



Effects of Grazing, Wind Erosion, and Dust Deposition on Plant Community Composition and Structure in a Temperate Steppe

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ABSTRACT

Grazing can affect plant community composition and structure directly by foraging and indirectly by increasing wind erosion and dust storms and subsequently influence ecosystem functioning and ecological services. However, the combined effects of grazing, wind erosion, and dust deposition have not been explored. As part of a 7-year (2010–2016) field manipulative experiment, this study was conducted to examine the impacts of grazing and simulated aeolian processes (wind erosion and dust deposition) on plant community cover and species richness in a temperate steppe on the Mongolian Plateau, China. Grazing decreased total cover by 4.2%, particularly the cover of tall-stature plants (> 20 cm in height), but resulted in 9.1% greater species richness. Wind erosion also reduced total cover by 17.0% primarily via suppressing short-

stature plants associated with soil nitrogen loss, but had no effect on species richness. Dust deposition enhanced total cover by 5.7%, but resulted in a 7.3% decrease in species richness by driving some of the short-stature plant species to extinction. Both wind erosion and dust deposition showed additive effects with grazing on vegetation cover and species richness, though no detectable interaction between aeolian processes and grazing could be detected due to our methodological constraints. The changes in gross ecosystem productivity, ecosystem respiration, and net ecosystem productivity under the wind erosion and dust deposition treatments were positively related to aeolian process-induced changes in vegetation cover and species richness, highlighting the important roles of plant community shifts in regulating ecosystem carbon cycling. Our findings suggest that plant traits (for example, canopy height) and soil nutrients may be the key for understanding plant community responses to grassland management and natural hazards.

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Key words: dust storm; plant diversity; plant height; plant–herbivore interaction; selective foraging; soil nutrient; species richness; vegetation cover.

HIGHLIGHTS

- Grazing decreased plant community cover but increased species richness.
- Wind erosion reduced plant community cover but did not affect species richness.
- Dust deposition enhanced plant community cover but decreased species richness.

INTRODUCTION

Grazing, the most widespread land-use practice in grasslands (Blüthgen and others 2012), occurs on more than 25% of the Earth's land surface (Asner and others 2004; Monfreda and others 2009). It has been widely accepted that grazing can play a crucial role in regulating grassland plant community composition and structure, with subsequent effects on ecosystem functioning and services (Ward and others 2007; Masunga and others 2013; Eldridge and others 2016; Wang and others 2019). Selective foraging by grazing animals can influence plant communities directly by defoliation and changing interspecific competition (Gwynne and Bell 1968; Harris and others 2003; Evju and others 2009; Ylänne and others 2015), and indirectly by modulating light availability (Collins and others 1998; Borer and others 2014). For example, livestock foraging may suppress species dominating in the canopy layer with higher competitiveness for light, and thus increase light availability for sub-canopy species (Huntly 1991; Borer and others 2014). However, trampling by grazing animals has been documented not to affect plant communities (Yang and others 2018). In addition, substantial debate remains on the effects of grazing on grassland plant diversity. Positive (Collins and others 1998; Liu and others 2015; Köhler and others 2016), neutral (Zhu and others 2012; Masunga and others 2013; Eldridge and others 2016; Jamsranjav and others 2018), and negative (Safford and Harrison 2001; Li and others 2017; Ren and others 2018) responses of species richness to grazing have been reported.

In addition to the direct impacts of grazing on grassland plant communities, defoliation and trampling by grazing animals may increase the wind erodibility of grassland soils, especially in arid and semi-arid regions, for several reasons (Neff and others 2008; Sørensen and others 2009; Aubault and others 2015; Munkhtsetseg and others 2017). First, livestock trampling can destroy soil crusts, compact the topsoil, and decrease water infiltration rate and soil stability (Eldridge and Leys 2003; Zhou

and others 2010; Tabeni and others 2014; van Klink and others 2015). Second, the expansion of bare soil areas associated with livestock trampling and the losses of standing vegetation under grazing may create greater wind flow along the soil surface and consequently higher wind speeds, providing favourable conditions for the occurrence of dust emission events (Zhao and others 2005; Ludwig and others 2007; Hoffmann and others 2008a; Belnap and others 2009; Nauman and others 2018). Grazing-driven aeolian processes including wind erosion and dust deposition may further impact plant community composition and structure (Okin and others 2006).

Wind erosion of soils can result in the loss of fine sediments, mainly silt/clay and fine sand, and associated nutrients such as nitrogen (N) by blowing off the most fertile topsoil (Neff and others 2005; Okin and others 2006; Li and others 2007, 2018; Lei and others 2019). This may alter plant community composition by accelerating shrub expansion (Li and others 2008a; Alvarez and others 2012) and increasing the dominance of plant species with high nutrient-use efficiency (Vitousek 1982; Wedin and Tilman 1996; Funk and Vitousek 2007). In addition, the process of surface soil removal and dust emission caused by wind erosion may damage young plant tissues, with subsequent effects on plant community composition and structure (Okin and others 2001; Alvarez and others 2012). After wind erosion, airborne fine dusts generally deposit less in the dust source areas but are gradually transported by winds to the regions downwind (Okin and others 2006; Neff and others 2008; Field and others 2010; Alvarez and others 2012). Contrary to the impacts of wind erosion, dust deposition may provide additional nutrients for plant growth (Reynolds and others 2001; Soderberg and Compton 2007; Neff and others 2008; Lawrence and others 2013), which may, in turn, lead to changes in interspecific competition and trade-offs, thus affecting plant community composition and diversity. For example, it has been documented that nutrient enrichment could enhance the dominance of plant species with high competitiveness for light and thus decrease species richness (Hautier and others 2009; Borer and others 2014; Harpole and others 2016). Given that wind erosion and dust deposition have opposite influences on soil nutrient pools, it is reasonable to expect that wind erosion and dust deposition may have contradictory impacts on plant community composition and diversity in grasslands. Nevertheless, how wind erosion and

dust deposition in combination with grazing affect grassland plant communities remain unexplored.

To address this gap in our knowledge, we examined the responses of plant community composition and structure to grazing and simulated aeolian processes (wind erosion and dust deposition) in a semi-arid temperate steppe of the Mongolian Plateau, China. Our experiment specifically tested the following three hypotheses: (1) Grazing and wind erosion would reduce vegetation cover via foraging and removing surface soil and associated nutrients, respectively. The decrease in vegetation cover, particularly the cover of tall-stature plants, under grazing and wind erosion would increase species richness by enhancing light availability for short-stature plants (Borer and others 2014; Figure 1). (2) Dust deposition would enhance vegetation cover by increasing soil nutrients. In contrast, dust deposition may directly reduce species richness by burying and killing short-stature plant species (Okin and others 2001, 2006). In addition, the dust deposition-induced eutrophication would indirectly decrease species richness by increasing tall-stature plant species that have high competitiveness for light and further excluding short-stature plant species (Hautier and others 2009; Harpole and others 2016). (3) Wind erosion may compound the negative impacts of grazing on plant growth, whereas dust deposition may ameliorate the negative impacts of grazing on plant growth. Given that shifts in plant communities

have been documented to affect ecosystem carbon cycling by mediating plant photosynthetic capacity, carbon substrate supply, and nutrient pools (Maestre and others 2012; Dieleman and others 2015; Musavi and others 2017), we also explored the potential effects of altered plant community composition and structure under grazing and simulated aeolian processes on carbon-cycling variables including gross ecosystem productivity (GEP), ecosystem respiration (ER), and net ecosystem productivity (NEP).

MATERIALS AND METHODS

Study Site

The study site is located in a semi-arid temperate steppe in Duolun County (42°02' N, 116°17' E, 1324 m a.s.l.), Inner Mongolia, China. Long-term (1954–2018) mean annual temperature is 2.4 °C with mean monthly temperature ranging from –17.5 °C in January to 18.9 °C in July (China Meteorological Data Sharing Service System). Mean annual precipitation is 382 mm with 91% of annual rainfall occurring during the growing season from May to October. Mean annual wind speed and annual maximum wind speed are 3.46 and 9.11 m s⁻¹, respectively, with gust winds up to 25.5 m s⁻¹. The sandy soils at this study site are classified as chestnut soils (Chinese classification) and Xeric Haplocalcids according to the US soil taxonomy classification system (Soil Survey Staff 1999), respectively, with 71.9% sand, 15.6% silt, and 12.5% clay at 0–10 cm depth (see also the detail information in Ma and others 2019). The vegetation is dominated by the perennial species *Artemisia frigida*, *Lespedeza davurica*, *Potentilla acaulis*, *Artemisia pubescens*, *Phlomis umbrosa*, *Agropyron cristatum*, *Stipa krylovii*, and *Leymus chinensis* (Table S1).

