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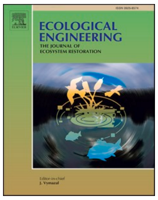

Wind disturbance on litter production affects soil carbon accumulation in degraded sandy grassland

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ABSTRACT

Plant litter derived from the living biomass is the primary source of soil carbon (C). However, the contribution and the mechanism of plant litter production to soil C remains uncertain in aeolian regions. In this study, the relationship between plant biomass, litter mass, and soil C content was analyzed after a spatial field investigation in Horqin sandy land, northeast China. Long-term monitoring of wind speed and plant litter production was also conducted in three habitats (mobile dune, semi-fixed dune, and fenced grassland). The soil C content was significantly affected by belowground biomass and belowground litter mass but not aboveground biomass and aboveground litter. The litter production in the desertified habitat (mobile dune and semi-fixed dune) significantly differed with that of the undesertified habitat (fixed dune and fenced grassland). In mobile dune, 38% of the aboveground primary production was lost, while there was a distinct enrichment of plant litter in semi-fixed dune and fenced grassland. Wind events (wind speeds of 7 and 8 m s^{-1}) at the end of the growing season significantly affected litter production rate, and wind was a major driver for litter transportation between habitats. In summary, plant litter production can be affected by wind events, and this influence differs among habitats in degraded grassland, leading to spatial heterogeneity of soil C accumulation. These results can strengthen the understanding of the relationship between soil properties and plant litter production in aeolian regions and furthermore, can provide information for ecological restoration of different types of desertified land, especially for the soil C accumulation.

1. Introduction

Arid and semi-arid regions are major climatic regions in the terrestrial ecosystem, comprising 47.2% of the world's land, and they also represent an important functional unit for carbon (C) storage in terrestrial ecosystems (FAO, 2004; Lal, 2009). Vegetation is considered as a key factor of the C cycle and the fluctuation of vegetation productivity is a controlling factor in the change of C storage in arid and semi-arid regions (Li et al., 2017). In addition, because of the low vegetation production, species diversity and soil nutrient content, alongside strong soil wind erosion and high human utilization intensity in arid and semi-arid areas, the vegetation is sensitive to human activities and climate change, and the plant productivity varies with high fluctuation, thus, the source–sink relationship for ecosystem C in the plant–soil system is also unstable (Knapp et al., 2002; Frank et al., 2015). For example, the global desertification caused by climate change and increased human activities led to a total loss of 19–29 Pg C from the plant–soil continuum (Lal, 2001). Li et al. (2006) showed that the ecosystem C storage decreased from 2186.7 to 516.9 g m^{-2} during fixed dune desertification. In contrast, some reasonable protections such as livestock exclusion can lead to a rapid accumulation of C and rapid desertification restoration. Taking the Naiman Banner for instance, located in southern part of the Horqin sandy land, northeast China, desertified area declined from 69.5% in the 1970s (Wang, 1989) to 46.8% in 2010 (Duan et al., 2014)

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because of a series of government protections and the change of land use patterns.

In semi-arid sandy grasslands, vegetation is a key factor in the ecosystem C cycle. The ecosystem C loss caused by vegetation usually occurs through two processes. The direct process involves the large amount of C loss from vegetation degradation (Li et al., 2006; Zuo et al., 2009). The second process relates to soil C loss via the transformation of the fine particulate matter in soil caused by enhanced wind erosion (Su and Zhao, 2003; Li et al., 2005; Zhao et al., 2007). The soil wind erosion was strongly suppressed by vegetation cover (Zhang, 2003; Li et al., 2005). It has been shown that the fine particulate matter was the major component of soil C storage in degraded sandy grassland, and its transformation was the major pathway of soil C loss during wind erosion (Su et al., 2004; Zhao et al., 2007). Thus, beneficial measures for vegetation restoration such as grazing exclusion or plantation can lead to the rapid increase of the ecosystem C. For example, the amount of C sequestered at 0–20 cm soil depth increased from 146.1 to 962.7 g m^{-2} after 26 years of grazing exclusion in Horqin sandy land (Li et al., 2012). The shrub *Caragana microphylla* enhanced the soil organic C storage (0–100 cm) by 88%, 74%, and 145% at 9, 15, and 31 years after plantation in Horqin sandy land, respectively (Li et al., 2017).

The terrestrial ecosystem C cycle depends on C sequestration via photosynthesis, C release via plant litter, and soil C decomposition via respiration (Luo et al., 2015; Cai et al., 2020). Organic C inputs into soil are derived from aboveground organic matter sources, including leaves, twigs, seeds, and coarse woody debris, as well as belowground inputs from roots, root exudations of C compounds, and organic matter from the rhizospheric microbial community (Nadelhoffer et al., 2004; Ekberg et al., 2007; Bowden et al., 2014). Litter dynamics is a critical biogeochemical process that controls soil organic matter formation and nutrient release, affecting atmospheric CO_2 concentrations, plant growth, and C accumulation (Cai et al., 2020). Conceptually, litter production is one of the most important pathways for soil C accumulation, and plant litter is derived from the falling of plant organs storing large amounts of photosynthesis products (Björn Berg and McClaugherty, 2003; Bowden et al., 2014). The amount of plant litter mass is a controlling factor on soil C concentration, and theoretically there would be a linear relationship between the soil C content and the litter or the aboveground net primary production (Bowden et al., 2014). However, there is little experimental evidence to support the assumption of a strong relationship between plant litter inputs and soil C accumulation (Lajtha et al., 2014). Even in field observations, a significant relationship is rare and the explanation proportion among the litter amounts or the aboveground net primary production to soil C content is typically low (Hashimoto et al., 2011; Agostini et al., 2015).

