Geoderma
Volume 385, 1 March 2021, 114828

Transformation of litter carbon to stable soil organic matter is facilitated by ungulate trampling

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https://doi.org/10.1016/j.geoderma.2020.114828

Highlights

- Trampling increased losses in litter mass and carbon by promoting soil-litter mixing.
- Trampling facilitated microbial assimilation and stabilization of litter carbon.
- Trampling increased soil organic carbon formation but did not affect priming effects.
- Trampling enhanced net soil organic carbon accumulation.

Abstract

Plant litter is an important source of soil organic carbon (SOC) in terrestrial ecosystem. The formation of SOC from plant litter and SOC mineralization to atmosphere is a critical determinant of long-term net ecosystem C balance. While it is generally understood that grazing plays a role in SOC cycling, what mechanisms are involved in driving SOC dynamic are not clear. Trampling enhances microbial processes by incorporating litter into the soil, likely influencing the fate of litter C and SOC mineralization. We conducted a controlled microcosm experiment to assess the role of trampling on the fate of litter C, litter-derived SOC mineralization (priming effect), and net C balance through incubation of ^{13}C isotopically labelled *Stipa krilovii* litter placed on the soil surface, or incorporated into soil via simulated trampling, for 6 months. Litter C transferred into the SOC pool was further fractionated into mineral-associated soil organic carbon pool (MASOC, <53 µm) and particulate organic carbon pool (POC, >53 µm). We analyzed soil enzyme activities and litter-derived microbial biomass carbon (MBC) to determine microbial activities. We found trampling increased overall losses in litter mass (+16%) and litter C (+14%), with proportionally more decomposed litter C transferred to SOC pools (MASOC + 47% and POC + 157%), compared to absence of trampling. The litter-derived MBC was positively correlated with SOC formation, which was increased (+40.78%) by trampling, indicting a stronger microbial contribution to SOC formation. The disturbance of trampling did not induce significant positive priming effects, consistent with invariant soil total MBC and soil enzyme activities following trampling. As a result, trampling induced an increase in SOC formation and invariant priming effect, which contributed to positive net soil C balance (-230.74 ± 89.44 vs 100.33 ± 32.65 mg C/kg soil). Our results show trampling incorporates litter into soil and promotes microbial uti

C and physiochemical stabilization of decomposed litter C, suggesting trampling is an important mechanism of SOC storage with litter C efficiently transferred into SOC pool. We demonstrate the importance of trampling in SOC formation and stabilization. Our findings indicate SOC formation efficiency from C input should be included in SOC predictive models in managed ecosystems.

Previous Next

Keywords

Grazing; Grasslands; Mineral-associated organic carbon; Particulate organic carbon; Soil organic carbon

1. Introduction

Globally, soil organic matter (SOM) is the largest organic carbon (C) pool in terrestrial ecosystems, containing more organic C than the atmosphere and global terrestrial vegetation combined (Lehmann and Kleber, 2015). Therefore, small changes in soil C pools may dramatically influence atmospheric CO_2 concentrations (IPCC, 2013). The balance between the formation of stable SOM and SOC mineralization is an important determinant of long-term ecosystem C dynamic (Cotrufo et al., 2013, Lehmann and Kleber, 2015). Grasslands cover ca. 40% of the earth's land surface and play a critical role in the global C cycle (Wang and Fang, 2009). Grazing is essentially universal in grassland ecosystems and is likely responsible for major processes of C cycling (Chen and Frank, 2020, McSherry and Ritchie, 2013, Zhang et al., 2013, Zhao et al., 2017). In fact, changes in the quality (Chen et al., 2015; Liu et al., 2015b; Wang et al., 2016, Wang et al., 2019) and quantity (Klumpp et al., 2009, Wang et al., 2016, Wang et al., 2019) of plant carbon inputs following grazing have been proposed to be the most important direct indicators explaining SOC. However, effects of grazing on cycling of plant inputs (i.e. contribution to SOC pools and effects on SOC mineralization) have not been quantified.

Plant litter (i.e. shoot and root litter) (Cotrufo et al., 2013, Hatton et al., 2015, Lorenz and Lal, 2005) and living root inputs (i.e. rhizodeposits) (Kuzyakov and Schneckenberger 2004) are the primary source of soil organic matter in terrestrial ecosystems. Up to 90% of plant photosynthate goes into soil in the form of litter (Cebrian 1999), and our understanding of how litter C stabilizes in soil is under-gonging a shift. A previous model for SOM formation reported litter C, which decomposes at a very slow rate, contributed substantially to stable SOM formation (Berg et al., 2008), and revised models emphasize the contribution of microbial catabolism and/or anabolism processes to SOM persistence (Cotrufo et al., 2015, Liang et al., 2017). Both field experiments (Cotrufo et al., 2015) and theoretical models (Liang et al., 2017) indicate that facilitation of SOM formation from litter decomposition involves two critical processes: (1) microbial carbon pump (i.e. litter C assimilated by microbes); (2) entombing effect (i.e. microbial necromass which includes dead microbial products and residues combined with metabolite stabilization via physical protection and/or chemical bonding). These two models also indicate greater SOM formation efficiency, as proportionally more litter C is incorporated into SOC pool after litter decomposition, benefiting soil C storage (Cotrufo et al., 2013). Additionally, plant inputs can accelerate or retard SOC decomposition, resulting in a positive or negative priming effect (Kuzyakov, 2010). The priming effect has been described as preferential substrate use (Cheng 1999), microbial mining of nitrogen from SOM (Fontaine et al. 2003; Fang et al., 2018a, Fang et al., 2018b), and/or co-metabolism of SOM with the utilization of added litter (Fang et al., 2018a, Fang et al., 2018b). The net C balance between accelerated SOC mineralization and newly formed SOC derived from added plant C determines soil C long-term storage (Fontaine et al., 2003). However, these current models do not include impacts and mechanisms of land management, such as grazing, on SOM formation processes and extent of priming effect, restricting our ability to predict soil C cycling in managed ecosystems.