Experimental Design

Our two-factor (grazing and aeolian processes) experiment was established in April 2010 (see also Ma and others 2017, 2019). There were two grazing levels (without and with grazing) and three aeolian process levels (control, wind erosion, and dust deposition). The experiment used a randomized complete block design with six treatments including control, wind erosion (WE), dust deposition (DD), grazing (G), wind erosion plus grazing (WE + G), and dust deposition plus grazing (DD + G), and five replicates for each treatment. Thirty 4-m × 4-m plots were arranged into six rows and five columns with a 1.5-m buffer zone between any

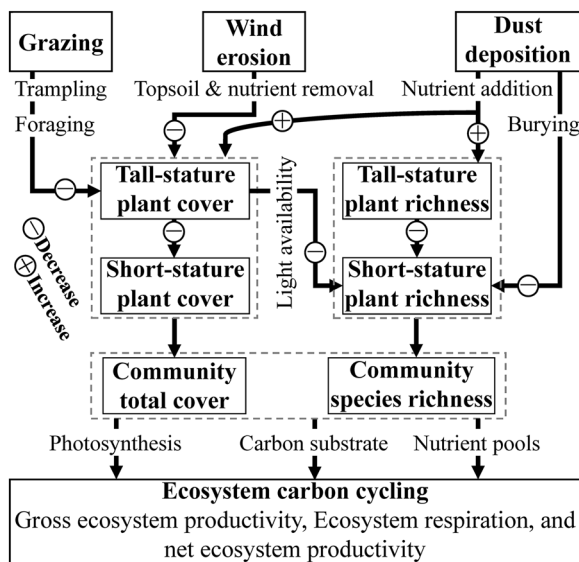


Figure 1. Conceptual model of the direct and indirect effects of grazing, wind erosion, and dust deposition on vegetation cover and species richness as well as ecosystem carbon cycling.

two adjacent plots. One of the six plots in each column was randomly assigned to one of the six treatments (see Figure S1 for experimental layout). Polyvinyl chloride (PVC) boards protruding 10 cm above the ground were used in each plot to prevent the disturbance of natural wind and deposited soil from adjacent plots. All the measurements were conducted in 3-m \times 3-m central area of each plot to reduce any possible edge effect.

Experimental Manipulations

Grazing was conducted using a 1-year-old sheep to forage for 4 h per month from June to September each year from 2010 to 2016 (grazing intensity was equivalent to 1 sheep for an $\text{h m}^{-2} \text{y}^{-1}$; see Figure S1 for treatment pictures). The grazing intensity of this study was within the range of grazing intensity gradients (1 sheep for 0.2–3.6 $\text{h m}^{-2} \text{y}^{-1}$) imposed by other grazing experiments in Inner Mongolia grasslands, which were close to our experiment site (Lin and others 2010; Qian and others 2017).

Simulated aeolian processes were manipulated in early May of each year from 2010 to 2016. Wind erosion was mimicked by blowing off a 1 cm layer of topsoil using a portable pneumatic extinguisher (Taining Machinery Ltd. Co., Taizhou, Jiangsu, China). During the wind erosion simulations, a cloth bag was used to collect soil blown off from the wind erosion plots. The collected soil was sieved through a 5-mm mesh to remove litters, mixed, and spread evenly on the surface of the dust deposition plots to mimic dust deposition. During the simulations of aeolian processes, 17 short rulers were evenly inserted into the surface of each wind erosion and dust deposition plot to mark the wind erosion and dust deposition depths (Figure S2). The erosion and deposition intensities used in this study were within the range of previous observations in several grassland sites close to our experiment. For example, a grazing intensity of 1 sheep for 0.29–0.88 $\text{h m}^{-2} \text{y}^{-1}$ could result in a 0.4–4.3 cm y^{-1} loss of surface soil in a sandy rangeland (Zhao and others 2005). In a temperate steppe, winds could blow off a 0.76 cm layer of topsoil in spring when vegetation cover is 10–30% (Meng and others 2018). In addition, another study assessing wind erosion rates has observed a 1.3 cm thickness of dust deposits on the surface of Inner Mongolia grasslands (Hoffmann and others 2011).

Although our methodologies simultaneously mimic grazing and aeolian processes in one of the first studies to date (also see Hoffmann and others 2008b), it is still worth noting that there are several

shortcomings in our experimental manipulations. First, our aeolian process manipulations could not mimic the abrasion effects of wind erosion on young plant tissues throughout the spring in this experimental grassland, which might influence plant growth (Okin and others 2001, 2006). Second, different from the actual aeolian processes, the soil added to the dust deposition plots was collected from the adjacent wind erosion plots in our experiment. As the surface soil of the wind erosion plots was gradually removed by the wind erosion treatment, it is expected that N content of the soil added to the dust deposition plots would decrease over time. By comparison, naturally deposited dusts generally come from other dust source areas and consist of mostly silt/clay and fine sand with generally high nutrient contents (Hoffmann and others 2008b; Neff and others 2008; Field and others 2010). Therefore, it is possible that our study may have underestimated the nutrient enrichment effects of dust deposition on grassland communities. Third, our experimental simulations decoupled grazing and wind erosion that usually occurred simultaneously in grasslands (Belnap and others 2009; Nauman and others 2018). For example, although livestock trampling showed little impact on plant communities in Inner Mongolia grasslands (Yang and others 2018), the effects of sheep trampling on soil crusts, which could affect the intensity of wind erosion, were neglected in the wind erosion plots. We acknowledge that these methodology constraints might reduce the ability of our experimental design in detecting the realistic interactions between grazing and aeolian processes.

Vegetation Monitoring

Since the experiment was designed as a long-term manipulative experiment, all vegetation sampling was conducted nondestructively at peak biomass (early August) once a year from 2010 to 2016. In May 2010, one permanent 1-m \times 1-m quadrat was established in each plot. The per cent cover of each plant species was visually estimated in each quadrat. The cover of all species was summed to obtain functional group and total cover. Thus, total cover of plant community can exceed 100% due to the canopy overlap of different species. In this study, only 10 out of the 210 observations (30 plots \times 7 years) were above 100% (Figure S3). In addition, the number of plant species in each quadrat was recorded as species richness. Moreover, canopy height of each species within the quadrats was also monitored and calculated as the average height

based on at least three randomly selected individuals.

Given that grazing and aeolian processes may have differential impacts on plants with different canopy heights (Huntly 1991; Borer and others 2014), we classified plants into short- (< 20 cm in height) and tall-stature species (> 20 cm in height; Yang and others 2011). In addition, plant species within short- and tall-stature functional groups were further categorized based on their relative cover. If the mean relative cover of a species in the control plots exceeded 5%, the species was classified as ‘dominant’. *Artemisia frigida*, *P. acaulis* and *P. umbrosa* were the dominant species within the short-stature functional group, accounting for > 54% of the total short-stature plant cover (Table S1). *Lespedeza davurica*, *A. pubescens*, *A. cristatum*, *L. chinensis*, and *S. krylovii* dominated the tall-stature functional group, contributing more than 92% of the total tall-stature plant cover. However, our analyses for individual species did not include *P. umbrosa* and *L. davurica* because the two species appeared in no more than 2 of our 6 treatments.

Measurements of Soil N Content and Ecosystem Carbon Fluxes

In early August of each year, three soil cores (5 cm in diameter and 10 cm in depth) were collected from two opposite corners and the centre of each experimental plot. Soil samples were mixed to form a composite sample of the plot. A 2-mm mesh was used to remove roots and organic debris from the samples. The soil samples were then air-dried and ground. Nitrogen content of the soil samples was analysed using an element analyser (Vario MACRO CUBE, Elementar Inc., Germany).