Litter production is affected by many factors such as phenology, vegetation type, and climate (Bray and Gorham, 1964; Scherer-Lorenzen et al., 2007). For example, in forest ecosystems, especially in the high-latitude taiga forest, litter yield is relatively low compared with aboveground primary productivity or aboveground biomass, and only a few organs fall (e.g. needle, fruit, and deadwood) to the surface and become plant litter (Chale, 1996; Schimel et al., 1999; Yanai et al., 2012). In contrast, for the herbs, especially annual species, most or all of the organs fall off at the end of the growing season and become plant litter (Henry et al., 2008; Liu et al., 2012). The process of plant organs falling to the soil surface is affected by factors such as climate and topography. For example, in Mauna Loa tropical rainforest, the litter production was negatively correlated with the increase of latitude (Raich et al., 1997). This relationship was also observed in rainforest located in Malaysia (Veneklaas, 1991; Kitayama and Aiba, 2002). However, the existing research has mainly focused on forest ecosystems, and to our knowledge, no studies have been carried out in semi-arid sandy grassland, in which the wind and sand activity are both strong.

Wind is one of the key factors affecting litterfall and litter distribution. Wind speed was considered as a driving factor on plant litter production. This relationship have been fully evidenced in forest ecosystem (Welbourn et al., 1981; Staelens et al., 2003; Hasanuzzaman and Hossain, 2014; Kamruzzaman et al., 2016). However, related studies in semi-arid degraded grassland are still rare (Wang et al., 2016). Wind can directly influence the production of litter. For example, the strong wind events at the end of the growing season can promote the formation of plant litter via the rapid falling of the organs or other necromass from the branches. Moreover, the strong wind events affect the distribution of the litter present at the soil surface (Wang, 2016). In addition, the varied roughness of underlying surfaces can also affect the intensity of surface wind erosion (Li et al., 2005), and thereby affect the influence of wind events on litter redistribution. Therefore, it can be speculated that the litter production ratio from the in-situ vegetation is large in areas with high vegetation coverage, because of the blocking effect of living plants or standing litter on litter movement, and some of the litter transported by wind may be captured. Moreover, the stability of the litter–soil system is high, which benefits material transformation. Accordingly, in areas of low vegetation coverage, the produced plant litter may be transported to varying degrees by strong wind events. Thus, we hypothesized that, in aeolian regions, there would be a distinct source or sink for plant litter in different habitats because of the heterogeneity of the surface landscape (especially in terms of vegetation).

In semi-arid degraded grassland, there remains no clear description of the influence of wind events on litter production. One possibility we speculated is that wind events may affect litter distribution during the litterfall season (i.e. at the end of the growing season), because litter is more affected by the wind when falling. Another possibility is that windy events affect litter redistribution throughout the non-growing season because this period is relatively long and there are many wind events with high speed during this period. Identifying the critical period in which the wind events affect plant litter production is necessary for human intervention on ecosystem restoration (especially for the soil C and soil nutrition) in areas of low vegetation coverage. The extent to which the wind speed affects litter distribution also remains unclear. Determination of the threshold of the wind speed affecting litter distribution could further facilitate manual interventions.

Therefore, the aims of this study were as follows: 1) to clearly describe the distribution patterns of the litter amount, the biomass, the soil C contents and their correlation in aeolian regions of Horqin sandy land through the analysis of field survey data; 2) to clarify the difference of the plant litter production among habitats by analysis of the relationship between biomass and litter amount; and 3) to determine the critical period and wind speed threshold for the impact of wind events on litter production or distribution in aeolian regions. This study would strengthen the understanding of the relationship between soil properties and plant litter production in aeolian regions, and thereby provide information for ecological restoration, especially for the soil restoration in areas of low vegetation coverage.

2. Material and method

2.1. Study site

Our study took place at the Naiman Desertification Research Station of the Chinese Academy of Sciences (42°58′N, 120°43′E; altitude 360 m a.s.l.), located in the Naiman Banner of Tongliao City, in the eastern part of the Inner Mongolia Autonomous Region of China. The region belongs to the cold temperate zone, with a semi-arid continental monsoon climate. Annual mean precipitation from 1971 to 2015 averaged 335 mm. The annual mean temperature is about 6.7 °C and the annual evaporation ranged from 1500 to 2500 mm. The average annual wind speed ranges from 3.4 to 4.5 m s^{-1}, but the mean wind speed during the non-growing season (October to April) with the most severe wind erosion ranges from 5.0 to 10.0 m s^{-1}. There were 16.2 wind events with a speed over 10 m s^{-1} (2-min mean wind speed per hour) between 2007 and 2016. These severe and intensive wind events accelerated some biotic or abiotic processes including land desertification (Zhu and Chen, 1994), wind erosion (Li et al., 2005; Zhao et al., 2010), and plant litter redistribution (Wang, 2016). The soil is classified as sandy chestnut soil according to the Chinese soil classification system, which is mostly equivalent to the Orthi-sandic Entisols of sandy origin in terms of the FAO-UNESCO system (Li et al., 2011). Soil C comprised 1.04 g kg^{-1} organic C (determined using the Walkley–Black dichromate oxidation procedure) and 0.07 g kg^{-1} inorganic C ($CaCO_3$, determined using the volumetric method) in grazing exclosure plots at 0–10 cm soil depth (Li et al., 2011). This region includes a wide variety of landscape types because of intensive land use (particularly overgrazing) in the last century, a series of governmental protection programs in recent decades, and climatic fluctuations. The desertified area accounted for 69.5% of the total area of Naiman Banner by the late 1970s, when the region's landscape became dominated by mobile dunes (Wang, 1989), while the desertified area in 2010 declined to 46.8% and the severely desertified area (vegetation coverage of <30%) was 12.9% (Duan et al., 2014). Although vegetation in this region varies with habitat, the vegetation is dominated by annual species (Zuo et al., 2009). This vegetation character combined with strong wind events in winter, led to a distinct litter flux among habitats (Wang, 2016).