Grazing is a complex interaction of livestock and grasslands, involving three mechanisms: defoliation, dung and urine return, and trampling, each of which may strongly influence processes of soil C storage (Liu et al., 2015b, Mikola et al., 2009). Trampling occurs in a high frequency and impacts feeding and non-feeding areas across grazed sites (Hobbs, 2010), and effects of trampling on ecosystem ecological processes are unexplored and likely underestimated (Heggenes et al., 2017, Rosenthal et al., 2012). Previous studies addressing effects of livestock trampling focus on: (1) effects on seed dispersal and germination (Eichberg and Donath, 2017, Horn et al., 2013); (2) plant cover (Heggenes et al., 2017), plant composition (Ludvikova et al. 2014),

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production (Drewry et al. 2008); (3) soil physical condition (Drewry et al., 2008, Ludvikova et al., 2014) and nutrient cycling (Schrama et al. 2013). Few studies have assessed the effects of trampling on soil C storage and cycling, although Liu et al. (2015b) demonstrated trampling may increase SOC storage through the promotion of plant allocation belowground, with subsequent increases in fungal abundance. It is known that trampling fragments plant material and promotes incorporation of litter into soil (Mancilla-Leytón et al., 2013), and this in turn promotes litter decomposition by facilitating microbial activity across diverse ecosystems (Hewins et al., 2013, Hewins et al., 2017, Lee et al., 2014). However, previous studies have focused on effects of trampling (or soil-litter mixing) on litter mass loss following microbial decomposition and photodegradation (Barnes et al., 2012, Hewins et al., 2013, Hewins et al., 2017, Lee et al., 2014, Liu et al., 2015a, Liu et al., 2018), and it is currently not known how trampling influences litter C contribution to SOC formation. Mixing plant material into soil induced greater C priming compared to surface applied treatments (Mitchell et al., 2016), indicating trampling may also increase mineralization of soil C. Positive priming effect following soil-litter mixing is most likely due to the promotion of enzyme production or increasing enzyme activity leading to a co-metabolic decomposition of SOC (Mitchell et al., 2016), indicating trampling may play an important role in litter-derived SOC dynamic and net soil C balance. Clarifying the role of trampling on litter decomposition, SOM formation and SOC mineralization is essential in determining C cycling in managed grasslands. The overall objectives of our work were to assess the influences of trampling on the fate of litter C and net C balance of SOC by regulating the processes of microbial degradation. We hypothesized that: (1) trampling promotes litter decomposition and SOC formation by facilitating litter-soil mixing and microbial assimilation of litter C and; (2) microbial activities are higher following trampling, compared to without trampling, with a concomitant greater priming effect.

2. Materials and methods

2.1. Soil and ^{13}C-labeled litter

Soil was collected from a typical steppe in the Duolun Restoration Ecology Station of the Institute of Botany of the Chinese Academy of Sciences (42°20′N,116°17′E), Inner Mongolia, China. After removing all aboveground plant material, soil was collected from the top 10 cm, sieved (2 mm) to remove rocks, roots, and other visible plant debris, and air-dried. The soil was derived from a semi-arid steppe with pH 6.4; sand = 495.8 g kg^{-1}; clay = 433.7 g kg^{-1}; silt 70.5 = g kg^{-1}; total carbon = 25.92 g kg^{-1}; total nitrogen = 2.20 g kg^{-1}.

Stipa krilovii seeds were collected from grasslands adjacent to the research station. *Stipa krilovii* is a perennial C_3 grass and a dominant species in this semi-arid steppe (Lu et al., 2017). Seeds were seeded into pots filled with soil (nutrient soil: buldymite: organic material = 1: 1: 1). Plants were watered twice a week to maintain growth, and after one month Hoagland's nutrient solution was added once each week. All pots were placed in an artificial climate chamber with an average humidity of approximately 60% under a 16/8h light/dark regime and 25/20°C. After three months, the plants were labelled with ^{13}C-CO$_2$ every ten days for one month. At each application, plants were labelled for three consecutive days. At each application, plants were placed into a sealed polyethylene plastic chamber (110 cm × 60 cm × 120 cm) filled with ^{13}C-CO$_2$ for 4 h (Lu et al., 2017). HCl was injected into labelled NaH^{13}CO$_3$ (98 atom%) positioned in the chamber on either side corner, and fans were installed above the NaH^{13}CO$_3$ to mix the air. Following the third and final application, ^{13}C- *S. krilovii* material (litter) was harvested, dried at 45°C, cut to 1–2 cm pieces, and homogenized. δ^{13}C value of the litter was +475.27‰, as determined by an isotopic ratio mass spectrometer (Isoprime 100, UK). These final values were considerably higher than natural abundance (average of −22‰). The litter contained 461.5 g C kg^{-1} and 16.2 g N kg^{-1}, yielding a C:N ratio of 28.5. The litter C:N ratio is lower than natural litter in the field (approximately 60–80), but we intended to obtain high δ^{13}C labelled litter to trace the fate of litter C with limited interest in the effects of litter quality.

2.2. Experimental design

Each 1.2 L incubation jar (d = 14 cm) was filled with 320 g of sieved and dried soil. The soil moisture was adjusted to 50% of water holding capacity (WHC) and soil density was adjusted to field density of 1.14 g cm^{-3} dry soil. Sixteen microcosms were preincubated at a 14/10 h light/dark regime and 30/20°C for one week. Litter was added to half of the microcosms, and the remaining half were set as controls with no litter addition. 1.2 g of δ^{13}C labelled litter was evenly spread on the surface of pre-incubated soil for each litter addition microcosm. Soil moisture was adjusted to 60% of WHC (approximately 15.75%) and was controlled gravimetrically throughout the incubation. Trampling treatments (without trampling and with trampling) were imposed onto both litter addition and control microcosms with four replications. Two empty jars were included

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controls (without litter and soil) to measure the background CO_2. Jars were hermetically sealed to avoid CO_2 and H_2O loss, incubated for 120 days, and opened every 5 (day 10 to 30) or 7 (day 30 to 120) days to allow aeration.