A 0.5-m-long × 0.5-m-wide × 0.5-m-high transparent chamber connected to a Li-6400 Photosynthesis System (LI-COR Inc., Lincoln, NE, USA) was used to measure ecosystem carbon fluxes (see also Song and others 2019). The chamber was sealed to the surface of an iron frame, which was inserted into the soil at 3-cm depth in each plot. Nine consecutive logs of CO₂ concentrations were recorded at 10-s intervals on each frame during a 90-s period. The decreases in the rates of CO₂ concentrations were used to calculate NEP. Following the measurements of NEP, the chamber was vented, covered with an opaque cloth, and put back on the same iron frame. The CO₂ exchange was measured again to calculate ER rate as light was eliminated (and hence photosynthesis). Gross ecosystem productivity was estimated as ER plus

NEP. Positive and negative NEP values represent net carbon uptake and loss, respectively.

Statistical Analysis

First, to investigate the main effects of grazing, two-way repeated-measures analyses of variance (RM-ANOVAs) using a mixed effect model were conducted to examine the effects of grazing (two levels including with and without grazing), aeolian processes (three levels including control, wind erosion, and dust deposition), and their interactions on soil N content as well as vegetation (including vegetation cover and species richness) and carbon-cycling variables (including GEP, ER, and NEP) across all the six treatments, where grazing and aeolian processes were considered as fixed between-subject effects and year was considered as within-subject effects. In addition, to examine the main effects of wind erosion and its interactions with grazing on these parameters, two-way RM-ANOVAs were also performed with data from four of the six treatments including the control, WE, G, and WE + G. Moreover, two-way RM-ANOVAs were conducted with data from 4 of the 6 treatments including the control, DD, G, and DD + G to investigate the main effects of dust deposition and its interactions with grazing on these parameters.

Second, simple linear regressions (SLRs) and backward multiple linear regressions (BMLRs; see Figure S4 for code) were used to examine the relationships of treatment-induced changes in total cover with treatment-induced changes in the cover of short- and tall-stature plant functional groups as well as the dependences of treatment-induced changes in the cover of short- and tall-stature plant functional groups on treatment-induced changes in the cover of dominant short- (*A. frigida* and *P. acaulis*) and tall-stature (*A. pubescens*, *A. cristatum*, *L. chinensis*, and *S. krylovii*) plants, respectively. In addition, the relationships of treatment-induced changes in the cover of dominant short- and tall-stature plants with treatment-induced changes in soil N content were also explored with SLRs.

Third, the dependences of treatment-induced changes in species richness on treatment-induced changes in the richness of short- and tall-stature plant functional groups were investigated using SLRs and BMLRs. In addition, SLRs were also performed to examine the relationships of treatment-induced changes in short-stature plant richness on treatment-induced changes in tall-stature plant cover. Moreover, the dependences of treatment-induced changes in carbon-cycling variables (GEP, ER, and NEP) on treatment-induced changes

in vegetation cover, species richness, and soil N content were examined with SLRs and BMLRs. All statistical analyses described above were performed with SAS 9.0 (SAS Institute, Cary, North Carolina, USA).

RESULTS

Soil N Content

Averaged across all the six treatments, soil N content fluctuated substantially among the seven experimental years (Figure 2A; $P < 0.001$, Table 1). There was no effect of grazing on soil N content averaged over the 7 years. When wind erosion and dust deposition were separately analysed with grazing, wind erosion significantly decreased soil N content by 12.3% ($P = 0.031$) whereas dust deposition did not affect soil N content (Table 2). No interaction of wind erosion or dust deposition with grazing on soil N content was found. However, wind erosion interacted with year to influence soil N content ($P < 0.001$), such that a sustained decrease in soil N content over time was found in the wind erosion plots (Figure 2B).

Cover of Total, Functional Groups, and Dominant Species

During the seven experimental years, total cover as well as short- and tall-stature plant functional group cover showed strong interannual variability (Figure 3; all $P < 0.001$, Table 1). Grazing and wind erosion significantly decreased total cover by

4.2% (Figure 3A; absolute change, $P = 0.041$) and 17.0% ($P < 0.001$, Table 2), respectively, averaged across the 7 years. Dust deposition increased total cover by 5.7% ($P = 0.023$). Short-stature plant cover was enhanced by 7.3% under grazing (Figure 3B; $P = 0.048$), decreased by 13.2% under wind erosion ($P = 0.002$), and showed no response to dust deposition. Grazing significantly reduced tall-stature plant cover by 11.4% (Figure 3C; $P = 0.002$). Wind erosion did not affect tall-stature plant cover, but dust deposition stimulated tall-stature plant cover by 5.6% ($P = 0.012$). No interactive effect between wind erosion/dust deposition and grazing on plant community or functional group cover was found.

Averaged over the 7 years, grazing significantly increased the cover of *A. frigida* by 7.7% ($P = 0.021$), decreased the cover of *A. cristatum* by 1.9% ($P < 0.001$), but did not affect the cover of the other four species (that is, *P. acaulis*, *A. pubescens*, *L. chinensis*, and *S. krylovii*; Figure 4; Table 1). Wind erosion significantly reduced the cover of *A. frigida* by 14.7% ($P = 0.002$, Table 2). Dust deposition did not affect the cover of the six dominant species. No interaction of wind erosion/dust deposition with grazing on the cover of the six dominant species was detected.

Plant Species Richness

Averaged across all the six treatments, species richness as well as short- and tall-stature plant richness varied with year (Figure 5; all $P < 0.001$,

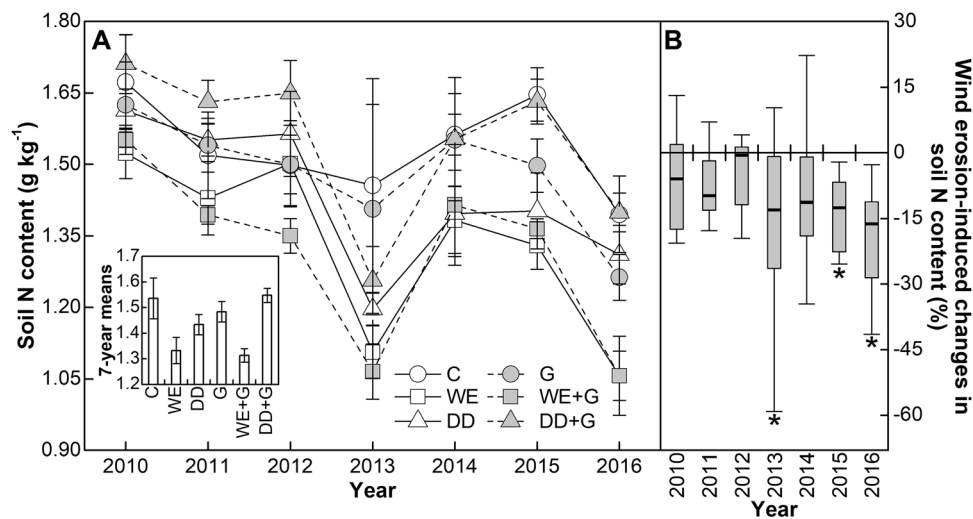


Figure 2. Annual dynamics and 7-year means (2010–2016, insets) of soil nitrogen (N) content under the six treatments (A). Data represent mean \pm 1 SE, $n = 5$. Box plots of wind erosion-induced changes in soil N content along the seven experimental years (B). C control, WE wind erosion, DD dust deposition, G grazing, WE + G wind erosion plus grazing, DD + G dust deposition plus grazing.

Table 1. Summary (*P* values) of Two-Way RM-ANOVAs on the Effects of Grazing (*G*), Aeolian Processes (*A*), Including Three Levels of Control, Wind Erosion, and Dust Deposition), and Their Interactions Across All the Six Treatments on Soil Nitrogen (*N*) Content, Total Cover (TOT), Short-Stature (SHS) and Tall-Stature (TAS) Plant Cover, the Cover of Six Dominant Species, Species Richness at Community (COM) and Functional Group Levels (SHS and TAS Plants), Gross Ecosystem Productivity (GEP), Ecosystem Respiration (ER), and Net Ecosystem Productivity (NEP)

Source of variation	Soil N content	Vegetation cover			Dominant species cover				Species richness				Carbon-cycling variables			
		TOT	SHS	TAS	<i>A. frigida</i>	<i>P. acutis</i>	<i>A. pubescens</i>	<i>A. cristatum</i>	<i>L. chinensis</i>	<i>S. krylovii</i>	COM	SHS	TAS	GEP	ER	NEP
<i>G</i>	0.718 ⁺	0.041 [−]	0.048 ⁺	0.002 [−]	0.021 ⁺	0.900 [−]	0.064 [−]	< 0.001 [−]	0.213 [−]	0.354	0.002 ⁺	0.001 ⁺	0.294 [−]	0.017 [−]	0.056 [−]	0.024 [−]
<i>A</i>	0.003	< 0.001	0.007	0.083	0.001	0.943	0.388	0.970	0.409	0.594	0.062	0.020	0.003	< 0.001	< 0.001	0.006
<i>G</i> × <i>A</i>	0.217	0.359	0.690	0.243	0.054	0.150	0.332	0.151	0.857	0.527	0.526	0.641	0.241	0.233	0.472	0.235
Year	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.063	< 0.001	< 0.001	0.024	0.012	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
<i>G</i> × year	0.881	< 0.001	< 0.001	0.018	< 0.001	0.181	0.131	< 0.001	0.203	0.180	0.810	0.616	0.793	0.051	0.014	0.036
<i>A</i> × year	0.014	< 0.001	< 0.001	0.012	< 0.001	0.148	0.324	0.004	0.227	0.078	0.010	< 0.001	0.175	< 0.001	< 0.001	0.004
<i>G</i> × <i>A</i> × year	0.225	0.226	0.041	0.101	0.018	0.684	0.805	0.080	0.411	0.040	0.346	0.053	0.412	0.077	0.821	0.003

These analyses were used to examine the main effects of grazing.