2.2. Experimental design and sampling

2.2.1. Experiment 1

At the peak of the growing season of 2018 (mid-July to the end of August), 210 plots in Naiman banner were selected for investigation, including four habitats: mobile dune (MD), semi-fixed dune (SFD), fixed dune (FD), and fenced grassland (G). Details of this classification are shown in Zhao et al. (2008) and Luo et al. (2016). Sample sizes and detailed descriptions of each habitat are given in Table 1. In each plot, the living plant in a quadrat with a size of 1 m × 1 m was clipped along the ground as the aboveground biomass (AB). Then the dead plant body including the standing litter and surface litter was in each quadrat was collected as the aboveground litter (AL). Belowground samples at 0–10 and 10–20 cm soil depth were collected by a soil auger (diameter 100 mm). In each quadrat, we collected three samples and mixed them together in every layer; these mixed samples were taken into the laboratory and washed with tap water, then the live roots (which had lighter colors and higher elasticity) were chosen by hand as the belowground biomass (BB) and the remaining necromass was classified as the belowground litter (BL). After the belowground sample collection, soil samples of each layer (0–10 and 10–20 cm) were collected with a thinner soil auger (diameter 28 mm). In each quadrat, we collected 5–7 samples and mixed them together for each layer.

Table 1
Detailed description of habitats of mobile dune (MD), semi-fixed dune (SFD), fixed dune (FD), and grassland (G) in this study.

Habitat	Sample size	Soil Crust	Vegetation Cover	Note
MD	81	No or a little soil crust and 100% shifting sand.	0–30%	If the land surface is covered by shifting sand and vegetation cover is 30%–60%, it is an MD.
SFD	69	10%–30% biological crust or even more physical crust, 70%–80% shifting sand.	30%–60%	If soil crust is <30%, even the vegetation cover ranges from 30%–60%, it is an SFD.
FD	40	>80% soil stratum or crust, and < 20% shifting sand.	60%–100%	If soil crust is 100% and vegetation cover is less than 60%, it is an FD.
G	20	No shifting sand.	90%–100%	The land surface is covered with plants or litter.

2.2.2. Experiment 2

To further understand the relationship between wind traits and plant litter production, we used the data from a long-term monitoring program conducted at Naiman Desertification Research Station (http://nmd.cern.ac.cn/). In this program, three types of habitats with varying degrees of desertification (MD, FD, and G) were targeted for monitoring, and many ecological parameters were measured for 20–30 years. The AL data in April from 2007 to 2016 and AB data in August from 2006 to 2015 were analyzed in this study. They were produced with ten quadrats with a size of 1 m × 1 m as replication in each habitat. The sampling process of AL and AB was the same as Experiment 1.

2.3. Measurements

All parts of the mass (including aboveground biomass, aboveground litter mass, belowground biomss and belowground litter mass) of each quadrat were weighed after oven-drying at 65 °C for 48 h. The soil samples were sieved at 2 mm and gravel, litter, and live and dead roots were removed after air-drying in the shade. The soil C content was measured by an elemental analyzer (Vario Macro cube, Elementar, Germany). The climate data was collected from a nearby automatic meteorological station, located near the center of our study area. Wind events of various speeds from 4 to 11 m s^{-1}) in the non-growing season (October to the April of the next year) from 2006 to 2016 were recorded for analysis.

2.4. Statistical analysis

Statistical analysis of the data was conducted using version 20.0 of the SPSS software (www.ibm.com/software/analytics/spss/). Differences among habitats for aboveground mass (i.e. biomass and litter mass) were tested by means of multiple comparisons using the least significant difference (LSD) test whenever one-way ANOVA indicated a significant difference among habitats ($P < 0.05$). We analyzed differences in the belowground litter mass, belowground biomass, and soil C content among four habitats (H) and two layers (L) by means of two-way ANOVA with H and L as factors. We performed multiple comparisons using the LSD test whenever the ANOVA indicated a significant difference ($P < 0.05$). We used the stepwise regression analysis to test the relationship between soil C content and dry matter. The relationships between AB and litter (including AL and BL) among desertified (including the MD and the SFD) and undesertified (including the FD and G) habitats were described with a general linear model after natural logarithmic transformation.

To test the influence of wind events on plant litter production, we determined the parameter of litter production rate (LPR), to describe how much litter was present before the growing season (end of April) divided by the aboveground primary productivity (the aboveground green biomass in the previous August). Then we compared the difference of LPR among three habitats (MD, FD, and G) by means of multiple comparisons using the LSD test whenever one-way ANOVA indicated a significant difference among habitats ($p < 0.05$). The relationship between LPR in each habitat and wind events at different speeds (4–11 m s^{-1}) was tested by Pearson correlation analysis. To further understand the relationship between wind events and LPR at the beginning period of litter production (October, in when all species dead and the wind become strong), a linear regression analysis was conducted between wind events with wind speeds of 7 and 8 m s^{-1} (because of the significant correlation coefficients) and LPR, respectively.

3. Results

3.1. Patterns of biomass, litter, and soil C distribution

The aboveground biomass increased gradually but significantly ($p < 0.01$) from MD to G. In MD, aboveground biomass was only 49.90 g m^{-2}, whereas it was 175.84 g m^{-2} in G (Fig. 1a). The aboveground litter masses in G and FD were significantly higher ($p < 0.01$) than those in MD and SFD. In MD and SFD, aboveground litter masses were relatively lower (21.51 and 14.61 g m^{-2} in MD and SFD, respectively) and there was no significant difference among MD and SFD (Fig. 1a).

The belowground litter mass varied among both habitats and depth, and there was a significant interaction among these two factors for the belowground litter mass ($F_{interaction} = 8.259$, $p < 0.001$). The belowground litter mass at 0–10 cm soil depth was significantly higher ($p < 0.05$) than that at 10–20 cm in all habitats. At 0–10 cm soil depth, belowground litter mass increased from MD to G, and was significantly higher ($p < 0.05$) in G than that in other habitats. At 10–20 cm soil depth; however, the belowground litter mass varied little among habitats, except for FD, which was significantly higher ($p < 0.05$) than that in other habitats (Fig. 1b).