Trampling was simulated by a trampling device with a natural cattle hoof, using a standardized up- and down-movement of the hooves based on the principle of a second-class lever (Eichberg and Donath, 2017, Striker et al., 2006) (Fig. S1). The device simulates the effects of one 400 kg breeding cow, assuming an equal distribution of its weight on each of the four hooves (~82 cm^2 per hoof). The static load at the hoof is ≈120 kPa [(100 kg per 82 cm^2) × (98 · 06 kPa cm^2 kg^{-1})], and is dropped from 0.25 m high, simulating cattle trampling movement (Striker et al., 2006). In the first half of the incubation period (on days 0, 30, and 60), we conducted cattle trampling with one hoof drop each time to simulate the effects of trampling induced litter incorporation into soil (Fig. S2). The last half of the incubation period (from days 61 to 120) was included to further determine the effects of litter incorporation induced by repeated trampling. Each trampling treatment was coupled with water adjustment and aeration. Trampling processes were applied prior to water adjustment to minimize the influence of water loss during trampling. As the water was added frequently, soil moisture remained consistent throughout the study. If any soil adhered to the device after trampling, it was returned to the corresponding microcosm.

2.3. Measurements of total and ^{13}C mineralization

C mineralization was measured by an alkali trap placed on the soil surface. Specifically, a 50 mL bottle was filled with 18 mL 1 M (or 2 M) NaOH to absorb CO_2. At 2, 4, 6, 10, 20, 30, 45, 60, 75, 90, 105, and 120 days, NaOH was replenished in each jar, and the amounts of CO_2 and ^{13}C-CO_2 were determined. A 1 mL (or 0.5 mL) NaOH solution from each trap was titrated against 1 M HCl in the presence of excess 0.5 M $BaCl_2$ and 1 drop of phenolphthalein indicator using an autoanalyzer (Titrette 50 mL, Brand, Germany). The CO_2 derived from litter (CO_2-litter) was determined by precipitating a 10 mL aliquot of NaOH with 10 mL 0.5 M $BaCl_2$, and $BaCO_3$ precipitate was washed by distilled water for several times to obtain a neutral pH value. Finally, precipitate was vacuum filtered and dried at 40°C to quantify ^{13}C abundance using an elemental analyzer (vario PYRO cube, Elementar, Germany) coupled to an isotope ratio mass spectrometer (Isoprime 100, UK).

2.4. Sampling and analyses of litter and soil

Following 120 days of incubation, microcosms were destructively harvested. All litter was removed from each jar using tweezers, dried at 65°C for 2 days, and weighed. Litter was ground and litter C and N concentrations were analyzed by a CN elemental analyzer (vario MASOC cube, Elementar, Germany). The soil of each jar was uniformly mixed. A subsample of fresh soil was collected to measure microbial biomass carbon (MBC) and ^{13}C–MBC. Soil was air-dried and soil C% and ^{13}C%, SOC fraction and C% and ^{13}C% of each fraction, and enzyme potential activities were analyzed.

Air-dried soil was then ground to analyze C and ^{13}C, as described above for ^{13}C-$BaCO_3$. Soil C was fractionated into two distinct C pools: mineral-associated soil organic carbon pool (MASOC, <53 μm) and particulate organic carbon pool (POC, >53 μm) (Poeplau et al., 2018). The MASOC pool is stable over long time scales and considered to be slower-cycling than the POC pool (Lehmann and Kleber, 2015). A physical fractionation method was performed to separate SOC into these two pools, where soil samples (10 g air-dried soil) were shaken with 30 mL of chemical dispersant (sodium hexametaphosphate: NaHMP, 50 g L^{-1}) for 18 h at 200 rpm (Sokol et al. 2019a). After shaking, samples were passed through a 53 μm sieve in a vibratory sieve shaker (AS 200 control, Retch, Germany) with running water to ensure all MASOC was rinsed. Both fractions were dried at 65°C and weighed. Dried samples were milled and analyzed for C and ^{13}C as described above.

The MBC was assessed through the chloroform-fumigation-extraction method (Vance et al., 1987). Briefly, one subsample (20 g) was extracted with 50 mL 0.5 M K_2SO_4 solution and a second subsample (20 g) was fumigated with ethanol-free chloroform in the dark for 24 h, followed by extraction with 50 mL 0.5 M K_2SO_4 solution. The extracting solution was used to analyze total organic C concentration using a rapid CS analyzer (Multi N/C 3100, Analytik jena, Germany). MBC were calculated as the difference between fumigated and non-fumigated samples, adjusted by a proportionality coefficient 0.45. To analyze ^{13}C concentration of each solution, a 12-mL extracting solution was freeze-dried, and approximately 8 mg of resultant K_2SO_4-C were analyzed using mass spectrometry (Delta plus XP, ThermoFisher Scientific, America).

The potential activities of β-1,4-glucosidase, α-1,4-glucosidase and cellobiohydrolase involved in soil C cycling were measured using a 96-well microplates assay following modified methods of (Bell et al., 2013, Fang et al., 2018a). For each soil sample analysis, ~3 g air-dried soil was weighed and homogenized in 90 mL of 50 mM sodium acetate buffer and shaken for 30 min at 200 rpm. 800 μL of soil slurries and 200 μL of 200 μM of substrate (labeled with the 4-methylumbellifery (MUB) w

2 mL deep 96 well plate. The sample plates were incubated in the dark at 25°C for 3 h. In parallel, a 4-MUB standard plate was prepared for each soil sample. Serial dilutions of a 2 mM stock standard solution were performed to prepare seven different concentrations (0, 2.5, 5, 10, 25, 50, 100 μM). The standard plates were prepared similarly to sample plates, by adding 200 μL of each standard dilution to 800 μL of soil slurry followed by incubation. The quantity of fluorescence was measured using an automated fluorometric plate-reader (SpectraMax i3x, Molecular Devices, America) at 365 nm for excitation and 450 nm for emission. The enzyme activities were expressed as nmol activity g^{-1} dry soil h^{-1}.

2.5. Data analysis

We calculated the following:

The percentage of litter mass loss during decomposition (D):

$$\mathrm{D}(\%)=[(\mathrm{M_0}-\mathrm{M_t})/\mathrm{M_0}]\times 100 \tag{1}$$

where M_0 and M_t are the weights of dried litter before and after incubation, respectively. The percentage of litter C loss during decomposition:

$$\mathrm{D_C}(\%)=[(\mathrm{M_0}\times\mathrm{L_0}-\mathrm{M_t}\times\mathrm{L_t})/(\mathrm{M_0}\times\mathrm{L_0})]\times 100 \tag{2}$$

where D_C represents the C loss from litter, L_t and L_0 represents the final and initial C concentrations, respectively.