Dominant SHS species: *A. frigida*, *Artemisia frigida*; *P. acutis*, *Potentilla acutis*; Dominant TAS species: *A. pubescens*, *Artemisia pubescens*; *A. cristatum*, *Agropyron cristatum*; *L. chinensis*, *Leymus chinensis*; *S. krylovii*, *Stipa krylovii*.

The bold numerals highlight the significance at $P < 0.05$.

The superscripts ‘–’, ‘+’, and ‘+’ represent negative and positive treatment effects, respectively.

Table 1). Species richness was increased significantly by 9.1% under grazing (Figure 5A; relative change, $P = 0.002$), unaffected by wind erosion, but reduced by 7.3% under dust deposition ($P = 0.004$, Table 2). Grazing resulted in 16.6% greater short-stature plant richness (Figure 5B; $P = 0.001$). Wind erosion did not influence short-stature plant richness, but dust deposition significantly decreased short-stature plant richness by 11.6% ($P = 0.019$). Tall-stature plant richness showed no response to grazing or dust deposition (Figure 5C), but was reduced by 15.9% under wind erosion ($P = 0.003$). The interaction between wind erosion/dust deposition and grazing did not impact species richness.

Abiotic and Biotic Factors Influencing Vegetation Cover

Regression analyses revealed that grazing-induced decrease in total cover was not associated with grazing-induced changes in the cover of either short- or tall-stature plants (Figure 6A). However, grazing-induced increase in short-stature plant cover was mostly explained by grazing-induced increase in the cover of *A. frigida* (Figure 6B; $R^2 = 0.93$, $P < 0.001$). Likewise, grazing-induced reduction in tall-stature plant cover could be mainly attributed to grazing-induced changes in the cover of *A. pubescens* (Figure 6C; $R^2 = 0.92$, $P < 0.001$) and *L. chinensis* ($R^2 = 0.85$, $P = 0.003$).

The decreased total cover under wind erosion was primarily due to wind erosion-induced reduction in short-stature plant cover (Figure 6D; $R^2 = 0.99$, $P < 0.001$). In addition, wind erosion-induced suppression in *A. frigida* cover mostly accounted for the decrease in short-stature plant cover under wind erosion (Figure 6E; $R^2 = 0.99$, $P < 0.001$), and was associated with the reduction in soil N content under wind erosion (Figure 6F; $R^2 = 0.71$, $P = 0.018$).

The interannual variation of dust deposition-induced changes in total cover was mainly controlled by the changes in short-stature plant cover under dust deposition (Figure 6G; $R^2 = 0.71$, $P = 0.018$). Dust deposition-induced increase in tall-stature plant cover linearly increased with the change in *L. chinensis* cover under dust deposition (Figure 6H; $R^2 = 0.67$, $P = 0.025$). Multiple regression analyses confirmed the above results from simple linear regressions (Table S2).

Table 2. Summary (*P* values) of Two-Way RM-ANOVAs on the Effects of Grazing (*G*), Wind Erosion (WE)/Dust Deposition (DD), and Their Interactions Across the Four Treatments Included the Control, WE, *G*, and WE + *G* (for WE × *G*) and the Four Treatments Including the Control, DD, *G*, and DD + *G* (for DD × *G*). Respectively, on Soil Nitrogen (N) Content, Total Cover (TOT), Short- (SHS) and Tall-Stature (TAS) Plant Cover, the Cover of Six Dominant Species, Species Richness at Community (COM) and Functional Group Levels (SHS and TAS Plants), Gross Ecosystem Productivity (GEP), Ecosystem Respiration (ER), and Net Ecosystem Productivity (NEP)

Source of vari- ation	Soil N content	Vegetation cover			Dominant species cover					Species richness				Carbon-cycling variables			
		TOT	SHS	TAS	<i>A. frigida</i>	<i>P. acaulis</i>	<i>A. pubescens</i>	<i>A. cristatum</i>	<i>L. chinensis</i>	<i>S. krylovii</i>	COM	SHS	TAS	GEP	ER	NEP	
<i>G</i>	0.638	0.336	0.153	0.010	0.534	0.515	0.265	< 0.001	0.121	0.937	0.008	0.008	0.371	0.041	0.081	0.038	
WE	0.031 [−]	< 0.001 [−]	0.002 [−]	0.160 [−]	0.002 [−]	0.707 ⁺	0.260 [−]	0.835 [−]	0.268 [−]	0.731 ⁺	0.284 [−]	0.610 ⁺	0.003 [−]	< 0.001 [−]	< 0.001 [−]	< 0.001 [−]	
<i>G</i> × WE	0.823	0.614	0.797	0.439	0.363	0.083	0.215	0.078	0.530	0.939	0.570	0.826	0.091	0.051	0.155	0.042	
Year	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.028	0.015	< 0.001	0.114	0.002	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	
<i>G</i> × year	0.664	0.009	0.011	0.001	0.028	0.112	0.120	0.002	0.084	0.016	0.880	0.630	0.362	0.049	0.014	0.311	
WE × year	< 0.001	< 0.001	< 0.001	0.149	< 0.001	0.208	0.121	0.004	0.479	0.117	0.056	0.003	0.452	< 0.001	< 0.001	< 0.001	
<i>G</i> × WE × year	0.002	0.721	0.102	0.146	0.015	0.149	0.076	0.548	0.241	0.181	0.415	0.027	0.228	0.040	0.813	0.002	
<i>G</i>	0.542	0.022	0.092	0.010	0.028	0.203	0.055	0.036	0.535	0.317	0.001	0.010	1.000	0.222	0.130	0.331	
DD	0.705 [−]	0.023 ⁺	0.985 [−]	0.012 ⁺	0.804 [−]	0.822 ⁺	0.762 ⁺	0.835 [−]	0.667 ⁺	0.372 ⁺	0.004 [−]	0.019 [−]	0.938 [−]	0.476 ⁺	0.049 ⁺	0.592 [−]	
<i>G</i> × DD	0.121	0.357	0.592	0.345	0.243	0.821	0.761	0.957	0.988	0.417	0.150	0.453	0.537	0.248	0.207	0.346	
Year	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.118	0.002	< 0.001	0.031	0.028	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	
<i>G</i> × year	0.907	0.113	< 0.001	0.126	< 0.001	0.456	0.210	0.003	0.193	0.135	0.570	0.181	0.572	0.044	0.448	< 0.001	
DD × year	0.048	0.071	0.092	0.018	0.149	0.114	0.662	0.044	0.325	0.439	0.071	< 0.001	0.463	0.377	0.131	0.310	
<i>G</i> × DD × year	0.204	0.193	0.209	0.250	0.725	0.589	0.801	0.062	0.571	0.159	0.147	0.030	0.820	0.311	0.826	0.095	

These analyses were used to examine the main effects of wind erosion and dust deposition as well as their interactions with grazing.

Dominant SHS species: *A. frigida*, *Artemisia frigida*; *P. acaulis*, *Potentilla acaulis*. Dominant TAS species: *A. pubescens*, *Artemisia pubescens*; *A. cristatum*, *Agropyron cristatum*; *L. chinensis*, *Leymus chinensis*; *S. krylovii*, *Stipa krylovii*.

The bold numerals highlight the significance at $P < 0.05$.

