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Original article

Changes in carbon and nitrogen storage along a restoration gradient in a semiarid sandy grassland

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ABSTRACT

Understanding carbon (C) and nitrogen (N) pools in degraded ecosystems is useful to predict future C and N sequestration potential during restoration. Here we examined the distribution of C and N pools in plant–soil system at four successional stages: mobile dune, semi-fixed dune, fixed dune and grassland. The four stages reflect the successional sequence during sandy grassland restoration in Horqin Sandy Land, Northern China. C and N storage in plant biomass, litter and soil increased significantly with advancing sandy grassland restoration. With the conversion from mobile dune to semi-fixed dune, fixed dune and grassland, total ecosystem C and N storage increased by 1.9, 4.8, 7.1 and 3.3, 15.7, 20.6 times, respectively. More than 80% of C and N storage were stored in soil in sandy grassland restoration. C or N storage in plant and root biomass, litter and soil was positively correlated to species richness. Soil C and N storage was positively correlated to the C and N in plant and root biomass. These results suggest that sandy grassland restoration has a high potential to sequester C and N in the soil. Increasing plant production and species diversity via restoration likely enhance the C and N sequestration in sandy grassland ecosystems.

1. Introduction

Arid and semi-arid regions cover approximately 45% of the earth's surface (Schimel, 2010), and store a substantial amount of carbon (C) and nitrogen (N) within the vegetation and the soil (Lal, 2004; Nosetto et al., 2006). Yet, most of these areas are prone to desertification, because of human activity and climate changes. With sandy desertification productivity sharply declines and a large amount of C and N is lost (Lal, 2004; Tschakert, 2004). These C and N losses due to desertification are a globally significant pool and contribute to the increase in atmospheric CO_2 (Lal, 2009). However, because desertified areas lost a large amount of C and N, ecosystem restoration not only increases productivity, but also sequesters a large amount of C and N.

Within the arid and semiarid regions of northern China, grasslands with sandy soils are highly vulnerable to wind erosion (Li et al., 2009). Sandy grasslands also contribute to a substantial proportion of the C flux in terrestrial ecosystems (Li et al., 2012; Peichl et al., 2012; Xie et al., 2005). Within sandy grasslands more than 90% of C and N is stored in the soil (Chen et al., 2012; Li et al., 2009). Several studies have shown that the identity of the dominant species during restoration can have a significant impact on C and N accumulation (Bardgett et al., 1999; Jiang et al., 2011). Many studies have also suggested that species richness increases plant biomass which can increase C and N accumulation in the soil (Dijkstra et al., 2005; Fornara and Tilman, 2008; Reich et al., 2001; Steinbeiss et al., 2008). Within sandy grasslands we have also found a positive relationship between species diversity and plant biomass (Zuo et al., 2012). Thus, to understand how sandy grassland restoration influences soil C and N accumulation, we need to consider plant biomass, the identity of the dominant species and the diversity of the plant community.

Horqin Sandy Land is located in the semi-arid area of southeast

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Inner Mongolia and is one of the most severely desertified regions of northern China (Li et al., 2009; Zhao et al., 2005). Since the 1970s, grazing exclusions had been implemented to stabilize dunes and restore the natural vegetation. Desertified sandy grasslands are characterized as mobile dunes, with more than 90% baer soil. Because Horqin Sandy Land has an annual precipitation of 350–500 mm and abundant seed sources remain (Li et al., 2012; Liu et al., 2009b), grazing exclusions allow pioneer plants to establish and survive and a succession from mobile dunes to semi-fixed and to fixed dunes occurs. To understand the restoration process, studies on vegetation (Qiao et al., 2012; Zuo et al., 2009), soils (Chen et al., 2012; Huang et al., 2012), soil macro faunal and microbial communities (Liu et al., 2009b; Wang et al., 2011) and vegetation-soil relationships (Zuo et al., 2014) have been carried out in recent years. However, potential changes in C and N sequestration after restoration remain to be evaluated.

The objective of this study was to examine how ecosystem C and N pools are distributed across a sandy grassland restoration sequence, and thus to evaluate the potential of C and N increases as sequestration restoration advances. We tested three hypotheses: 1) total ecosystem C and N storage increase with restoration; 2) soil stored the majority of C and N; and 3) species richness and biomass positively increase C and N sequestration.