The belowground biomass also varied with both habitat and depth; however, the interactive effect between these two factors was not significant ($F_{interaction} = 2.036$, $p = 0.089$). At both soil depths, the belowground biomass increased from MD to G. Moreover, the belowground biomass at 0–10 cm soil depth was significantly higher ($p < 0.05$) than that at 10–20 cm in SFD and G (Fig. 1c).

The soil C content varied among both habitats and depth, and also there was a significant interaction among these two factors ($F_{interaction} = 4.833$, $p < 0.001$). The soil C content increased from MD to G in both layers, and was significantly higher ($p < 0.05$) at 0–10 cm than at 10–20 cm soil depth in all habitats except FD (Fig. 1d).

3.2. *Relationship between soil C and dry matter*

Stepwise regression analysis (Table 2) indicated that soil C content at 0–20 cm soil depth was significantly affected by the aboveground biomass, the belowground biomass, and the belowground litter mass. The aboveground litter played insignificant effect on soil C content. Further analysis demonstrated that, in both layers, soil C content was only significantly affected by the belowground biomass and the belowground litter mass. Furthermore, the explanation ratio of these two factors on soil C content was relatively low, especially at 10–20 cm soil depth. The belowground biomass and the belowground litter mass accounted for 41.0% and 19.5% of the variance in soil C content at 0–10 and 10–20 cm soil depth, respectively.

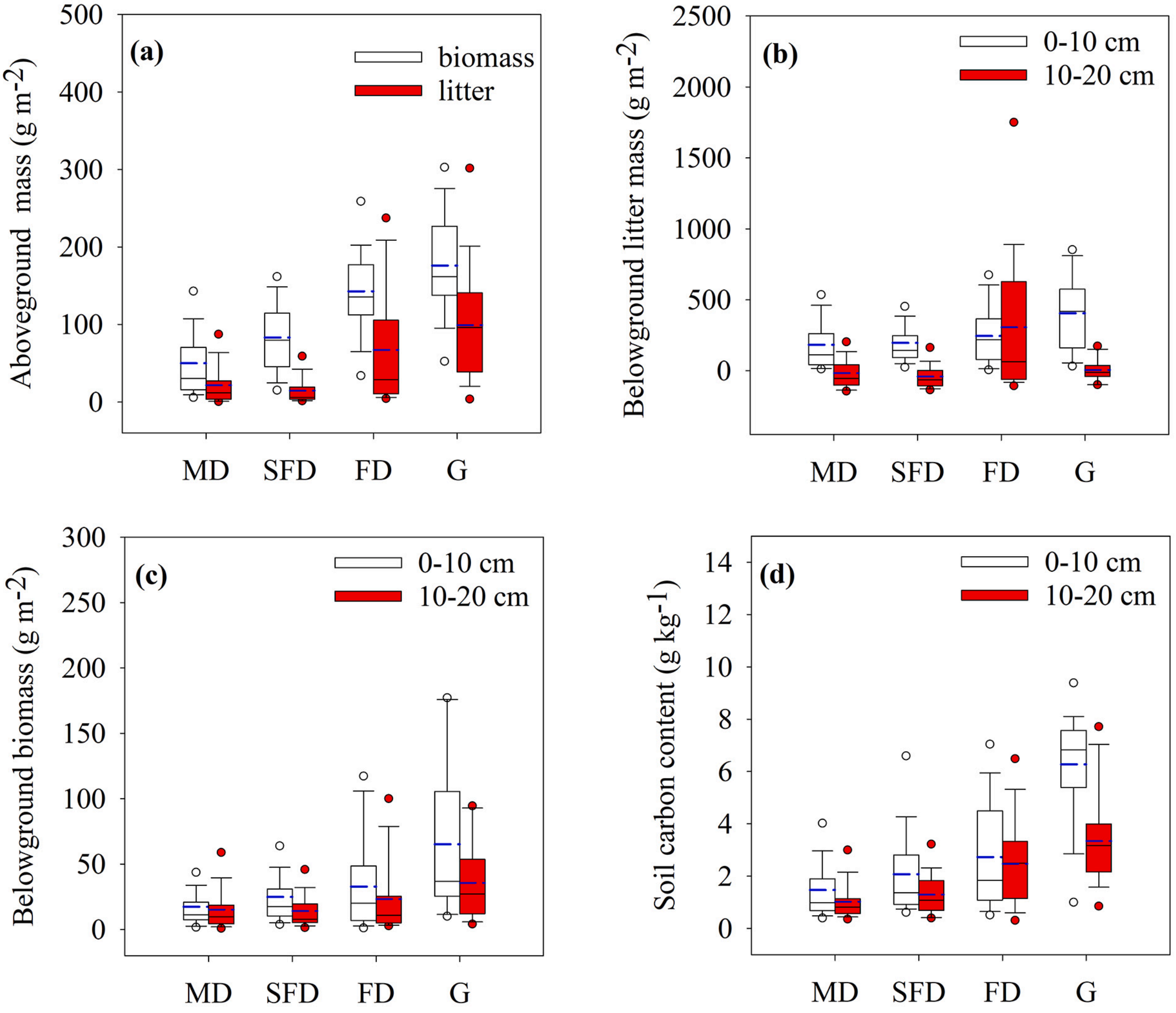

Fig. 1. Aboveground biomass (a), belowground litter mass (b), belowground biomass (c) and soil carbon content (d) for mobile dunes (MD), semi-fixed dune (SFD), fixed dunes (FD), and fenced grassland (G). Box plot labeled with different letters differ significantly (one-way ANOVA followed by LSD test, $P < 0.05$). Ranges represent the 5th percentile to the 95th percentile, boxes represent the 25th to 75th percentiles, and blue dash lines represent the mean value. In (a) the lowercase and capital letters represent differences of the biomass and litter mass, respectively. In (b), (c), and (d) the lowercase and capital letters represent differences at 0–10 cm and 10–20 cm, respectively, the underlined asterisks represent the significant differences at $P < 0.05$ among soil depths. Ranges represent the 5th percentile to the 95th percentile, boxes represent the 25th to 75th percentiles, and green dash lines represent the mean value. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2

Stepwise regression analysis of soil carbon (C) contents at 0–10 and 10–20 cm soil depth and related factors. AB, BB, and BL indicate the aboveground biomass, the belowground biomass, and the belowground litter mass, respectively.