The superscripts “−” and “+” represent negative and positive treatment effects, respectively.

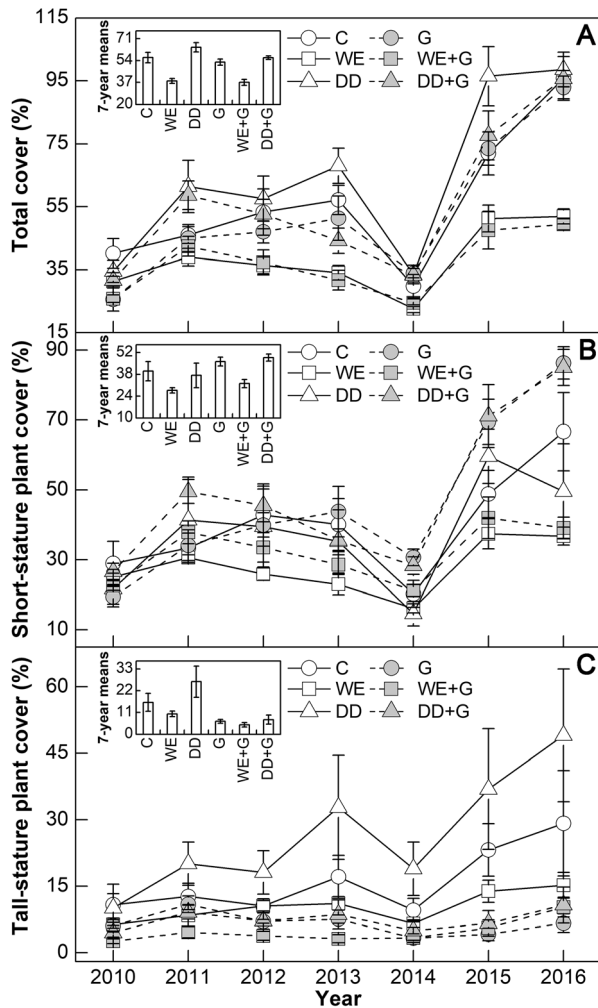


Figure 3. Annual dynamics and 7-year means (insets) of total cover (A), and short- (B) and tall-stature (C) plant cover under the six treatments. Data represent mean \pm 1 SE, $n = 5$. See Figure 2 for treatment abbreviations.

Factors Controlling Species Richness

Simple linear regressions showed that increased short-stature plant richness under grazing was associated with grazing-induced suppression in the tall-stature plant cover (Figure 7A; $R^2 = 0.67$, $P = 0.050$). In addition, dust deposition-induced decrease in species richness showed linear and positive dependences on the change in short-stature plant richness under dust deposition (Figure 7B; $R^2 = 0.89$, $P = 0.002$). Multiple regression analyses confirmed the above results (Table S3).

Ecosystem Carbon Fluxes Mediated by Shifted Community Composition and Structure

Across the seven experimental years, GEP was significantly decreased by 9.5% and 21.4% under grazing (Figure 8A; $P = 0.017$, Table 1) and wind erosion ($P < 0.001$, Table 2), respectively. However, neither dust deposition nor the interactions between grazing and wind erosion/dust deposition affected GEP. In addition, ER was reduced by 22.5% under wind erosion ($P < 0.001$), increased by 9.2% under dust deposition ($P = 0.049$), but was not influenced by grazing or its interactions with wind erosion/dust deposition. Moreover, grazing and wind erosion significantly decreased NEP by 11.7% ($P = 0.024$) and 20.1% ($P < 0.001$), respectively. Dust deposition did not influence NEP. Furthermore, there was a significant interaction between grazing and wind erosion on NEP ($P = 0.042$). Grazing reduced NEP by 0.2% without wind erosion and by 21.7% with wind erosion. Wind erosion decreased NEP by 10.5% without grazing and by 29.7% with grazing.

Simple linear regressions showed that wind erosion-induced decreases in GEP linearly increased with wind erosion-induced reductions in total cover (Figure 8B; $R^2 = 0.78$, $P = 0.008$) and short-stature plant cover ($R^2 = 0.77$, $P = 0.010$). The interannual variation of wind erosion-induced suppressions in ER was also controlled by the reductions in total cover (Figure 8C; $R^2 = 0.75$, $P = 0.018$) and short-stature plant cover ($R^2 = 0.74$, $P = 0.013$) under wind erosion. In addition, wind erosion-induced decreases in NEP were mostly explained by wind erosion-induced reductions in total cover (Figure 8D; $R^2 = 0.69$, $P = 0.020$) and short-stature plant cover ($R^2 = 0.67$, $P = 0.024$). Moreover, dust deposition-induced changes in ER showed linear and positive dependences on dust deposition-induced changes in species richness (Figure 8E; $R^2 = 0.53$, $P = 0.063$) and short-stature plant richness ($R^2 = 0.51$, $P = 0.070$). Multiple regression analyses partly confirmed the above results based on simple linear regressions (Tables S4-S5).

DISCUSSION

Grazing Effects on Grassland Plant Communities

Our finding that grazing reduced plant cover agrees with our Hypothesis 1 as well as the results of numerous previous studies (for example, Gwynne

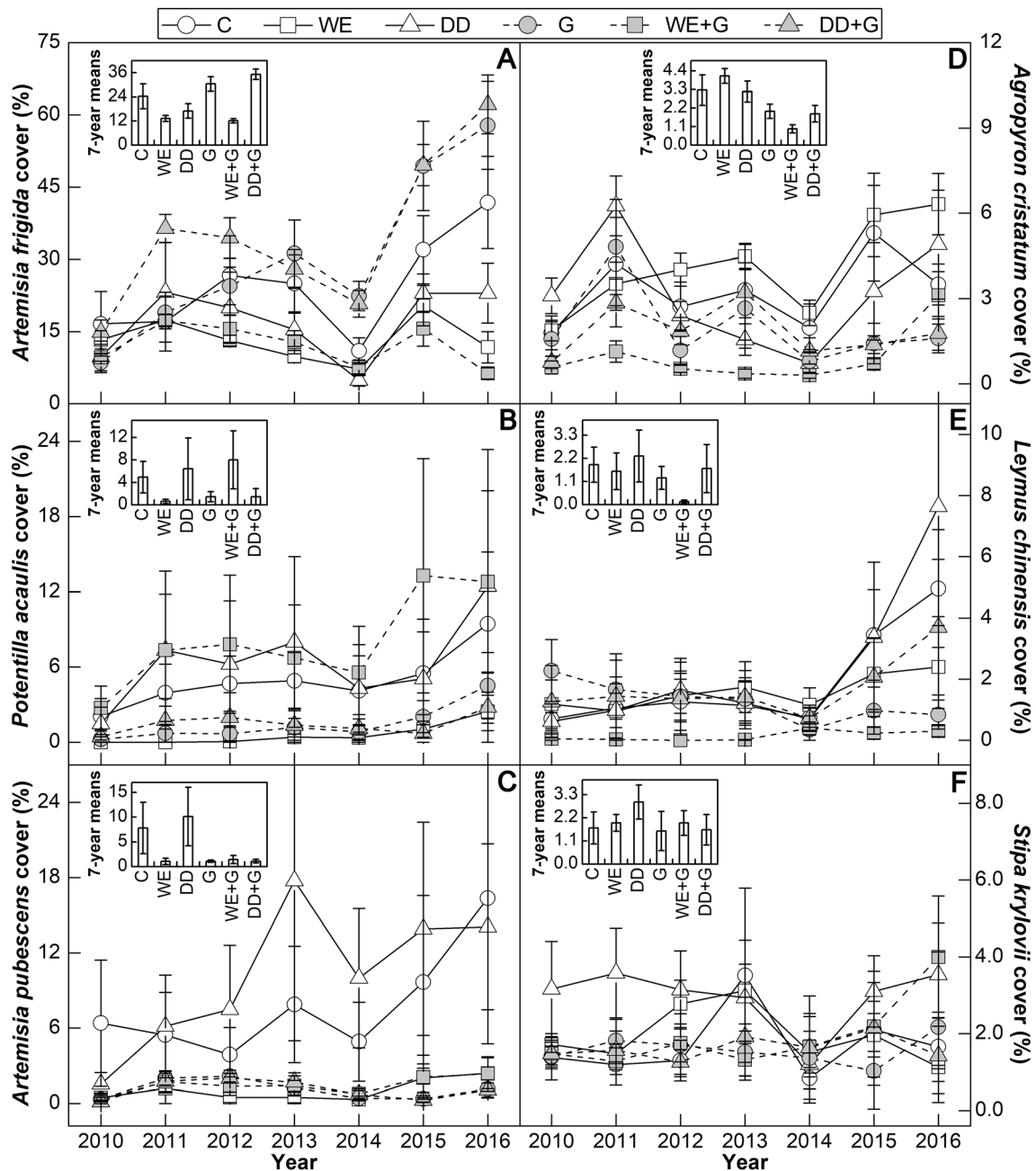


Figure 4. Annual dynamics and 7-year means (insets) of dominant short- (*A. frigida*, **A**; and *P. acaulis*, **B**) and tall-stature (*A. pubescens*, **C**; *A. cristatum*, **D**; *L. chinensis*, **E**; and *S. krylovii*, **F**) plant cover under the six treatments. Data represent mean \pm 1 SE, $n = 5$. See Figure 2 for treatment abbreviations.