The contribution of litter-derived C to CO_2, soil SOC, SOC fractions and MBC pools followed the isotopic mixing model:

$$f_{litter} = (\delta_\mathrm{S} - \delta_\mathrm{B})\,/(\delta_\mathrm{litter} - \delta_\mathrm{B} \tag{3}$$

where f_{litter} is the fraction of litter-derived C contributing to CO_2, soil pools, and MBC; δ_S , δ_{litter}, and δ_B are the δ^{13}C of specific CO_2, soil pools, or MBC sample from the litter treatment (δ_S), the initial litter (δ_{litter}), and the control (δ_B) treatment, respectively. The pool size of litter-derived C was calculated by the specific C pool size multiply by f_{litter}.

Recovery of added litter carbon measured and calculated with above methods was 67% to 77% across all treatments (Fig. 2a). While our method is commonly used to track the fate of litter carbon (Córdova et al., 2018, Shahbaz et al., 2017a, Shahbaz et al., 2017b, Wu et al., 2019), incomplete recovery occurs in laboratory and field studies. For example, alkali traps absorb CO_2, but do not absorb other forms of C, such as CO and CH_4. Also, microbial colony adhering on litter surface may fall off during drying and weighing, resulting in C loss. However, our study focused on the formation of new SOC from litter C and balances of SOC pools, and inherent biases of litter carbon recovery likely had little influence on our results and conclusions.

Calculating the contribution of litter-derived C to MBC, the δ^{13}C of MBC was assessed following the isotopic mixing model (Fang et al., 2018b):

$\delta^{13}C_{MBC} = (\delta^{13}C_{fumi} \times C_{fumi} - \delta^{13}C_{non-fumi} \times C_{non-fumi})/(C_{fumi} - C_{non-fumi})$ (4)where C_{fumi}, $C_{non-fumi}$ are the mass of C in fumigated and non-fumigated samples, and $\delta^{13}C_{fumi}$, $\delta^{13}C_{non-fumi}$ are the δ^{13}C value of the fumigated and non-fumigated samples, respectively.

Efficiency of SOC formation, which evaluates the contribution of litter C to the SOC pool, was obtained as the ratio of litter-derived SOC to total litter C loss. The total litter C loss was calculated by the initial litter C content multiplied by the percentage of litter C loss (D_C).

The observed priming effect (cumulative primed C), defined as the acceleration or retardation of SOM decomposition by adding substances to soil, was calculated as the difference in the cumulative SOC mineralization between the 'with litter addition' and the 'without litter addition' treatments (Kuzyakova et al., 2000). The cumulative SOC mineralization was calculated by cumulative C mineralization minus the litter-derived C mineralization in each microcosm. We quantified the net soil C balance by calculating the trade-off between cumulative priming effect and the gain of litter-derived SOC.

The mineralization rate of litter C or soil C during decomposition under the trampling treatments was tested by repeated two-way ANOVAs with trampling and time as within-subject factors. The normality and homogeneity of variances of repeated data were examined with Shapiro-Wilk test and Mauchly's test, respectively. The mineralization rate of litter C at day 30 and 60, soil

C with litter at day 20 and 90, and priming effect at day 20 and 90 were determined to be non-normal, but we still included all data as the significance of within-subject factors did not differ between assessments with inclusion of non-normality data and assessments excluding these data. We used one-way ANOVAs for all the other data with trampling as fixed factor. When necessary, data were transformed using log or reciprocal functions to improve homogeneity of variance and /or normality of the data. The non-normality and/or non-homogeneity datasets were tested by Mann-Whitney *U* test. The normality of residues following ANOVAs were examined by Shapiro-Wilk test. Analysis was conducted in SPSS 19 (IBM Statistics, US). Figures were performed in OriginPro 9. The correlation between litter-derived SOC and litter-derived MBC and the significance of the correlation model were tested by basicTrendline packages in R software (3.6.0).

3. Results

Trampling significantly increased losses in litter mass ($P \leq 0.01$) and marginally significantly increased losses in litter C ($P \leq 0.10$) (Fig. 1a). Trampling increased litter mass loss and litter C loss by 16% and 14%, respectively, compared to the control (not trampled). Litter C mineralization rates were significantly influenced by the main effects of trampling and time, and interactive effects of trampling and time (Fig. 1b). Litter C mineralization rates were initially high in both treatments and decreased over time (Fig. 1b). Litter C mineralization rates increased following trampling, particularly early in the incubation (Fig. 1b), likely due to increased microbial proximity to litter.