ID	Parameter	Equation	R^2	*F*	*P*
1	$C_{0\text{-}20}$	$Y = 0.334 + 0.011AB + 0.007BB + 0.001BL$	0.457	59.256	< 0.001
2	$C_{0\text{–}10}$	$Y = 0.738 + 0.005BL + 0.019BB$	0.410	66.037	< 0.001
3	$C_{10\text{–}20}$	$Y = 1.062 + 0.003BL + 0.013BB$	0.195	22.911	< 0.001

3.3. Relationship between dry matter biomass and litter

There was a significant linear relationship between aboveground biomass and aboveground litter mass for both desertified ($R^2 = 0.220$) and undesertified ($R^2 = 0.347$) habitats. The slope of the regression line was 0.66 for the desertified habitat and 1.66 for the undesertified habitat, and the interaction among these two habitats were both significantly ($P < 0.05$). This indicates that the pattern for aboveground litter production in desertified and in undesertified habitat differed significantly, and the aboveground litter increased faster in the undesertified habitat than in the desertified habitat through the increase of aboveground biomass (Fig. 2a). A similar linear relationship was also observed for the belowground litter mass (Fig. 2b).

3.4. Litter production and its response to wind events

The ten years of monitoring data showed that litter production rate varied significantly among habitats ($F = 18.696$, $p < 0.001$), with values of 61.83%, 287.57%, and 271.82% for MD, FD, and G, respectively (Fig. 3). In MD, only 61.83% of the aboveground primary production remained at the soil surface as aboveground litter before the next growing season (end April), and thus about 40% of the aboveground primary production was transformed. In contrast, the aboveground litter present before the growing season was 2.88 and 2.72 times the aboveground primary production of the former growing season for FD and G, respectively. This indicates that there was a distinct enrichment of aboveground litter in FD and G, suggesting that litter mass from other places was transported into FD and G.

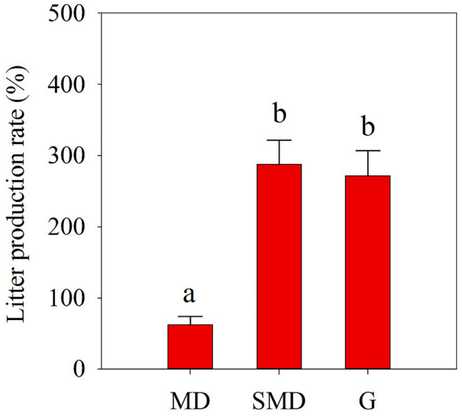

Fig. 3. Litter production rate (i.e. litter mass present at the soil surface before the growing season at the end of April divided by the aboveground primary productivity, which was presented by the aboveground green biomass in the previous August) for mobile dunes (MD), fixed dunes (FD), and fenced grassland (G). Box plot labeled with different lowercase letters differ significantly (one-way ANOVA followed by LSD test, $P < 0.05$). Ranges represent the 5th percentile to the 95th percentile, boxes represent the 25th to 75th percentiles, and green dash lines represent the mean value. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Correlation analysis showed that the litter production rate was affected by wind events (Table 3), and this effect varied among habitats and times. In MD, the Pearson's correlation coefficient was consistently non-significant, whereas in FD, wind events with speeds of 5–6 m s^{-1} only were significantly negatively ($p < 0.05$) correlated with the litter production rate. In G, some Pearson's correlation coefficients were positive before February and negative in March, but only significant ($p < 0.05$) at the speed of 4 m s^{-1}.