and Bell 1968; Evju and others 2009; Ylänne and others 2015). When analysed separately by plant functional groups, grazing had negative impacts on tall-stature plants only, similar to previous studies reporting that grazing by herbivores could suppress competitively dominant species (Huntly 1991; Harris and others 2003; Borer and others 2014). Increased sub-canopy light availability for short-stature plants (Figure S5), as the result of grazing-

induced decline in tall-stature plant cover, may have been responsible for the observed increase in short-stature plant cover (Borer and others 2014).

Although grazing only significantly decreased the cover of *A. cristatum* within the tall-stature plant functional group, the responses of the cover of *A. pubescens* and *L. chinensis* to grazing explained much of the interannual variation of the grazing effects on tall-stature plant cover, suggesting that sheep

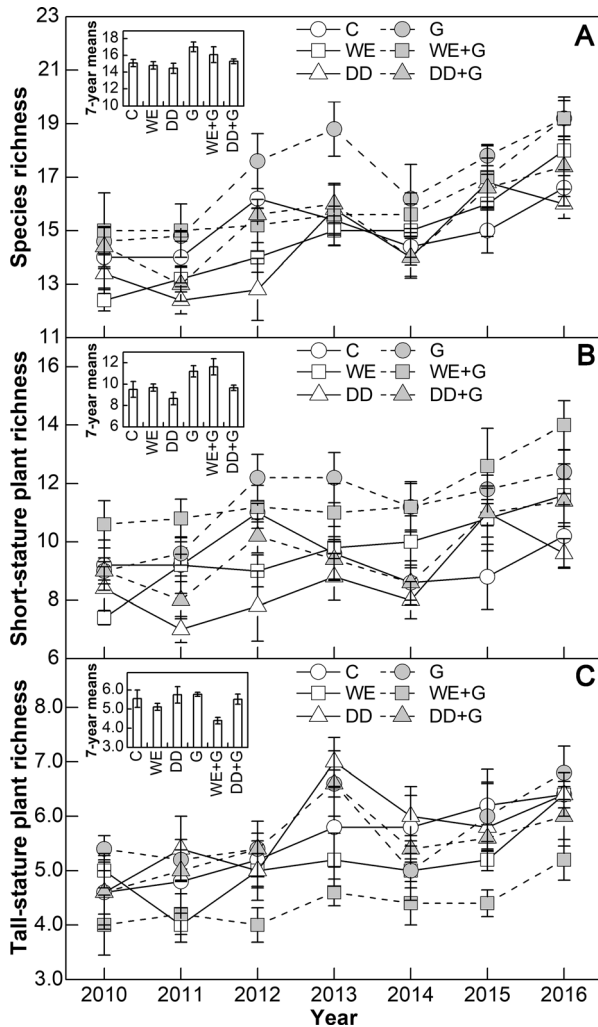


Figure 5. Annual dynamics and 7-year means (insets) of species richness (A), and short- (B) and tall-stature (C) plant richness under the six treatments. Data represent mean ± 1 SE, $n = 5$. See Figure 2 for abbreviations.

may selectively forage plants. These results agree with the findings of several previous grazing studies conducted in the grasslands of Inner Mongolia, that herbivores may preferentially forage *L. chinensis* (Chen and others 2005; Li and others 2008b; Zhao and others 2009). In addition, our result of grazing-induced sustained increase in the cover of *A. frigida* (Figure S6), as a member of the short-stature plants, is consistent with the widely held perception that *A. frigida* can be an indicator of grassland degradation due to overgrazing in Inner Mongolia (Chen and others 2005; Li and others 2008c; Wang and others 2014). In contrast, two other studies conducted in *A. frigida*-dominated grasslands in Inner Mongolia have revealed that grazing could reduce the cover of both *L. chinensis* and *A. frigida* (Barger and others 2004; Wang and others 2017).

This discrepancy could be primarily attributed to the emergence of *Potentilla acaulis* that is more adaptive to grazing than *A. frigida* in *A. frigida*-dominated grasslands (Li and others 2005).

Increased species richness under grazing is also consistent with our Hypothesis 1 and the findings of several previous studies (Collins and others 1998; Liu and others 2015; Köhler and others 2016), but is at odds with other studies reporting that grazing shows neutral or negative influences on plant diversity (Safford and Harrison 2001; Zhu and others 2012; Eldridge and others 2016; Li and others 2017; Jamsranjav and others 2018; Ren and others 2018). The different responses of species richness to grazing may be ascribed to the differences in grazing intensity, herbivore assemblages, pre-grazing plant diversity, and grassland types (Bullock and others 2001; Liu and others 2015; Su and others 2017). In our study, the reduction in tall-stature plant cover under grazing increased sub-canopy light availability, leading to increased coexistence of short-stature plants (Borer and others 2014; Niu and others 2016). These results imply that light availability may play an important role in regulating plant diversity responses to grazing (Hautier and others 2009; Borer and others 2014).

Impacts of Wind Erosion on Grassland Plant Communities

Decreased total cover under wind erosion in our experiment supports our Hypothesis 1. Our results indicate that decreased cover of short-stature plants, particularly that of *A. frigida*, was primarily responsible for the reduced total cover under wind erosion. In line with several previous studies that wind erosion could reduce soil nutrients (Neff and others 2005; Okin and others 2006; Li and others 2018; Lei and others 2019), the suppression in soil N content may potentially explain the decrease in the cover of *A. frigida* under wind erosion. In addition, as a dominant species in the functional group of short-stature plants (Table S1), *A. frigida* generally produces more adventitious roots, which mainly distribute in topsoil, rather than taproots (Zhanbula and others 1999; Li and others 2005). Probably also because of this reason, *A. frigida* suffers the most when wind erosion occurs and destroys biological and physical crusts of topsoil. The sustained reduction in soil N content under wind erosion, coupled with the vulnerable traits of *A. frigida*, may have been responsible for the increasing negative impacts of wind erosion on the cover of *A. frigida*, the short-stature plant functional