2. Materials and methods

2.1. Site description

The study was conducted in a sandy grassland ecosystem in Horqin Sandy Land (42°55′ N, 120°42′ E; 360 m elevation), Inner Mongolia, Northern China. The area has a continental semi–arid climate, the annual mean temperature is around 6.4 °C, with a minimum monthly mean temperature of −13.1 °C in January and a maximum of 23.7 °C in July. Annual average precipitation is 360 mm, with 75% during the growing season of June to September. The annual mean wind velocity ranges from 3.2 to 4.1 m s^{-1}, and the prevailing wind direction is northwest.

This region is characterized by a mosaic of mobile dune, semi-fixed dune, fixed dune and grassland patches (Chen et al., 2012; Guo et al., 2008; Liu and Yan, 2010; Qiao et al., 2012). Soils are classified as sandy chestnut soils, vulnerable to wind erosion and plant distributions strongly respond to soil variability (Zuo et al., 2009). The dominant pioneer species on mobile sand dunes is *Agriophyllum squarrosum*. In semi-fixed dunes, the dominant species is *Artemisia halodendron*, an asexually-reproducing shrub adapted to slight sand burial. Fixed dunes are dominated by the forb *Artemisia scoparia*, and grasslands are dominated by the annual forb *A. scoparia* and the perennial grasses *Phragmites communis and Pennisetum centrasiaticum*.

2.2. Sampling design

All field sampling was conducted in August of 2013. We selected 24 sampling sites corresponding to the four typical successional habitats (6 replicate sites per habitat) along a restoration gradient of sandy grasslands, including mobile dune (MD) with less than 10% vegetation cover, semi-fixed dune (SFD) with 10–60% vegetation cover, and fixed dune (FD) with more than 60% vegetation cover and grassland (G) with more than 60% vegetation cover (Liu et al., 2009a; Zuo et al., 2012). These sites were located at 0.5–8 km distance from each other (Fig. 1). Semi-fixed dunes and fixed dunes were naturally restored from mobile dunes by fencing out livestock at some point between 1980 and 1995. Grassland sites were fenced to exclude livestock in 1996, thus grassland represents a relatively good vegetation type in this region.

At each site, we established one 20 × 20 m plot in an area with flat topography (slope < 5°). Five 1 × 1 m quadrats were set up at the four corners and the center in each plot to survey the vegetation and collect soil samples. The number of plant species and plant cover by species was recorded in each quadrat. Above-ground biomass was harvested and litter was collected within each quadrat.

After the litter layer was removed in each quadrat, roots were sampled at four depth layers (0–10, 10 to 20, 20 to 40 and 40–60 cm) using an 8 cm-diameter soil auger. Concurrently, three random soil samples were collected at each layer within each quadrat using a 3 cm-diameter soil auger, and pooled to form one composite sample for laboratory analysis. Soil samples were air-dried and hand-sieved through a 2-mm screen to remove roots and other debris. For soil bulk density, soil samples were collected in 5 cm increments using a soil auger equipped with a stainless-steel cylinder (5 cm in both diameter and height) and the bulk density was calculated as the average of two or four samples for each of the above mentioned four soil layers (Li et al., 2013).

Roots were washed and handpicked over a 1-mm screen to remove all soil, pebbles and debris. The aboveground biomass, litter and roots were dried at 60 °C for 48 h and were ground using a mill (Pulverisette 14, Germany). Soil samples for bulk density were dried at 105 °C for 24 h. Soil total C and total N concentrations were determined with an elemental analyzer (Vario Macro cube, Elementar, Germany). Data from different depths of five quadrats were averaged to calculate the root biomass, soil C and N content and bulk density at each depth in every plot.

Soil % C and % N were converted to g C and N m^{-2} with the corresponding soil bulk density. Plant and root % C and % N were converted to g C and N m^{-2} by considering the biomass sampled per area unit. Data from five quadrats were averaged to allow us to estimate the mass of C and N in aboveground plant, litter, root, soil, plant system (aboveground plant, litter and root) and total ecosystem (plant–soil system) at each plot.

2.3. Statistical analysis

All data were expressed as mean ± 1 SE (n = 6). Overall patterns in the aboveground biomass, C and N content in plant and litter and total C and N pools data in the different restoration stages was compared with a one-way analysis of variance (ANOVA). The effects of successional habitat and soil layer on soil variables, root biomass and its C and N content were analyzed by a two-way ANOVA. We used a least-significant-difference (LSD) test to compare different restoration stages, if a measured variable was significant ($P < 0.05$) in the ANOVA. All tests were performed with SPSS (version 16.0).