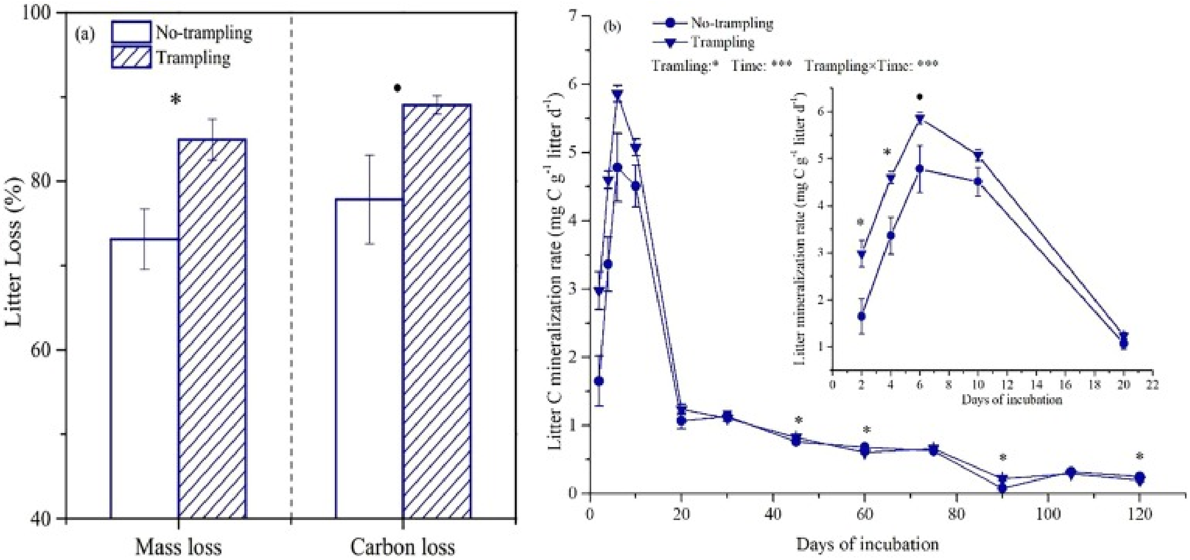

Fig. 1. The effects of trampling on litter mass loss and carbon loss (a). Litter C mineralization rate under trampling treatments (b). The data are the means of four replicates. The effects of trampling and sampling time on litter C mineralization rate were tested by repeated two-way ANOVA. Significant differences of litter C mineralization rate at day 30 and 60 were tested by Mann-Whitney *U* test. Significant differences of all the other data were tested by ANOVA; •: $0.05 < P < 0.1$; *: $0.01 < P < 0.05$; ***: $P < 0.001$.

The distribution of litter C was significantly influenced by trampling ($P \leq 0.05$) (Fig. 2a, Table 1). Specifically, compared to without trampling, trampling increased litter-derived SOC and cumulative litter C mineralization by 76% and 12%, respectively (Fig. 2a, Table 1). Trampling promoted the accumulation of litter-derived C into MASOC ($P \leq 0.\ 1$) and POC ($P \leq 0.05$) pools. C inputs following trampling formed 157% greater POC and 47% greater MASOC, compared to without trampling (Fig. 2a, Table 1). Trampling significantly increased efficiency of SOC formation by 58% ($P \leq 0.05$), compared to without trampling (Fig. 2b).

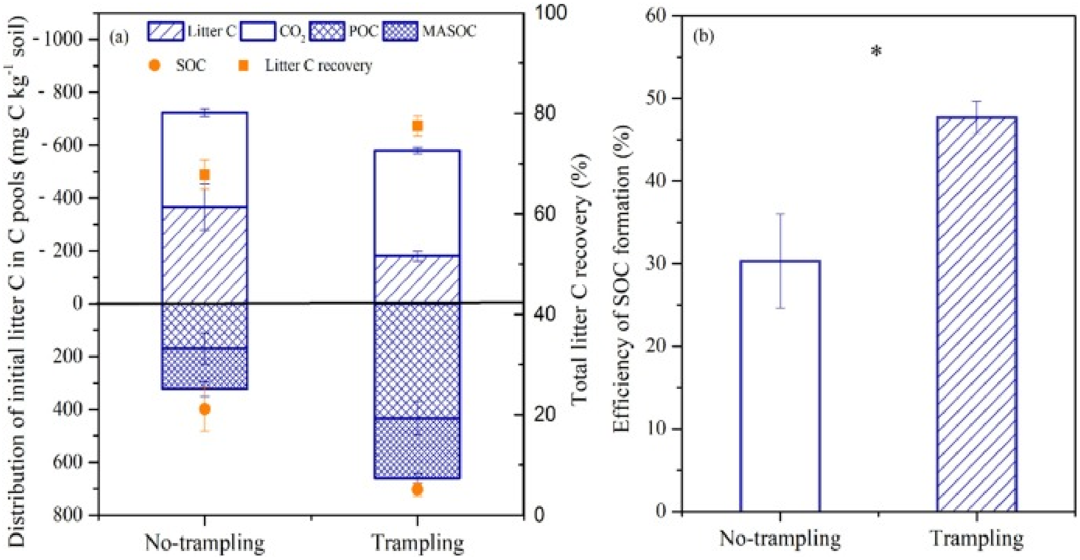

Fig. 2. The distribution of litter C into various pools following trampling or no trampling (control) (a), and efficiency of SOC formation derived from litter C following trampling (b). The data are the means of four replicates. Significant differences between treatments were tested by one-ANOVA; *: $0.01 < P < 0.05$.

Table 1. Effects of trampling on litter-derived soil organic carbon (SOC), cumulative litter C mineralization, litter-derived mineral-associated soil organic carbon pool (MASOC, <53 μm) and particulate organic carbon pool (POC, > 53 μm).

Response variable	**Df**	**F**	**P**
Litter-derived SOC (mg C kg^{-1} soil)	1	12.361	0.013
Cumulative litter C mineralization (mg C kg^{-1} soil)	1	5.213	0.063
Litter-derived MASOC (mg C kg^{-1} soil)	1	4.551	0.077
Litter-derived POC (mg C kg^{-1} soil)	1	9.156	0.023

Note: Significant differences between treatments were tested by ANOVA. Data provided in Fig. 2a.

Trampling did not significantly change activities of β-1,4-glucosidase, α-1,4-glucosidase, or total C-enzyme ($P > 0.05$) (Fig. S3). Litter addition alone significantly increased soil MBC (Fig. S4) and ^{13}C retention in microbial biomass was significantly increased by trampling ($P \le 0.05$), but the soil MBC after litter addition was not influenced by trampling ($P > 0.05$) (Fig. 3a). There was a positive relationship between litter-derived MBC and litter-derived SOC ($R^2 = 0.65$, $P \le 0.05$) (Fig. 3b).

