paleoecological information indicates that the natural vegetation in the area probably has been dominated by herbaceous plants rather than trees throughout most of the last 100 ky (Sun et al. 1997). The present study confirms a variety of general patterns about grassland ecosystem responses to N fertilization and provides some new insights into the causes of these responses in the specific context of the Keerqin Sandy Lands.

Nitrogen effects on semi-arid grassland vegetation

Nitrogen addition has commonly been observed to change plant species composition and to reduce plant diversity in herbaceous vegetation (Wedin and Tilman 1996; Gough et al. 2000; Stevens et al. 2004). Our observations confirm previously reported patterns for temperate herbaceous communities, with a decrease in warm-season C_4 grasses and an increase in C_3 plants (Table 2). In addition, the dominance and diversity of legumes also decreased, and an increase in the dominance of annual plants was observed. These responses are probably explained by a combination of differing N acquisition strategies, N-use efficiency and maximum growth rates of these different functional types (Xia and Wan 2008) and the increased competition for light resource under nutrient addition (Wamelink et al. 2009). These shifts in composition were also accompanied by a loss of diversity, with a decrease in species richness by 50% (Table 3). The magnitude of species loss has been observed to increase with greater N stimulation of productivity (Clark et al. 2007; Xia et al. 2009). Both the decrease in species diversity (Table 3) and increase in aboveground C storage (Fig. 1b) were at the upper end among published reports, confirming the observations of Clark et al. (2007).

We observed a small but significant reduction in root biomass with N addition, as has been noted in most other studies (Ennik et al. 1980; Bardgett et al. 1999; but see Power 1980). It is generally recognized that more C is allocated belowground in N poor sites and increasing soil N availability often leads to decline in fine root biomass (Nadelhoffer et al. 1985). Moreover, the root:shoot ratio of the vegetation declined by more than half. Presumably this response reflects a change in plant allocation for N acquisition. The increase in the proportion of annual plants probably also contributed to this response, as the root:shoot ratio of herbaceous perennials generally exceeds that of annual plants (Reynolds and D'Antonio 1996). Steinbeiss et al. (2008) suggested that higher plant diversity can increase root production and lead to greater soil C storage in managed grasslands.

Ecosystem carbon and nitrogen pools

The effects of N addition on ecosystem C storage have received increasing attention. Our study supported the general observation that additional N stimulates increased aboveground C storage in grasslands (Wedin and Tilman 1996; Foster and Gross 1998; Xia and Wan 2008). This increased C storage was associated with both live biomass and litter pools (Fig. 1a). However, despite these increases, total ecosystem C storage did not respond significantly to 5 years of N addition (Fig. 1b). The mineral soil was by far the largest C pool in these grasslands (Fig. 1a), and this large pool did not respond to N addition (Table 1).

The effect of N addition on total ecosystem C storage depends on the balance between production and decomposition (Mack et al. 2004). In contrast to the straightforward direct effects on aboveground production and C storage, the response of decomposition processes to N addition is more uncertain (Fog 1988; Schlesinger and Andrews 2000; Manning et al. 2008). Moreover, feedbacks between decomposition and production may occur; for example, if N addition stimulates decomposition it could accelerate N recycling (Nowinski et al. 2008) and consequently plant growth might be stimulated more than decomposition, resulting in increased ecosystem C storage (Hyvönen et al. 2008). In the present study we observed decreased C:N ratios in plant litter under N addition (control = 33.9 ± 1.3 and N treatment = 28.4 ± 0.5) that might be expected to stimulate litter decomposition; however, the litter C pool increased in about the same proportion as the aboveground C pool (Fig. 1a). Increased litter C inputs may exert a priming effect on soil respiration, resulting in decreased surface soil C storage (Sulzman et al. 2005; Schaefer et al. 2009). Moreover, the reduced root C allocation probably depressed soil C inputs in the N treated plots. These results indirectly provide support for the contention of Fornara and Tilman (2008) that soil C accumulation in N-limited grasslands is strongly influenced by plant species composition. The decrease in C_4 perennials and legume species may have contributed to the decrease in belowground biomass and thus soil C inputs under N fertilization because legumes have unique access to N, and C_4 grasses take up and use N efficiently thereby increasing belowground biomass in N-limited grasslands where fixation is the main source of N for plants (Fornara and Tilman 2008). Whether such compositional changes under short-term N addition lead to longer-term influences on soil C pools requires more extended experimental studies.

The addition of 100 g N m^{-2} over 5 years resulted in an increase in N storage in aboveground pools (Fig. 1d) but not soil pools, even though the total doses were comparable in magnitude to the total N pool size in the upper 30 cm soil (~140 g N m^{-2}). About 5.1% of the added N could be accounted for in increased aboveground N pools, indicating relatively low N retention and suggesting high N losses. The low N retention may be due to potential N loss pathways such as N leaching (Wedin and Tilman 1996), and gaseous N loss in denitrification (Peterjohn and Schlesinger 1990; Tilsner et al. 2003), nitrification (Bremner and Blackmer 1978; Neff et al. 1994) or ammonia volatilization (Schlesinger and Peterjohn 1991) after fertilization. In addition, apparently microbial immobilization in these coarse soils with relatively low C contents was not sufficient to retain soil N, and soil C:N ratios did not respond significantly to the treatment (Table 1). Accurate assessments of the fate of N added to sandy grasslands and regulating mechanisms will require consideration in future research.

No data on atmospheric N deposition are available for our study site. However, an observation in a grassland ecosystem in the Songnen Plain of Northeast China (~200 km away from our study site) showed that atmospheric N deposition was 14.88 kg N ha^{-1} y^{-1} during December 1994 to November 1995, and that NH_4^+-N and NO_3^--N are the main forms of N deposition in that study area (Li et al. 2000). The magnitude of N addition in the present experiment exceeded the highest pollutant deposition rates (Galloway et al. 2004); therefore, interpretations of the patterns and magnitude of responses should be made with due caution.

In conclusion, we observed that N addition over 5 years did not promote increased ecosystem C storage in semi-arid sandy grasslands in China. Whereas the shifts in species composition and aboveground plant growth stimulated higher aboveground C storage under N addition, the large belowground C pool did not respond and could even decline because of reduced root C allocation. In the long term more gradual responses as well as the interaction of coincident CO_2 fertilization with N pollution could modify this result and deserve further experimental study (Dijkstra et al. 2005).

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