3. Results

3.1. Characteristic of biomass, C and N contents in plant systems

Aboveground plant biomass, litter mass and their C and N contents were significantly different among the four successional habitats (Table 1, $P < 0.01$). Plant biomass and litter mass increased with advancing sandy grassland restoration. Grassland had the highest aboveground plant C content and mobile dune had the highest aboveground plant N content. The litter C content in mobile dune and semi-fixed dune was higher than that of fixed dune and grassland, and semi-fixed and fixed dune had a lower litter N content, as compared to the mobile dune and grassland. Root biomass and C and N contents significantly differed between the 0–10 cm and 10–20 cm depth layers ($P < 0.01$). Root biomass also differed between the 20–40 cm and 40–60 cm depth layers ($P < 0.05$), but not for C and N content (Table 2).

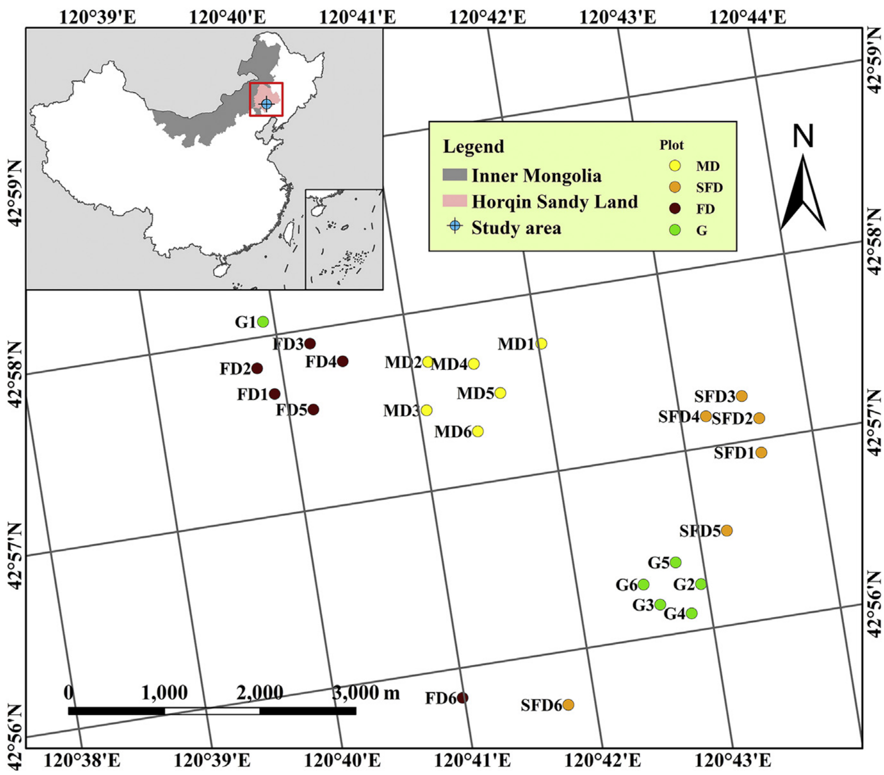

Fig. 1. Location of study area and the sampling sites.

Table 1
Characteristics of aboveground biomass, litter mass and carbon (C) and nitrogen (N) contents in aboveground biomass and litter at four successional stages (Mean ± SE, n = 6).

	Aboveground plant				Litter		
	Species richness	Biomass (g m^{-2})	C (g kg^{-1})	N (g kg^{-1})	Mass (g m^{-2})	C (g kg^{-1})	N (g kg^{-1})
MD	1.83 ± 0.17^a	2.20 ± 0.39^a	390.27 ± 2.67^a	23.15 ± 1.29^a	2.40 ± 1.05^a	443.04 ± 9.71^a	10.78 ± 0.81^a
SFD	6.53 ± 0.59^b	98.10 ± 7.27^b	418.13 ± 1.75^b	15.56 ± 0.19^b	63.75 ± 9.66^b	463.22 ± 3.81^a	7.83 ± 0.18^b
FD	10.23 ± 0.44^c	131.41 ± 8.20^c	407.59 ± 2.52^c	16.09 ± 0.41^b	71.88 ± 15.93^b	400.02 ± 11.43^b	9.85 ± 0.75^b
G	7.47 ± 0.60^b	190.38 ± 19.15^d	424.33 ± 0.82^d	16.61 ± 0.39^b	166.34 ± 12.07^c	409.65 ± 8.37^b	10.64 ± 0.40^a
F	52.33	50.93	51.74	25.35	37.12	11.13	5.16
P	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.01

MD, Mobile dune; SFD, Semi-fixed dune; FD, Fixed dune; G, Grassland; Different letters in mean values indicate statistical difference among habitats of sandy grassland restoration at $P < 0.05$.