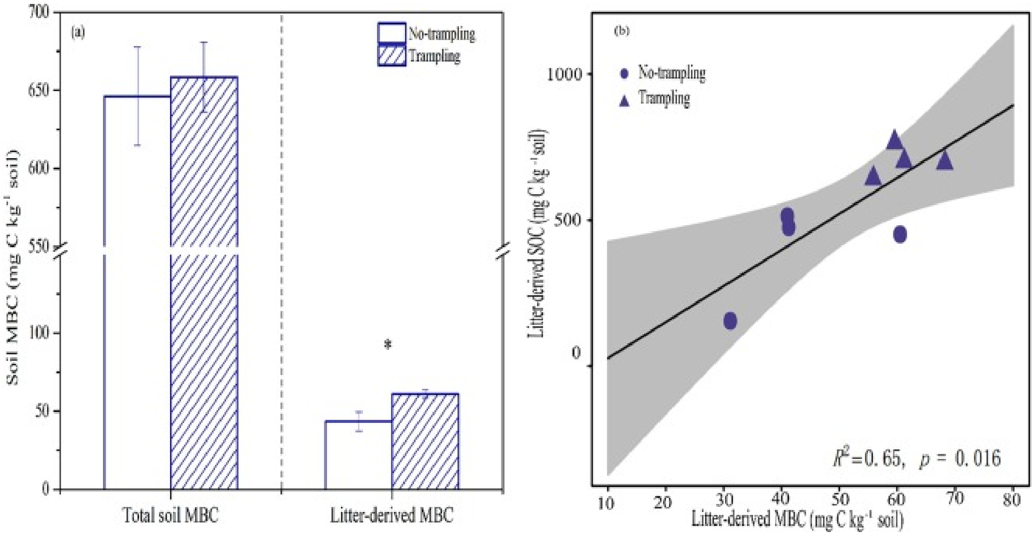

Fig. 3. Total microbial biomass carbon (MBC) and litter-derived MBC in soil following trampling (a), and the relationship between litter-derived MBC and litter-derived soil organic carbon (SOC) (b). The data are the means of four replicates for each treatment (trampling and no trampling) with litter additions. Significant differences between treatments were tested by ANOVA; *: 0.01 < P < 0.05.

SOC mineralization with litter addition was greater, as compared to without litter addition, which suggested litter addition stimulated positive priming effect (Fig. 4a). Rates of soil carbon mineralization and priming effect were initially high in both treatments and decreased over time (Fig. 4a).Trampling did not affect SOC mineralization rate and priming effect rate, nor did trampling effect cumulative SOC mineralization or cumulative priming effect (Fig. 4a). However, trampling did result in an increase in net soil C balance ($P \leq 0.05$), increasing net soil C balance by 27% (Fig. 4b).

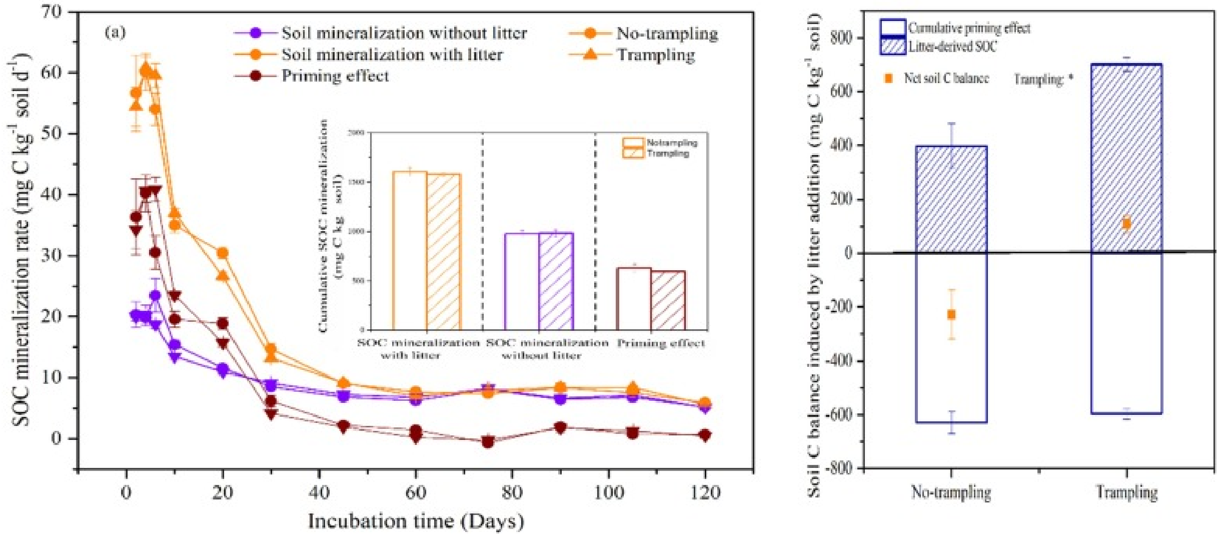

Fig. 4. Effects of tramping on cumulative soil organic carbon (SOC) mineralization with and without litter addition, and cumulative priming effect (PE) (a). Effects of tramping on net soil C balance (b). The data are the means of four replicates. The effects of trampling and sampling time on SOC mineralization rate were tested by repeated two-way ANOVAs. Significant differences in net soil C balance between treatments were tested by ANOVA; *: 0.01 < P < 0.05.

4. Discussion

Our study demonstrates trampling has significant effects on litter decomposition and SOC formation form litter C. The formation of stable SOM is critical to long-term net ecosystem C balances (Cotrufo et al., 2013, Lehmann and Kleber, 2015), however effects from grazing on SOM formation are not currently included in SOM predictive models. Our results show proportionally more litter-derived C is transferred to MASOC and POC pools, while SOC mineralization was not increased by litter addition following trampling, resulting in overall positive effects on net soil C balance. Our results indicate grazing influences litter derived soil C pools by influencing SOC formation efficiency, in which trampling plays a critical role in promoting soil C storage.

4.1. Trampling on litter decomposition and litter C transformation

Trampling induced burial of litter (Fig. S2) and subsequent formation of soil-litter films is considered to be one of the drivers that promote litter decomposition in drylands (Hewins et al., 2013, Liu et al., 2018). Under field condition, the major mechanism of soil-litter mixing is that attenuation of environmental extremes related to temperature, solar radiation, and litter moisture to create conditions favorable for microbial processes (Hewins et al., 2017, Lee et al., 2014). We found that trampling increased microbial incorporation of litter C in controlled favorable conditions, which supports previous suggestions that soil-litter mixing increases litter C accessibility for soil microbes by decreasing distance and promoting direct contact between litter and soil (Helgason et al., 2014, Mitchell et al., 2018, Mitchell et al., 2016). Moreover, trampling did not affect soil total MBC and soil enzyme activities, demonstrating that the larger contact surface between litter and soil due to soil-litter mixing under trampling increases opportunities for soil enzyme and microbes to break down litter C. Our results also indicate the positive effects of trampling on litter decomposition and SOC formation will become more pronounced when microbial activities are restricted by extreme environments.