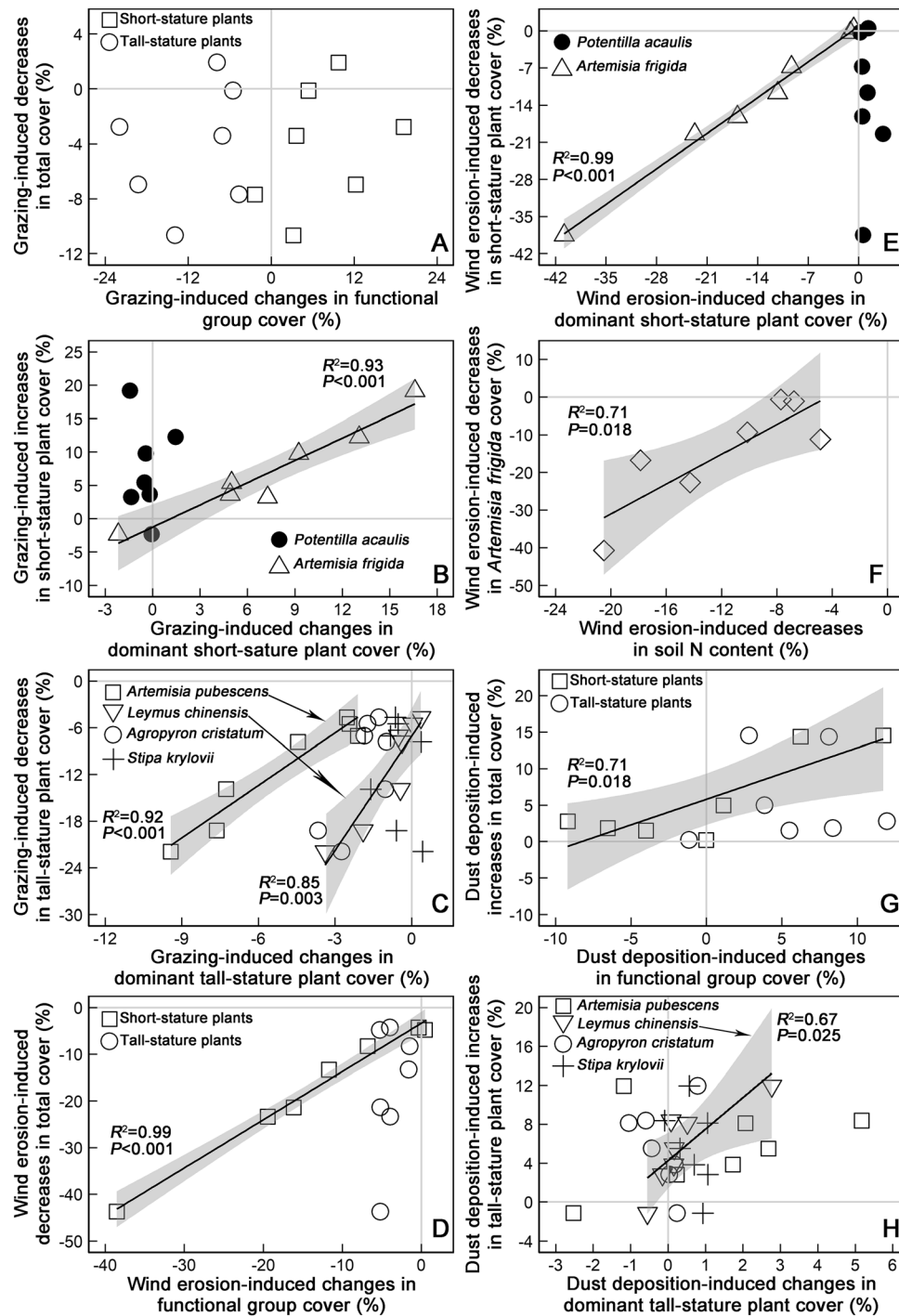


Figure 6. Dependences of grazing (G)-induced decrease in total cover on G-induced changes in short- (SHS) and tall-stature (TAS) plant functional group cover (A), of G-induced increase in SHS plant cover on G-induced changes in dominant SHS plant cover (B), and of G-induced decrease in TAS plant cover on G-induced changes in dominant TAS plant cover (C). Relationships of wind erosion(WE)-induced decrease in total cover with WE-induced changes in SHS and TAS functional group cover (D), of WE-induced decrease in SHS plant cover with WE-induced changes in dominant SHS plant cover (E), and of WE-induced decrease in *A. frigida* cover with WE-induced reduction in soil N content (F). Dependences of dust deposition (DD)-induced increase in total cover on DD-induced changes in SHS and TAS functional group cover (G) and of DD-induced increase in TAS plant cover on DD-induced changes in dominant TAS plant cover (H). Each data point represents treatment main effects on cover and soil N content in each year. Linear regression (solid line) and 95% CIs (shaded area).

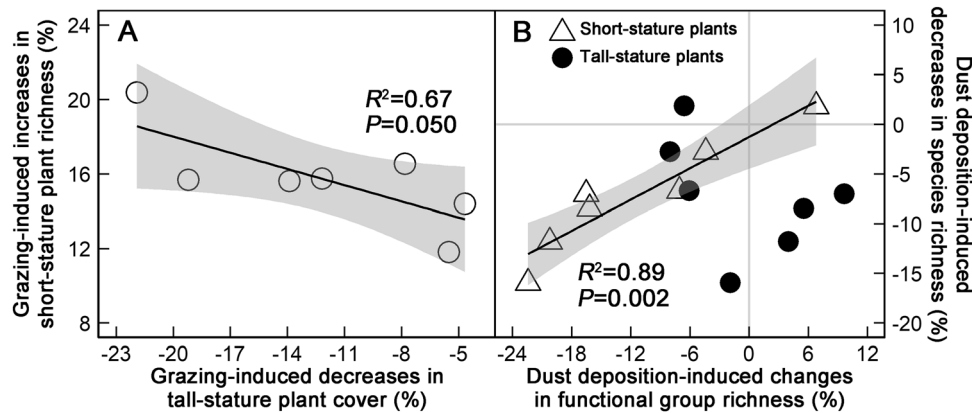


Figure 7. Dependences of grazing (G)-induced increase in short-stature plant richness on G-induced decrease in tall-stature plant cover (A) and of dust deposition (DD)-induced reduction in species richness on DD-induced changes in functional group richness (B). Each data point represents treatment main effects on species richness and cover in each year. Linear regression (solid line) and 95% CIs (shaded area).

group, and the whole community over the last several experimental years (Figure S6). Furthermore, the abrasion effects of wind erosion on young leaves of plants may be another potentially important mechanism suppressing plant growth and consequent vegetation cover (Okin and others 2001, 2006). Nevertheless, the methodology constraints in entirely mimicking natural wind erosion result in that this abrasion mechanism cannot be considered in this study. Thus, cautions should be taken when extrapolating our findings to other grasslands that are affected by natural wind erosion.

Our finding of the lack of species richness response to wind erosion is inconsistent with the component of our Hypothesis 1 that wind erosion-induced decrease in total cover may enhance light availability, and thus increase short-stature plant richness and consequent species richness (Hautier and others 2009; Borer and others 2014). This result emerged likely because wind erosion altered short-stature plant cover, but not tall-stature plant cover, resulting in little change in light availability (Figure S5). In addition, decreased tall-stature plant richness under wind erosion is, however, also partly at odds with our expectation that wind erosion could increase the dominance of plant species with high nutrient-use efficiency. For example, *S. krylovii* as a dominant tall-stature plant is known to have the highest leaf N-use efficiency among the 13 plant species measured in this study (Figure S7). Overall, our findings indicate that although wind erosion suppresses plant growth and tall-stature plant richness, short-stature plant richness and overall richness of this semi-arid temperate steppe show strong resistance to wind erosion-induced

topsoil disturbance imposed by our experimental manipulations.

Dust Deposition Effects on Grassland Plant Communities

Our finding of increased total cover under dust deposition is in agreement with our Hypothesis 2. Although no significant increase in soil N content under dust deposition was detected, dust deposition is known to increase soil nutrient pools in the dust deposited region (Reynolds and others 2001; Soderberg and Compton 2007; Neff and others 2008; Lawrence and others 2013), which presumably accounted for increased total cover of plant community in our experiment. Note that although dust deposition effects on short- and tall-stature plant cover together determine the interannual variation of total cover responses to dust deposition, increased tall-stature plant cover was primarily responsible for the enhancement in total cover. These findings emerged likely because that nutrient addition associated with dust deposition could increase the growth of species with higher light-competition ability (for example, *L. chinensis*, Figure 6H; Hautier and others 2009; Harpole and others 2016).