Mobile dune had the lowest root biomass in the layer from 0 to 10 cm and the lowest root C content in the layer from 10 to 20 cm. Semi-fixed dune had the highest root C content in the layer from 0 to 10 cm, and grassland had the highest root biomass at three depths, 10–20 cm, 20–40 cm and 40–60 cm. Root biomass in the layer from 0 to 10 cm accounted for 47.9%, 69.0%, 59.2% and 54.7% of total root biomass (0–60 cm) in mobile dune, semi-fixed dune, fixed dune and grassland, respectively. Within each habitat type, root biomass in the layer from 0 to 10 cm significantly differed from the three other soil layers ($P < 0.05$), but there was no difference among the three other soil layers. Root biomass at each soil layer below 10 cm did not differ among mobile dune, semi-fixed dune and fixed dune ($P > 0.05$). No differences in root biomass C and N contents among four soil depths was found in any habitat type ($P > 0.05$).

3.2. Soil bulk density and C and N contents

Habitat, depth and their interaction had significant effects on soil bulk density, soil C and N contents (Fig. 2, $P < 0.001$). Soil bulk density in the layer from 0 to 10 cm significantly decreased with advancing sandy grassland restoration ($P < 0.001$). Soil bulk density in the layer from 40 to 60 cm among habitats was significantly different ($P < 0.05$), because soil bulk density in grassland was lower than the other three habitats. Soil C and N contents significantly increased with advancing sandy grassland restoration ($P < 0.001$), but the soil C and N contents below 10 cm did not differ between mobile and semi-fixed dunes ($P > 0.05$). Within the vertical profile, the late successional fixed dune and grassland habitats had significantly lower soil bulk density in the upper 10 cm ($P < 0.05$), while soil C and N contents showed a reverse trend ($P < 0.05$). The earlier successional habitats, the mobile and semi-fixed dunes, showed no significant pattern in bulk density or soil C and N content.

3.3. Allocation and storage of C and N in the ecosystem

Total ecosystem C and N differed significantly among the four successional habitats (Table 3, $P < 0.05$). As compared to the degraded mobile dune, the other habitats, semi-fixed dune, fixed

Table 2
Characteristics of carbon (C) and nitrogen (N) contents in belowground root biomass at four successional stages (Mean ± SE, n = 6).

	0–10 cm			10–20 cm			20–40 cm			40–60 cm		
	Biomass ($g\ m^{-2}$)	C ($g\ kg^{-1}$)	N ($g\ kg^{-1}$)	Biomass ($g\ m^{-2}$)	C ($g\ kg^{-1}$)	N ($g\ kg^{-1}$)	Biomass ($g\ m^{-2}$)	C ($g\ kg^{-1}$)	N ($g\ kg^{-1}$)	Biomass ($g\ m^{-2}$)	C ($g\ kg^{-1}$)	N ($g\ kg^{-1}$)
MD	11.00 ± 2.74^{aA}	424.29 ± 3.90^{aA}	10.95 ± 0.74^{acA}	3.08 ± 1.30^{aB}	408.88 ± 4.13^{aA}	11.82 ± 1.20^{aA}	5.02 ± 2.25^{aB}	401.66 ± 18.51^{aA}	11.64 ± 1.05^{aA}	3.87 ± 1.66^{aB}	402.27 ± 9.82^{aA}	12.26 ± 1.47^{aA}
SFD	112.98 ± 25.74^{bA}	452.67 ± 2.40^{bA}	7.77 ± 0.16^{bA}	19.43 ± 5.43^{aB}	445.11 ± 7.25^{bA}	7.83 ± 0.42^{bA}	18.93 ± 5.52^{aB}	439.93 ± 7.53^{aA}	10.33 ± 0.87^{aA}	12.37 ± 2.40^{aB}	432.51 ± 13.54^{aA}	13.23 ± 1.77^{aB}
FD	62.66 ± 18.91^{bA}	431.30 ± 3.00^{aA}	11.89 ± 0.34^{aA}	13.64 ± 1.74^{aB}	440.90 ± 6.07^{bA}	10.94 ± 1.06^{aA}	15.72 ± 2.50^{aB}	440.71 ± 6.14^{aA}	11.16 ± 1.26^{aA}	13.82 ± 2.98^{aB}	425.4 ± 8.91^{aA}	11.57 ± 1.11^{aA}
G	122.52 ± 28.97^{bA}	429.54 ± 3.40^{aA}	9.67 ± 0.52^{cA}	49.77 ± 9.66^{bB}	434.23 ± 2.73^{bA}	8.01 ± 0.67^{cA}	36.14 ± 7.16^{bB}	430.07 ± 4.61^{aA}	8.92 ± 0.73^{aA}	15.46 ± 4.12^{bB}	439.63 ± 4.13^{aA}	7.44 ± 0.39^{bB}
F	5.56	15.08	13.32	12.60	9.24	5.15	7.16	2.91	1.43	3.10	2.79	3.91
P	<0.01	<0.001	<0.001	<0.001	<0.001	<0.01	<0.01	>0.05	>0.05	<0.05	>0.05	<0.05