The acceleration of fragmentation and comminution in response to trampling increased microbial and physical transfer of litter C into the SOM pool, as well as litter C mineralization. Trampling increased the proportion of decomposed litter C incorporated into the SOC pool, indicating that trampling has a positive effect on litter C preservation in soil C pools. There are two pathways of SOC formation: (1) *in vivo* microbial turnover in which litter C is first biosynthesized by microbes, followed by microbial necromass and metabolites incorporation into the SOC pool through associations with soil minerals; and (2) direct sorption of partially decomposed litter fragments (*ex vivo* modification) (Cotrufo et al., 2015, Liang et al., 2017, Sokol et al., 2019b). The greater litter-derived MBC in response to trampling, with positive relationships between litter-derived MBC and litter-derived SOC, indicates a promotion of litter C assimilated by microbes and a stronger potential of *in vivo* microbial pathways. The direct contact with soil microbes and mineral surfaces facilitates decaying litter fragments, microbial necromass, and metabolites for stabilization in aggregate C or organo-mineral associated C (Fulton-Smith and Cotrufo, 2019, Mitchell et al., 2018, Sokol et al., 2019b). Our research suggests trampling promotes an “entombing effect” and facilitates sorption and stabilization of litter-derived C. In addition, increasing stabilization of microbial necromass or metabolites decrease microbial reuse of newly formative SOC, with a concomitant increase in carbon use efficiency of decomposed litter C and SOM formation efficiency (Geyer et al., 2016). Higher efficiency of SOM formation following trampling does not necessarily correspond with high persistence of new soil C, and it may be important to consider cycling time (Cotrufo et al., 2015). Our results showed both the formation of fast-cycling (POC) and slow-cycling (MASOC) components of SOC were promoted by trampling, indicating that trampling increases the persistence of litter derived SOC through both SOC formation pathways.

Our experimental mesocosms design excluded positive effects of solar radiation which have been reported to play crucial roles in litter decomposition (defined as photodegradation) in arid and semi-arid ecosystems (Austin and Vivanco, 2006, Gallo et al., 2009, Wang et al., 2015). However, microbial decomposition has been previously reported to be more effective in altering lignin and other cell wall structures than photodegradation (Lin et al., 2018). Moreover, our results indicate litter burial also promotes an “entombing effect”, indicating trampling induced litter burial may show similar effects on litter decomposition (Liu et al. 2018), but stronger positive effects on SOC formation, compared to solar radiation exposure. Our results suggest the observed positive effects of trampling on SOC formation would remain unchanged in the presence of photodegradation.

Recent empirical evidence suggests soil-litter mixing is a crucial abiotic driver of relatively rapid litter decomposition rates, typically more rapid than what is predicted by models in arid and semi-arid ecosystems (Barnes et al., 2015). Ho

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researchers generalized soil-litter mixing was in response to wind- and water-borne soil movement (Hewins et al., 2017, Levi et al., 2020). Our research indicates disturbance from animal trampling is an important mechanism enhancing the process of soil-litter mixing. Furthermore, our results illustrate soil-litter mixing not only accelerates decomposition, but also promotes SOC formation efficiency from litter C. We propose the incorporation of soil-litter mixing into ecosystem models will not only improve the ability to predict decomposition rates and soil C dynamics (Hewins et al., 2017), but also SOC formation and storage in grasslands.

4.2. Trampling on priming effects and net SOC accumulation

Our study shows one mechanism driving positive effects of grazing on SOC is that trampling increases SOC formation from litter C, offsetting losses of SOC from mineralization, and ultimately enhancing net SOC accumulation. The addition of litter to soil induced a strong positive priming effect, which is in agreement with previous studies (Fang et al., 2018a, Wu et al., 2019). Litter addition alone significantly increased soil MBC (Fig. S4), indicating positive priming effect after plant C input is most likely due to co-metabolism of SOM (Chen et al., 2014, Fang et al., 2018a; Kuzyakova et al., 2000). Although trampling significantly influenced SOC mineralization rate at some sampling times (Table S1), trampling did not significantly influence the cumulative priming effect. Previous research reported C priming was enhanced when plant C was integrated into topsoil, compared to applications on the soil surface. This is likely because mixing disrupts soil structure and exposes previously inaccessible C to microbial activity (Mitchell et al., 2016). In our study, we observed little response in total MBC or soil enzyme activities following trampling. Our results suggest the disturbance strength of trampling was less than total mixing of soil and litter, and restricted trampling induced C priming. The effect strength of trampling on litter burial may be regulated by trampling intensity and plant coverage (Hewins et al., 2017, Levi et al., 2020). Trampling frequency in our experiment is likely lower than expected under field conditions (about 195 vs 405 steps m^{-2} per grow season under light grazing) (Chai et al., 2016). Levi et al. (2020) reported soil-litter mixing was greater in bare soil, compared to areas with grass cover, as bare soil is more sensitive to aeolian and fluvial disturbance than plant covered areas. Thus, the lower trampling in our study may underestimate the effects of trampling, while bare soil surface may amplify soil-litter mixing, counteracting low trampling intensity.

Previous studies have reported trampling may increase soil compaction and decrease soil pore space (Zhao et al., 2007), with a concomitant decrease in soil microbial activity and soil respiration (Chai et al., 2016, Hiltbrunner et al., 2012, Liu et al., 2015b). In our study, we focused on the direct effects of fragmenting and burial on aboveground litter decomposition and SOC formation. Additionally, the effect of trampling is expected to decrease soil mineralization with increased soil compaction (Chai et al., 2016), therefore it will not change the effect direction of trampling on net soil C balance if trampling results in substantial soil compaction.