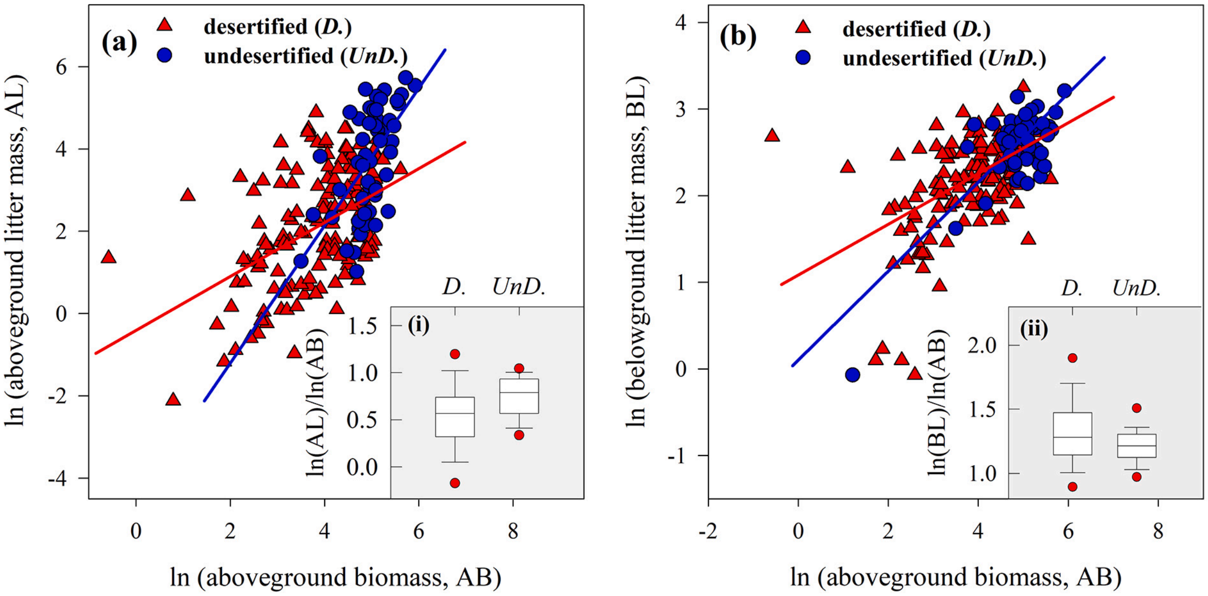

Fig. 2. Linear regression between aboveground biomass and aboveground litter mass (a) or belowground litter mass (b). The red triangle and the blue circle represent the relationship for desertified and undesertified habitats respectively. The box plots at the bottom right of each figure represent the ratio of aboveground biomass (i) and belowground litter mass (ii) to aboveground biomass in desertified and non-desertified habitats. Ranges represent the 5th percentile to the 95th percentile, boxes represent the 25th to 75th percentiles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 3
Pearson's correlation coefficients among frequency of wind events with different speed and litter production rate among different month in three habitats: mobile dune (MD), semi-fixed dune (SFD), and fenced grassland (G). Asterisk represents significance at $P < 0.05$, $n = 10$.

Habitat	Time	Wind speed ($m\ s^{-1}$)							
		4	5	6	7	8	9	10	11
MD	Oct	0.307	0.183	0.196	0.278	0.226	0.388	0.246	0.298
	Nov	0.515	0.388	0.395	0.271	0.279	0.141	0.315	0.315
	Dec	0.55	0.48	0.393	0.094	−0.064	−0.055	0.055	0.055
	Jan	0.074	0.05	0.074	0.032	0.018	−0.175	−0.089	−0.089
	Feb	−0.147	−0.238	−0.325	−0.031	0.089	0.133	0.065	0.065
	Mar	0.247	0.178	0.123	−0.115	−0.116	−0.155	−0.147	−0.147
	Apr	−0.012	0.088	0.207	0.244	0.104	−0.017	0.119	0.072
SFD	Oct	−0.07	−0.167	0.22	0.442	0.447	0.539	0.328	0.415
	Nov	0.171	0.169	0.225	0.024	0.099	−0.017	0.449	0.449
	Dec	0.477	0.510	0.495	0.437	0.353	0.526	0.615	0.615
	Jan	0.111	0.083	0.188	0.111	−0.018	−0.237	−0.045	−0.045
	Feb	−0.487	−0.641*	−0.685*	−0.478	−0.074	−0.406	−0.229	−0.229
	Mar	−0.498	−0.57	−0.471	−0.519	−0.500	−0.456	−0.436	−0.436
	Apr	−0.325	−0.362	−0.312	−0.246	−0.281	−0.446	−0.306	−0.425
G	Oct	−0.089	0.127	0.589	0.679*	0.654*	0.487	0.272	0.237
	Nov	−0.009	0.112	0.182	0.089	0.08	−0.049	0.261	0.261
	Dec	0.244	0.309	0.356	0.523	0.573	0.589	0.703*	0.703*
	Jan	0.581	0.632*	0.689*	0.721*	0.591	0.503	0.424	0.424
	Feb	−0.141	−0.335	−0.193	−0.083	0.054	−0.293	−0.391	−0.391
	Mar	−0.653*	−0.531	−0.386	−0.226	−0.201	−0.067	0.026	0.026
	Apr	−0.466	−0.513	−0.414	−0.302	−0.128	−0.254	−0.379	−0.424

Linear regression analysis of the ten years of monitoring showed that wind events at the end of the growing season (October) with speeds of 7 (Fig. 4a) and 8 $m\ s^{-1}$ (Fig. 4b) were positively and significantly correlated with litter production rate. This significant positive relationship was only observed in G, indicating that wind events (with speeds of 7 and 8 $m\ s^{-1}$) at the end of the growing season accelerated the litter production rate in G. Thus, the wind can be considered a major driver for litter transportation, especially in G, where wind increased aboveground litter.

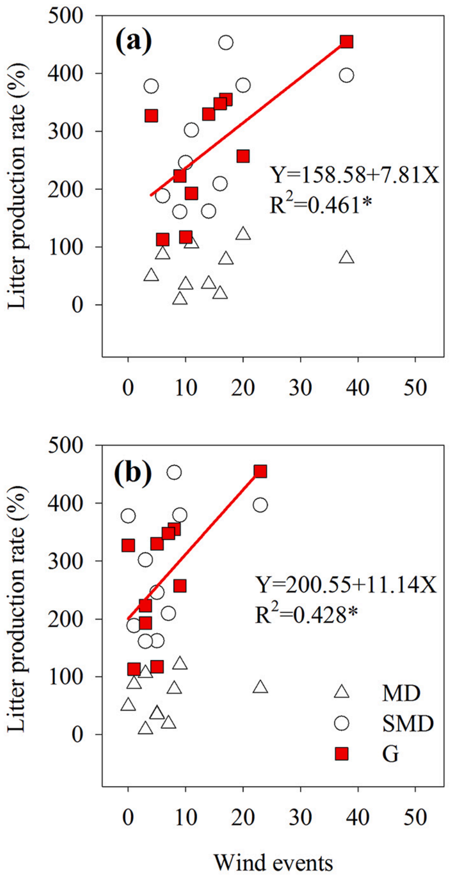

Fig. 4. Linear regression analysis of the ten years of monitoring between the frequency of wind events at the end of the growing season (October) with speeds of 7 (a) and 8 $m\ s^{-1}$ (b) with litter production rate in the mobile dunes (MD), fixed dunes (FD), and fenced grassland (G).

4. Discussion

4.1. Biomass, litter and soil C distribution

Carbon cycling in terrestrial ecosystems, especially that related to litter, is tightly related to soil organic C (Melillo et al., 1989; Atarashi-Andoh et al., 2012; Bowden et al., 2014; Novara et al., 2015). In this study, we measured soil C content via the combustion method. Therefore, the soil C content evaluated in this study included both the organic C and the inorganic C. A previous study in our study area (Li et al., 2011) demonstrated that soil C was mainly present in the form of organic C; the inorganic C at 0–20 cm soil depth ranged from 8.78% to 10.49% in the continuous grazing area and from 6.39% to 8.05% in the grazing exclosure area. Therefore, in the current study, it was reliable and feasible to analyze the relationship between plant litter and soil C content.