MD, Mobile dune; SFD, Semi-fixed dune; FD, Fixed dune; G, Grassland; Different lowercase letters in mean values indicate the statistical difference of same variable among different habitats at $P < 0.05$; Different capital letters in mean values indicate statistical difference of same variable among different depths in same habitat at $P < 0.05$.

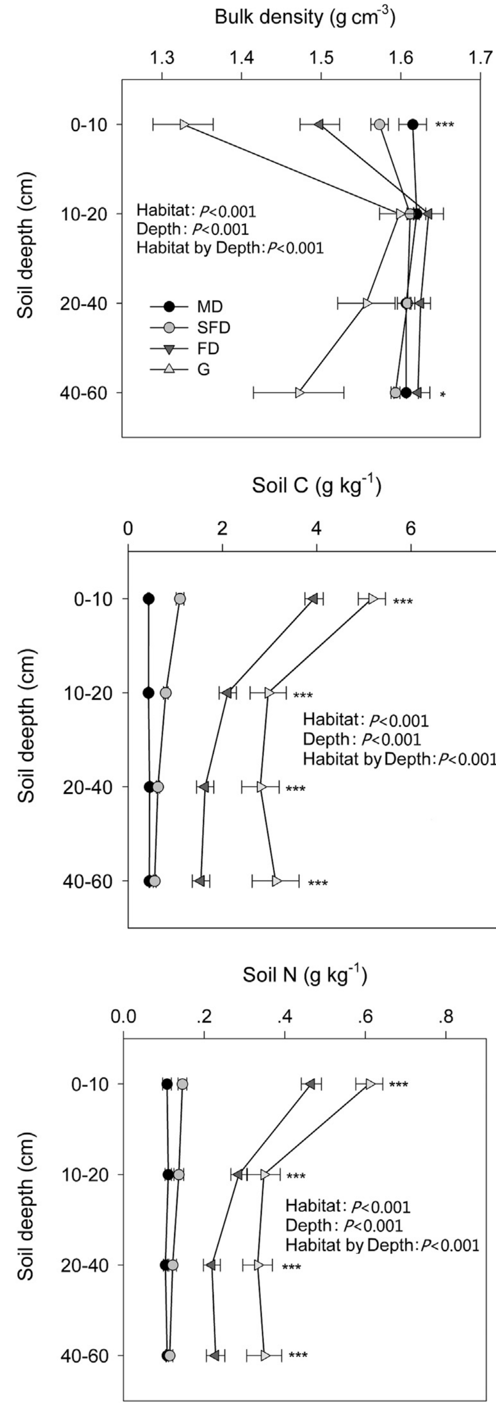

Fig. 2. Soil bulk density, carbon (C) and nitrogen (N) contents at four successional stages. MD, Mobile dune; SFD, Semi-fixed dune; FD, Fixed dune; G, Grassland. Values represent means ± standard errors (SE, n = 6). * and *** indicate significant levels of $P < 0.05$ and $P < 0.001$.

dune and grassland had 12.6, 11.4 and 21.4 times more C in the plant system; 8.2, 11.7 and 18.9 times more N in the plant system; 1.6, 4.6 and 6.7 times more C in the soil; 1.2, 2.5 and 3.3 times more N in the soil; 1.9, 4.8 and 7.1 times more total C; 3.3, 15.7 and 20.6 times more total N. The majority of C and N was stored in the soil in all four habitats; 97.7, 82.3, 93.7 and 92.0% of C and 99.7, 97.6, 98.4 and 98.0% of N in mobile dune, semi-fixed dune, fixed dune and grassland. Aboveground plant C and N storage also increased with

Table 3
Carbon (C) and nitrogen (N) storage in the plant–soil system at four successional stages (Mean ± SE, n = 6).