4.3. The potential effects of trampling in managed grasslands

In arid and semi-arid natural grasslands dominated by perennial grasses, there are considerable amounts of standing litter that requires several months or even years to fall to the soil surface (Frouz et al., 2011, Pettersson and Hansson, 1990, Wang et al., 2017). Standing dead litter, typically greater than half of the total litter biomass, receives greater solar radiation, higher atmospheric temperatures, and higher night-time relative humidity (Wang et al., 2017). These abiotic conditions can lead to a 94% faster decomposition rate compared to surface litter, with greater C loss released to the atmosphere (Wang et al., 2017), as the lack of contact between standing litter and soil mineral surfaces restrict microbial necromass and litter fragment transfer into soil C pools (Lehmann and Kleber, 2015, Liang et al., 2017). Therefore, the rapid decomposition rate of standing dead litter can be inconsequential in terms of SOM formation. Trampling promotes incorporation of standing litter into soil, which may decrease the negative effects of standing dead litter on SOC formation, further facilitating SOC formation.

The potential effects of trampling on grassland ecosystems are highly variable and remain uncertain. While a positive effect of trampling on SOC formation and seedling emergence has been reported (Eichberg and Donath 2017), intensive ungulate trampling may induce degradation of soil structure, physical properties, and microbial properties (Drewry et al., 2008, Hiltbrunner et al., 2012). Trampling may also damage plants, thereby reducing grassland production (Drewry et al. 2008). The direction and magnitude of trampling effects are strongly correlated with soil characteristics (Drewry et al. 2008), water content (Drewry et al., 2008, Heggenes et al., 2017, Menneer et al., 2005), trampling intensity and timing (Drewry et al., 2008, Heggenes et al., 2017, Miller et al., 1999). Thus, more research is needed to obtain a more holistic picture of abiotic and biotic processes across multiple grassland ecosystems to determine the overall benefits of trampling in grassland management.

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5. Conclusions

Our study demonstrates trampling has strong effects on litter decomposition and litter C allocations. Indeed, our study is the first to show trampling increases litter C transfer into soil during litter decomposition and promotes net soil C balance. Trampling resulted in 157% greater fast-cycling fraction (POC) and 47% greater slow-cycling fraction (MASOC) of SOM formation from litter C, suggesting trampling facilitates litter C storage in the SOC pool, extending C cycling time. Trampling presumably facilitates microbial assimilation of litter C (+40.80%) and increases the close connections of microbial necromass and litter fragments with soil minerals. Increase of SOC formation following trampling (398.66 ± 82.45 vs 701.94 ± 25.36 mg C/kg soil) offsets SOC mineralization (629.40 ± 19.91 vs 601.61 ± 12.59 mg C/kg soil), resulting in an overall positive effect on net soil C balance (-230.74 ± 89.44 vs 100.33 ± 32.65 mg C/kg soil) (Fig. 5). Our study indicates trampling is an important mechanism of SOC stabilization by increasing the efficiency of litter C transfer into the SOC pool, and therefore should be included in SOM predictive models. However, effects of trampling on C-cycling are controlled by both abiotic and biotic conditions (e.g. trampling intensity, soil moisture, atmospheric conditions, etc), and trampling may have indirect effects, such as injure to plants, decrease in plant production, or compaction of soil. Therefore, the biotic and abiotic effects of trampling across multiple grassland ecosystems should be considered and further studied, prior to an overall management recommendation for livestock trampling on grasslands to increase soil SOC stabilization.

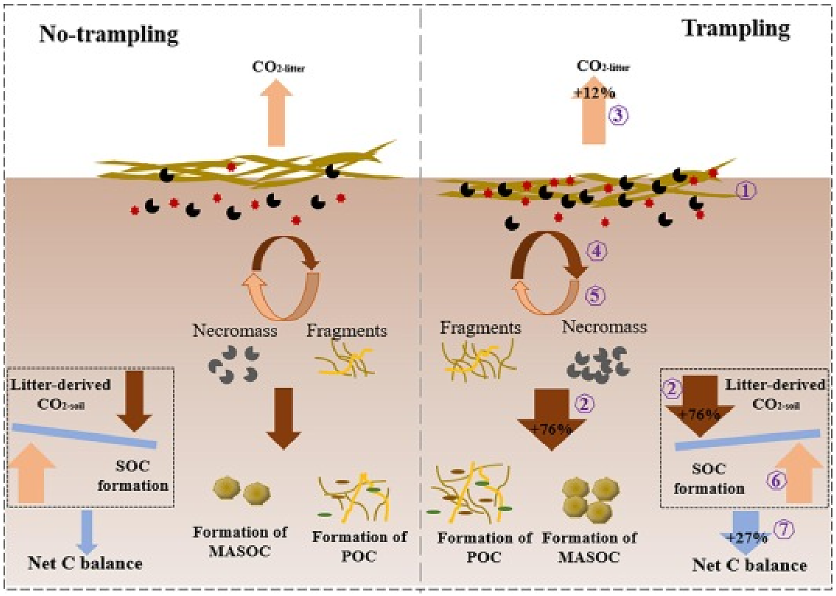

Fig. 5. The potential mechanisms regulating litter C distribution following trampling. Trampling facilitates litter mixing with soil (1) and promotes SOC formation from litter C (2) and litter C mineralization (3). Soil-litter mixing following trampling promotes microbial utilization of litter C (4) and decreases microbial reuse of necromass (5), thus may increase the microbial assimilation and physiochemical stabilization of litter C. As a result, more proportion litter C is transferred to soil MASOC and POC pools following trampling. Trampling shows limited influence on litter-derived SOC mineralization (priming effect) (6). Ultimately, trampling induced SOC formation offsets loss of SOC from mineralization after litter C addition, enhancing the net SOC accumulation (7).

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.

Acknowledgements

We thank the Duolun Restoration Ecology Station of the Institute of Botany of the Chinese Academy of Sciences for providing the research sites. We also thank Ye Wu and Ping Zhou for their assistance with trait measurements. We also thank Dr. Gaowen Yang for assistance with our schematic diagram and Dr. Junyi Liang for his edits on an earlier draft of our manuscript.

The research was supported by the earmarked fund for the National Natural Science Foundation of China (31971748), (31830092), innovation talent plan of national forestry and grassland science and technology (2019132608).

Appendix A. Supplementary data

The following are the Supplementary data to this article:

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Supplementary data 1.

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