In this study, our field investigation fully demonstrated that both the vegetation character (including living plant biomass and the litter mass) and the soil C content significantly differed among habitats (Fig. 1). This great variation in the plant–soil system has also been found in former studies in Horqin sandy land (Li et al., 2006; Zuo et al., 2009). In theory, the soil C is mainly derived from plant productivities via both aboveground and belowground litter production, and thus, there should be a strong relationship between soil C and plant productivity or plant litter production (Björn Berg and McClaugherty, 2003; Bowden et al., 2014). This relationship has been shown in other ecosystems (Sayer, 2006; Leff et al., 2012; Lajtha et al., 2014) but not yet for degraded sandy grasslands in semi-arid aeolian regions. Therefore, it is necessary to expound the relationship between soil C content and plant productivities or plant litter production.

4.2. Relationship between soil C content and dry matter biomass

Soil C is derived from plants, and thus the biomass or litter mass is considered to be the main source of soil C. Ecosystem C models assume a strong relationship between soil C accumulation and annual net primary productivities or and plant litter inputs (Bolinder et al., 2012; Quijano et al., 2017). However, there is little experimental evidence to support this assumption (Lajtha et al., 2014). The existing research conclusions are inconsistent; for example, in forest ecosystems, some studies have shown that there is a close relationship between aboveground biomass and soil C, and here the aboveground biomass is considered to be the most important factor to explain the variation of soil C stock (Huyler et al., 2014; Mehta et al., 2014). Leaf litter contributed more to soil organic C than fine roots in two 10-year-old subtropical plantations (Cao et al., 2020). Declines in leaf litter inputs can lead to rapid losses of soil C (Bowden et al., 2014). A study conducted in a temperate steppe of northern China demonstrated that there was a significant positive correlation between soil C content and abovementioned biomass (Jiang et al., 2011). However, other studies have reported that the belowground biomass had a more important effect on soil C accumulation than the aboveground biomass. The root-derived aliphatic compounds were found to be a source of soil organic matter with greater relative stability than leaf inputs (Crow et al., 2009b). Root litter inputs exerted a greater influence over soil C than aboveground litter in a subtropical natural forest (Liu et al., 2019). The significance of the underground part has also been verified in the study of farmland ecosystems (Kätterer et al., 2011; Bolinder et al., 2012; Mazzilli et al., 2015). This relatively high importance was also found in the current study, as the belowground biomass was significantly correlated with soil C content in both layers (Table 2). This could be because the litter fall was affected by many factors, especially climate change (Melillo et al., 1993; Raich et al., 2006), leading to uncertainty of the relationship between aboveground biomass and soil C content. However, the soil structure is relatively stable and thus the belowground biomass would more stably release C to soil via exudates or fine root turnover.

Litter is the key link for C exchange within the plant–soil system, and results from existing research on the relationship between litter and soil C remain controversial. Some studies have shown that the soil C pools in this forest do not respond linearly or immediately to aboveground or belowground litter inputs (Lajtha et al., 2014; Huang and Spohn, 2015), whereas others observed a significant relationship between soil C and litter mass (Sayer, 2006; Leff et al., 2012; Tanner et al., 2016). Moreover, the litter influence on soil C was also manipulated by the amount of the plant litter and the detrital input. A litter-removal experiment found that, after two decades of doubled litter addition, soil C did not increase, while declines in leaf litter inputs can lead to rapid losses of soil C (Bowden et al., 2014). Klotzbücher et al. (2012) found that reduced litter input did not change fluxes of dissolved organic C, while litter addition significantly increased the dissolved organic C fluxes. In the current study, we found that only the belowground litter mass was significantly correlated with soil C but not the aboveground litter mass (Table 2). The priming effect on soil C decomposition had been given as an explanation of the non-significant effect of aboveground litter addition on soil C accumulation (Sulzman et al., 2005; van Groenigen et al., 2014). However, this priming effect could be short-lived (Hoosbeek and Scarascia-Mugnozza, 2009) and thus may not be evident in field investigation because ground litter may have been present for a long time under natural field conditions. Furthermore, given that the wind erosion in this study area is severe (Wang, 1989; Li et al., 2005) and there was distinct litter flux among dunes (Wang et al., 2016), we inferred that the wind events increased the uncertainty of the relationship between aboveground litter and soil C.

4.3. Relationship between dry matter biomass and litter

The interaction between litter and living biomass is an important part of the material circulation of the terrestrial ecosystem. Current research has mainly focused on the impact of litter on vegetation productivity or on plant community composition and structure. For example, a study in a typical steppe showed that litter addition increased belowground net primary productivity via the influence of litter on soil moisture and soil nitrogen availability, ultimately increasing belowground water use efficiency and plant nitrogen uptake (Shen et al., 2016). In a typical steppe of Inner Mongolia, Wang et al. (2011) found that litter removal decreased the amount of grass (*Leymus chinensis*) that was produced. However, litter addition caused an inconsistent effect among years, with moderate applications producing the most positive effects due to the litter manipulation, which enhanced soil moisture and reduced soil heat units (Wang et al., 2011). This manipulation was also demonstrated in a neotropical savanna on the Brazilian plateau (Villalobos-Vega et al., 2011). In the current study, we demonstrated that, there was a large variation in both the aboveground biomass and the belowground biomass, and the mass of litter also varied greatly in our study region (**Fig. 1**). Moreover, even in a small scale of each habitat, taking the aboveground biomass for example, the variation remained high, with a variable coefficient (i.e. SD/mean) ranging from 0.36 to 0.92. Thus, it can be inferred that the patch distribution of litter leads to high spatial heterogeneity of vegetation. This hypothesis is consistent with the findings of a study in a Mediterranean semi-arid shrubland that plant litter accumulation and its patchy distribution have large impacts on landscape patch properties (Boeken and Orenstein, 2001).