	C Storage (g m^{-2})				N storage (g m^{-2})			
	MD	SFD	FD	G	MD	SFD	FD	G
Plant	0.85 ± 0.15^{a}	43.17 ± 3.72^{b}	57.33 ± 3.86^{c}	84.77 ± 8.79^{d}	0.06 ± 0.01^{a}	1.12 ± 0.07^{b}	2.23 ± 0.17^{c}	3.15 ± 0.37^{d}
Litter	1.02 ± 0.42^{a}	29.74 ± 4.53^{b}	29.49 ± 7.19^{b}	68.15 ± 5.27^{c}	0.03 ± 0.01^{a}	0.50 ± 0.08^{b}	0.76 ± 0.24^{b}	1.77 ± 0.13^{c}
Subtotal aboveground	**1.87 ± 0.54^{a}**	**72.92 ± 7.14^{b}**	**86.81 ± 9.85^{b}**	**152.91 ± 9.7^{c}**	**0.08 ± 0.02^{a}**	**1.62 ± 0.12^{b}**	**2.99 ± 0.32^{c}**	**4.92 ± 0.33^{d}**
Root (0–60 cm)	9.77 ± 3.19^{a}	73.53 ± 14.75^{bc}	45.77 ± 9.39^{ac}	96.3 ± 17.66^{b}	0.28 ± 0.11^{a}	1.36 ± 0.25^{b}	1.27 ± 0.35^{b}	1.93 ± 0.34^{b}
Plant system	**11.64 ± 3.72^{a}**	**146.44 ± 18.82^{b}**	**132.58 ± 18.93^{b}**	**249.21 ± 16.37^{c}**	**0.36 ± 0.13^{a}**	**2.99 ± 0.32^{b}**	**4.26 ± 0.64^{b}**	**6.85 ± 0.49^{c}**
Soil (0–60 cm)	431.44 ± 9.66^{a}	683.87 ± 36.16^{a}	1973.47 ± 176.60^{b}	2880.96 ± 212.09^{c}	103.79 ± 2.61^{a}	120.83 ± 7.68^{a}	262.53 ± 19.78^{b}	337.42 ± 21.01^{c}
Plant–Soil system	**443.07 ± 10.32^{a}**	**830.32 ± 33.59^{a}**	**2106.04 ± 162.45^{b}**	**3130.17 ± 212.55^{c}**	**104.15 ± 2.51^{a}**	**123.82 ± 7.56^{a}**	**266.78 ± 19.31^{b}**	**344.27 ± 20.83^{c}**

MD, Mobile dune; SFD, Semi-fixed dune; FD, Fixed dune; G, Grassland; Different letters in from mean values indicate statistical difference among different habitats at $P < 0.05$. Plant system included plant, litter and root.