Consistent with our Hypothesis 2, we found a negative impact of dust deposition on species richness. We hypothesize that the reduction in species richness under dust deposition might be attributed to increased tall-stature plant cover, which would, in turn, reduce sub-canopy light availability for short-stature plants. However, our result did not support this mechanism, as indicated by the lack of response of light availability to dust

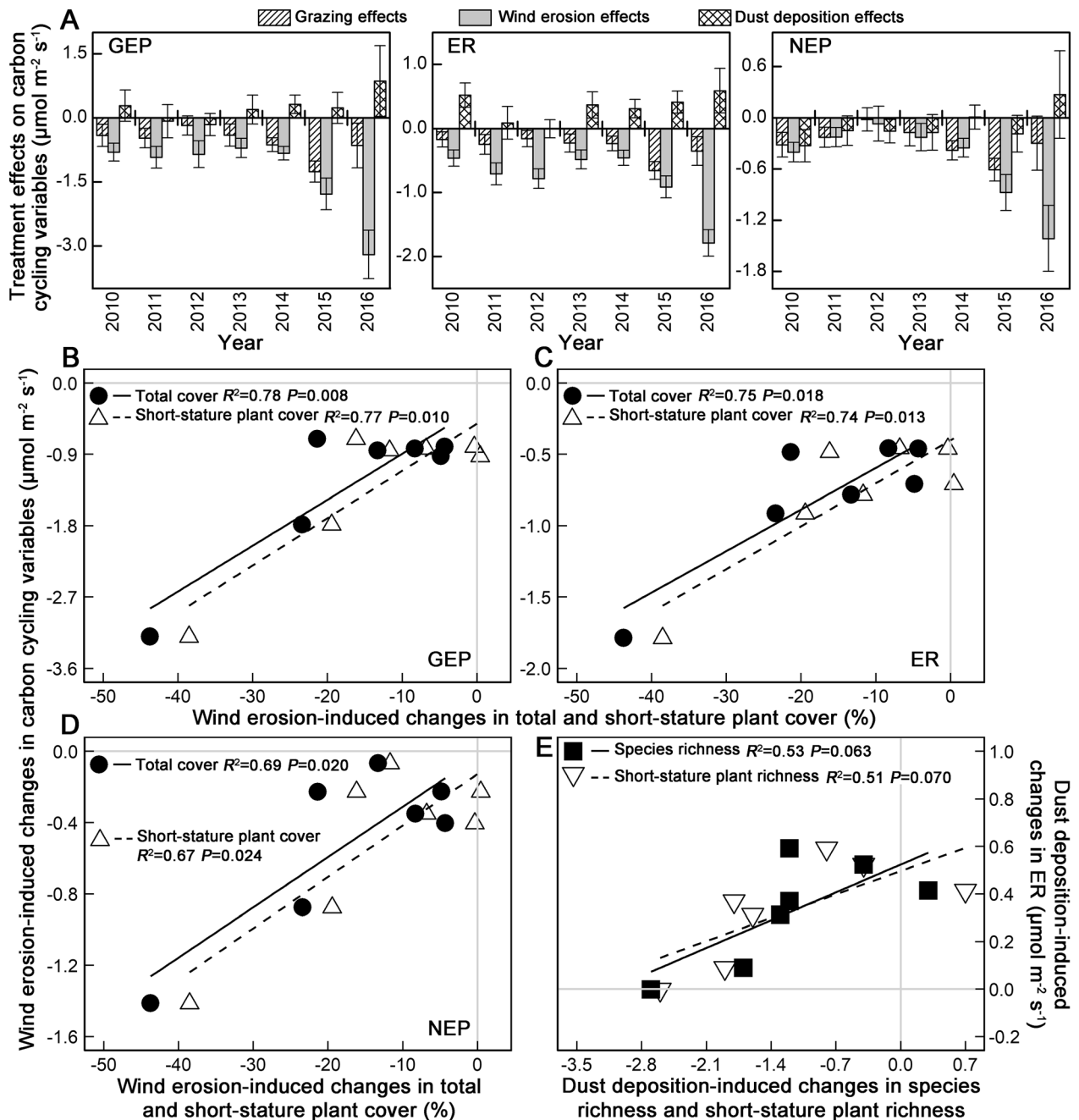


Figure 8. Main treatment effects on gross ecosystem productivity (GEP), ecosystem respiration (ER), and net ecosystem productivity (NEP) in the seven experimental years (**A**). Dependences of wind erosion (WE)-induced decrease in GEP (**B**), ER (**C**), and NEP (**D**) on WE-induced reductions in total and short-stature plant cover. Relationships of dust deposition (DD)-induced increase in ER with DD-induced reductions in species richness and short-stature plant richness (**E**). Each data point represents main treatment effects on carbon-cycling variables as well as vegetation cover and species richness in each year.

deposition (Figure S5) and the lack of association between the dust deposition-induced decrease in short-stature plant richness and the increase in tall-stature plant cover under dust deposition (Figure S8). Another possible mechanism, that the windblown dust deposited in the plots buried and

killed short-stature plants and plant seedlings (Okin and others 2001, 2006), may potentially explain the loss of short-stature plant richness under dust deposition (Figure 1). This mechanism is supported by the lower occurrence frequency for two short-stature plants (that is, *Astragalus scaber-*

rimus and *Astragalus galacties*, both canopy height < 5 cm) in dust deposition plots than plots without dust deposition (Table S6). Therefore, reduced short-stature plant richness under dust deposition primarily accounted for dust deposition-induced decrease in species richness (Figure 7B). It should also be noted that there was a shortcoming in our dust deposition simulation. Given that the surface soil of the wind erosion plots was gradually removed by the wind erosion treatments, the N content of the soil added to the dust deposition plots may decline over time (Figure 2B). By contrast, naturally deposited dusts always have high nutrient contents, because the process of dust emission can preferentially transport smaller particles of silt/clay and fine sand with higher nutrient contents to the deposited regions downwind (Okin and others 2006; Neff and others 2008; Field and others 2010). As a result, the effects of eutrophication associated with dust deposition on grassland communities might be underestimated in our study. When mimicking aeolian processes in further field studies, sieving the wind-eroded sediments with a finer mesh (for example, < 2 mm) and then spreading the collected soil with higher proportion of silt/clay and fine sand on the surface of dust deposition plots may better simulate natural dust deposition.

Interactive Effects of Grazing and Simulated Aeolian Processes

As demonstrated here and in previous studies (Gwynne and Bell 1968; Evju and others 2009; Yläne and others 2015), grazing may reduce plant community cover, leading to the loss of biological and physical soil crusts and the increase in bare soil area. Therefore, our Hypothesis 3 suggested that wind erosion may compound the negative impacts of grazing on plant community by further destroying the topsoil texture and accelerating nutrient loss. In addition, dust deposition may ameliorate the negative impacts of grazing on plant growth by increasing soil nutrient availability. However, in disagreement with our Hypothesis 3, we observed additive effects of grazing with wind erosion and dust deposition on both vegetation cover and species richness.

One possible mechanism to explain the additive effects between wind erosion and grazing in this experiment is that simulated wind erosion occurred earlier than grazing (early May vs. the middle of June–September) in each year and had stronger negative impacts on total cover than moderate grazing. For example, total cover was 19.4%

($P = 0.003$), 18.2% ($P = 0.004$), and 3.6% ($P = 0.476$) lower under the wind erosion plus grazing, wind erosion, and grazing treatments than in the control plots, respectively (Figure S9). By contrast, the additive effects between dust deposition and grazing may be attributed to that grazing effects overwhelmed the relatively small dust deposition effects.

Our experimental manipulations have decoupled grazing and wind erosion that usually occur simultaneously in grasslands (Belnap and others 2009; Nauman and others 2018). Therefore, the methodology used in this study can clearly reveal the independent effects of wind erosion and dust deposition on grassland plant communities by isolating the impacts of grazing, but might influence our ability to detect interactions between grazing and aeolian processes. Specifically, since our experimental design cannot account for the role of grazing in causing differing amounts of wind erosion due to trampling of crusts and decreasing vegetation cover, our results cannot directly infer how grazing and wind erosion interact to affect vegetation community parameters in a natural system. Caution should be taken when using our observations to parameterize wind erosion models or extrapolating our findings to the regional scale or other grasslands. Further studies need to be conducted to explore the interactive effects between grazing and wind erosion or dust deposition in natural setting as well as the interactive influences of wind erosion and dust deposition, and their interactive effects with grazing.

Implications of Grassland Plant Community Shifts for Carbon Cycling

Plant community composition and structure play important roles in regulating ecosystem carbon cycling (Maestre and others 2012; Dieleman and others 2015; Musavi and others 2017). Changes in community composition and structure in response to grassland management and natural hazards in the present study were driven by abiotic and biotic factors (that is, soil nutrients and plant canopy height). On the other hand, changes in community composition and structure could translate into changes in ecosystem functions. The observed positive dependences of wind erosion- and dust deposition-induced variation in ecosystem carbon-cycling exchanges (GEP, ER, and NEP) upon changes in vegetation cover and species richness point to close relationships of ecosystem carbon cycling with development and diversity of plant communities (Maestre and others 2012; Musavi

and others 2017). Our findings highlight the importance of changing plant community structure in response to grassland management and natural hazards in regulating ecosystem carbon cycling, with important implications for the sustainable management of ecosystem services under land-use practices and natural hazards in temperate grasslands.

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DATA AVAILABILITY

The data supporting our results in this manuscript were archived in figshare (<https://doi.org/10.6084/m9.figshare.12480077>).

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