Litter is completely derived from living plants and thus, in theory, plant productivity should determine the litter yield (Björn Berg and McClaugherty, 2003; Bowden et al., 2014). Therefore, there should be a relationship between biomass and litter mass; however, this relationship was rarely observed because of other influencing factors, especially the climate (Melillo et al., 1993; Raich et al., 2006). Litter production varied among the type of ecosystem (Chale, 1996; Liu et al., 2012; Yanai et al., 2012), and this variation was also evidenced in this study that the ratio of litter mass to aboveground biomass differed significantly between desertified and undesertified habitats (Fig. 2), and the litter production rate also differed significantly among habitats observed from the 10 years monitoring (Fig. 3). Furthermore, in grassland ecosystems, especially in semi-arid grassland, there remains a knowledge gap relating to the relationship between the living biomass and the litter mass. In our study area, the wind effects on plant litter production should be fully considered.

4.4. Litter production and its response to wind events

wind is considered as an important factor on litter production, existed study demonstrated that, leaf and stipule litterfall could be governed by monthly maximum wind speed in a subtropical mangrove of *Bruguiera gymnorrhiza* (Kamruzzaman et al., 2016). In a cropland agro forestry ecosystem, which located in southwestern Bangladesh, there was a significant correlation ($P < 0.05$) among litter production and wind speed for many species (Hasanuzzaman and Hossain, 2014). However, there was an insignificant relationship between wind speed and litter production in this study, only the frequency of wind events among different speed significantly ($P < 0.05$) correlated with the plant litter production (Table 3). This contradiction would lead by the surface roughness among different ecosystem. There have been no studies that directly show a relationship between litter production rate and wind events; existed studies on wind erosion in a degraded sandy land demonstrated that surface roughness was an important factor affecting the surface wind erosion intensity (Li et al., 2005). In a wind erosion region of Horqin sandy land, soil properties varied significantly among sites with different degree of desertification (Lian et al., 2013). In FD, the high surface roughness resulting from the high vegetation coverage is the key factor leading to low wind erosion intensity and high surface structural stability (Li et al., 2005). This relatively higher vegetation coverage can directly capture soil fine particulate matter during the process of wind erosion, resulting in the change of surface soil texture and in the surface soil C and nutrition enrichment (Li et al., 2005). In contrast, in areas with a high proportion of bare land, wind erosion can lead to the loss of soil fine particulate matter and C and N (Su et al., 2004; Zhao et al., 2007). Therefore, we infer that, similar to the fine particulate matter in the soil, the larger surface roughness not only captures the fine particulate matter in areas with high vegetation coverage (i.e. FD and G), but also captures a certain amount of litter during the process of litter movement. Thus, the amount of litter present is greatly higher than the maximum biomass, and these habitats should be considered as a sink of plant litter. In contrast, areas with a high proportion of bare land, such as MD, can considered as a source of plant litter because the wind erosion promoted the litter loss, resulting in a lower amount of litter present than the maximum biomass (Fig. 3). This relationship was also strengthened by our field investigation showing that as the aboveground (or underground) biomass increased, the increase in the slope of litter (or necromass) in undesertified grassland was significantly higher than that in desertified grassland (Fig. 2).

In this study, because of the long-term protective management, even though the area was originally a typical FD, the monitoring plots of the FD were similar to those of G, indicating successful vegetation restoration (Wang et al., 2016; Luo et al., 2016). This may also explain the non-significant difference of the litter production rate between FD and G (Fig. 3).

The present study demonstrated that the amount of belowground litter was an important factor affecting soil C concentration in Horqin sandy land. Moreover, the litter production varied among habitats and affected by wind events. Our results initially identified thresholds and critical periods of wind events that affect litter redistribution; however, these findings are based on the results of a long field survey. In-situ observations on the relationship between litter-flux and wind events among habitats with different micro-topographic conditions are necessary in further study. This approach would provide more accurate information on the increase of the litter production rate in areas with low vegetation coverage (i.e. MD and SFD) for the regional ecological restoration in semi-arid degraded grassland.

5. Conclusion

In this study, the spatial investigation demonstrated that the soil C varied greatly among habitats in degraded grassland of Horqin regions. The soil C content was significantly affected by belowground biomass and belowground litter mass but not aboveground biomass and aboveground litter at 0–10 and 10–20 cm soil depth. Furthermore, the explanation ratio of these two factors (belowground biomass and belowground litter mass) on soil C content was relatively low, especially at 10–20 cm soil depth. Patterns for litter production in desertified habitat (MD and SFD) significantly differed with the undesertified habitat (FD and G) through the increase aboveground biomass; both the aboveground litter and the belowground litter increased faster in the undesertified habitat than in the desertified habitat. The 10 years of monitoring indicated that, in MD, about 40% of the aboveground primary production was lost, while there was a distinct enrichment of aboveground litter in SFD and G. Wind events (with speed of 7 and 8 m s^{-1}) at the end of the growing season significantly affected litter production rate, and wind was the main driver for litter transportation between habitats in which most of the plant litter was falling. In summary, plant litter production was affected by wind events, and this influence differed among habitats in degraded grassland, this variation led to the spatial heterogeneity on soil C accumulation in Horqin sandy land. This result can strengthen the understanding of the relationship between soil properties and plant litter production and thereby can provide information for ecological restoration of different types of desertified land, especially for the soil C accumulation.

Author contributions

Yongqing Luo, Xueyong Zhao and Zhong Du conceived and designed the study. Yongqing Luo, Lilong Wang, and Xuyang Wang performed the experiments. Xinping Liu and Yuqiang Li analyzed the results. Yongqing Luo drafted the manuscript. All co-authors had a chance to review the manuscript before submission and contributed to discussion and interpretation of the data.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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