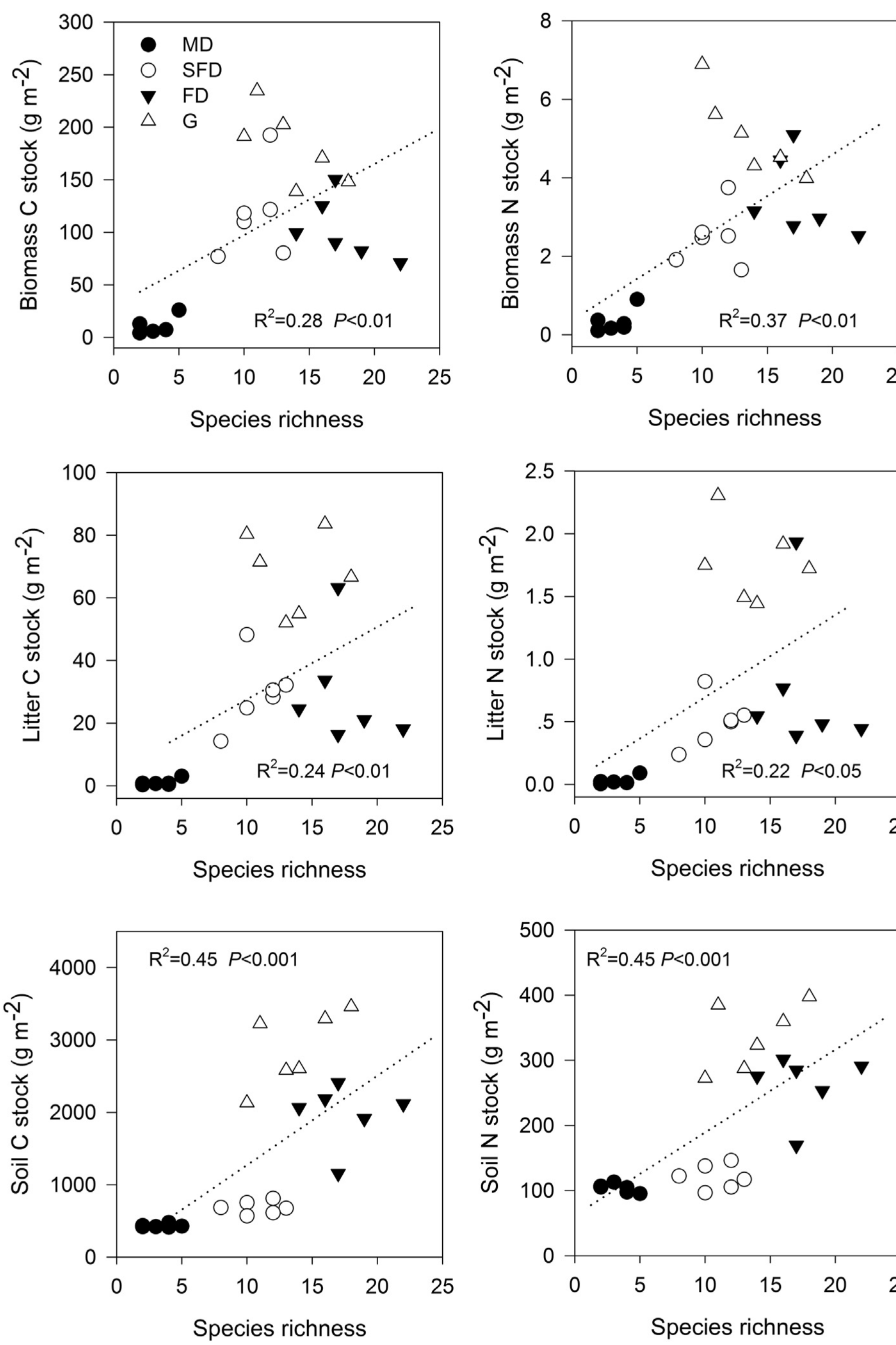

Fig. 3. Linear regression analyses between species richness and C and N stock in biomass (aboveground plant and root at depth of 0–60 cm), litter and soil (0–60 cm). MD, Mobile dune; SFD, Semi-fixed dune; FD, Fixed dune; G, grassland.

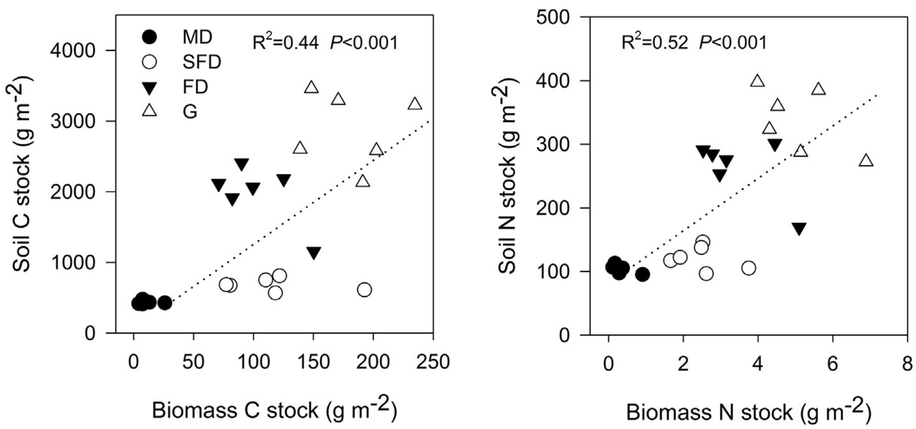

Fig. 4. Linear regression analyses of C and N stock between soil and biomass (aboveground plant and root at depth of 0–60 cm). MD, Mobile dune; SFD, Semi-fixed dune; FD, Fixed dune; G, grassland.

advancing sandy grassland restoration ($P < 0.05$), but there was no pattern in the root C and N.

3.4. Relationship between species richness and storage allocation of C and N in the ecosystem

Overall, we found a positive relationship between species richness and C or N storage in plant and root biomass, litter and soil with advancing sandy grassland restoration (Fig. 3, $P < 0.01$). C and N storage in the soil was positively correlated with the C and N storage in plant and root biomass, respectively (Fig. 4, $P < 0.01$).

4. Discussion

We found that species richness, plant biomass and litter mass consistently increased from mobile dune to fixed dune. However, root biomass and C and N contents of plant, litter and root did not consistently increase, which may be caused by the changes in dominant species in the four successional habitats. Compared to mobile dune and fixed dune, semi-fixed dune with the dominant shrub (A. *halodendron*) had a higher C content in aboveground plant and roots (0–10 cm). Aboveground plant biomass in semi-fixed dunes was lower than that in fixed dune and grassland, whereas root biomass did not differ, suggesting that the dominant shrub in semi-fixed dunes, A. *halodendron*, allocated more biomass into belowground roots. Mobile dune had a higher plant and litter N as compared to the two other dune habitats, because the dominant pioneer species, *A. squrrosum*, has a higher leaf N content and a smaller specific leaf area. These are adapted to environments with barren soils, high light incidences and strong wind erosion (Li et al., 2005).

Our results show that soil C and N increased from mobile dune to grassland, while soil bulk density at upper 10 cm decreased (Fig. 2). This is consistent with previous studies that show that habitat restoration can improve the soil environment, though this soil improvement here primarily affects in the upper 10 cm (Guo et al., 2008; Li et al., 2013; Liu and Yan, 2010; Zuo et al., 2014). Wolkovich et al. (2010) have found that herbaceous plants litter and dead roots are linked with an increase in soil carbon and nitrogen storage, and several other studies similarly have found that increased plant biomass increases soil C and N content (Fornara and Tilman, 2008; Peichl et al., 2012). Our study also shows that plant biomass is positively correlated with the soil C and N content.

In agreement with our hypothesis, mobile dune stabilization and habitat restoration via grazing exclusion leads to increased ecosystem C and N pools. Thus, sandy dune restoration has the potential to sequester C and N in these semiarid sandy grasslands, as shown in other studies (Pei et al., 2008; Su et al., 2003; Wu et al., 2010).

The last two successional stages, fixed dune and grassland, had the highest ecosystem C and N storage (Table 3). Zhou et al. (2008) has reported that grassland desertification in the last century has resulted in 107.5 Mt ecosystem C and 10.0 Mt N losses (0–100 cm deep). Sandy dunes (mobile, semi-fixed and fixed dunes) cover 24.1% of the total area, or 30,198.87 km^2 (in 2010) (Duan et al., 2013). If we assume that all sandy dunes will transform grasslands, total ecosystem C and N storage will reach 52.84 and 5.81 Mt.

In all study sites, 82–97% of C and N storage was in the soil (Table 3), suggesting that soil is an important location for C and N sequestration in grassland ecosystems (Lal, 2003; Preger et al., 2010; Wu et al., 2010). This likely occurs due to inputs from litter decomposition and root-decay processes (Kemp et al., 2003; Knops et al., 2007). Sandy grassland restoration should lead to a state where C and N inputs are greater than losses. From our results and other studies on C and N sequestration in semiarid and arid grasslands (Li et al., 2012; Nosetto et al., 2006; Preger et al., 2010) we predict that sandy grassland restoration in this region has the potential to result in significant C and N storage.

Our study supports the hypotheses that ecosystem C and N sequestration is strongly associated with plant C and N biomass production, which over time results in soil C and N sequestration. Increased plant biomass increases above- and belowground litter inputs and over time results in soil C and N sequestration (De Deyn et al., 2008; Wu et al., 2010). Across the restoration gradient, our study also shows that plant diversity is associated with increased soil C and N storage (Jiang et al., 2011; Steinbeiss et al., 2008). However, since the dominant species and plant biomass also differ across the restoration gradient, experimental studies are need to disentangle species richness, species identity and community productivity impacts on ecosystem C and N sequestration.

Within our sandy grasslands, mobile dunes are characterized by uniform low soil C and N. Semi-fixed dune are characterized by shrubs and shrubs in arid and semiarid ecosystem can cause “islands of fertility” with spatial patterns of C and N distribution across the landscape (Su et al., 2004; Zhao et al., 2007). Shrub-induced increases in soil fertility and altered microclimate under their canopies may facilitate herbaceous species colonization (Zuo et al., 2009). Thus, the spatial concentration of C and N in the semi-fixed dune stage may be a key step to allow later successional herb species to establish in the semi-fixed dune stage. Subsequently, these herbs established in the "islands of fertility" under shrub vegetation in semi-fixed dunes can spread into the herb dominated vegetation of the fixed dunes and grasslands communities with a spatial uniform soil C and N distribution (Zhang et al., 2005; Zhao et al., 2007; Zuo et al., 2009).

5. Conclusions

Our study illustrates large changes in biomass allocation and ecosystem C and N storage along a successional sequence during sandy grassland restoration. C and N storage in plants and soil, as well as species richness, aboveground biomass, litter mass and soil C and N content, increased with advancing sandy grassland restoration. Soil contains the majority of ecosystem C and N in all four restoration stages. Species richness is positively associated with the higher C and N storage in plant and root biomass, litter and soils, and plant C and N pools are positively associated with soil C and N pools. Therefore, increased species richness and biomass likely enhance ecosystem C and N sequestration in sandy grassland ecosystems.

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