Vegetation Biomass Dynamics and Its Relationship with Soil Carbon During the Restoration of Degraded Sandy Grasslands: Postprint

Authors: Zhou Jing, Sun Yongfeng, Jieping Ding, Bai Haojiang, Ma Xiang, Wang Xuyang, Luo Yongqing

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Abstract

Plant biomass allocation characteristics and material input to soil constitute critical processes in the restoration of degraded sandy grassland ecosystems, particularly regarding soil carbon content enhancement. This study examined mobile dunes, semi-fixed dunes, fixed dunes, and enclosed grasslands representing different restoration stages in the Horqin Sandy Land, investigating herbaceous vegetation biomass allocation patterns, root traits, and soil physicochemical properties to elucidate the interrelationships among biomass allocation, root traits, and soil carbon. Results demonstrated that with progressive restoration of desertified grasslands, aboveground biomass, root biomass, surface litter, and underground residues exhibited significant increasing trends ($P<0.01$). Compared with severely desertified mobile dunes, total plant dry matter (biomass + litter) in semi-fixed dunes, fixed dunes, and enclosed grasslands increased by 11.0%, 116.3%, and 151.2%, respectively. Soil carbon content increased significantly with grassland restoration ($P<0.05$), with higher accrual rates in the 0~10 cm layer than in the 10~20 cm layer. Structural Equation Modeling (SEM) analysis revealed that soil carbon content in the 0~10 cm layer was influenced by surface litter, underground residues, and root surface area, whereas soil carbon content in the 10~20 cm layer was affected only by underground residues and root surface area. Furthermore, soil carbon content in both layers showed no significant relationship with aboveground biomass. These findings indicate that during degraded sandy grassland restoration, soil carbon content is primarily regulated by litter input and root traits rather than by aboveground biomass per se.

Full Text

Changes in Vegetation Biomass and Its Relationship with Soil Carbon During the Restoration of Degraded Sandy Grasslands

ZHOU Jing[1], SUN Yongfeng[2], DING Jieping[1], BAI Haojiang[3], MA Xiang[4], WANG Xuyang[3], LUO Yongqing[3]

[1]Gansu Academy of Eco-environmental Sciences, Lanzhou 730020, Gansu, China
[2]CSCEC AECOM Consultants Co., Ltd., Lanzhou 730000, Gansu, China
[3]Northwest Institute of Eco-Environment and Resources, Chinese Academy of Sciences, Lanzhou 730000, Gansu, China
[4]Academy of Animal Science and Veterinary Medicine, Qinghai University, Xining 810016, Qinghai, China

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Abstract

The allocation pattern of plant biomass and its input into soil are critical processes for restoring degraded sandy grassland ecosystems, particularly for enhancing soil carbon content. This study investigated mobile dunes, semi-fixed dunes, fixed dunes, and fenced grasslands at different restoration stages in the Horqin Sandy Land. We analyzed herbaceous vegetation biomass allocation characteristics, root traits, and soil physicochemical properties to clarify the relationships between biomass allocation, root traits, and soil carbon. The results revealed that aboveground biomass, root biomass, surface litter, and underground necromass all increased significantly ($P<0.05$) as desertified grasslands were restored. Compared to severely desertified mobile dunes, the total dry matter (biomass plus litter) in semi-fixed dunes, fixed dunes, and fenced grasslands increased by 11.0%, 116.3%, and 151.2%, respectively. Soil carbon content also increased significantly ($P<0.01$) with restoration, with a higher accumulation rate in the 0–10 cm layer than in the 10–20 cm layer. Structural equation modeling showed that soil carbon content in the 0–10 cm layer was influenced by surface litter, underground necromass, and root surface area, whereas soil carbon content in the 10–20 cm layer was affected only by underground necromass and root surface area. Notably, soil carbon content in both layers showed no significant relationship with aboveground biomass. These findings indicate that during the restoration of degraded sandy grasslands, soil carbon content is primarily influenced by litter input and root traits rather than by aboveground biomass directly.

Keywords: degraded sandy grassland; soil carbon content; plant biomass; litter; root traits

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Introduction

Grasslands are among the most important terrestrial ecosystems on Earth, providing critical ecological benefits such as carbon sequestration, oxygen release, water conservation, climate regulation, and wind erosion prevention, alongside socioeconomic values like food production. However, since the mid-20th century, grasslands in northern China have experienced varying degrees of degradation due to intensified human activities and natural climate change. Research indicates that desertified land in northern China has been expanding at an accelerating rate since the 1950s, with national desertification area reaching 2.84×10^{6} km^{2} by 2009 and 3.34×10^{6} km^{2} by 2014. This desertification has substantially diminished ecosystem services including wind erosion control, hydrological regulation, and soil conservation.

Land desertification triggers structural changes and functional decline in ecosystems, manifested as reduced vegetation productivity, decreased species diversity, diminished carbon sequestration capacity, lower livestock productivity, and increased sandstorms. Since the mid-20th century, China has implemented major ecological restoration initiatives such as the "Three-North" Shelterbelt Program, which have effectively restored degraded sandy grasslands in northern China. Between 2009 and 2014, the area of mobile sand dunes decreased by 89.2×10^{3} hm^{2}. However, insufficient alignment between ecological projects and regional resource endowments—such as reduced water availability amid agricultural expansion—has led to declining stability of restored grassland ecosystems. Therefore, investigating the relationships among vegetation-soil system components across restoration sequences in degraded sandy grasslands and identifying the driving mechanisms of key ecosystem functional indicators can provide theoretical foundations for targeted restoration management and enhanced regional ecosystem services.

Soil carbon sequestration represents a vital function of grassland ecosystems, influenced by vegetation processes including productivity, root turnover, and litter production and allocation. In degraded sandy grasslands, vegetation restoration significantly promotes soil carbon sequestration capacity, with vegetation productivity considered a key factor affecting soil carbon storage. However, some studies have reported weak correlations between vegetation productivity and soil carbon content. While linear relationships between fine root length, root surface area, and soil carbon storage have been validated, the underlying mechanisms—including interrelationships among root traits and specific contributions of individual traits—remain unclear. Additionally, the influence of litter on soil carbon sequestration during restoration, particularly the specific processes through which litter input affects soil carbon, is not well understood. Systematic research on biomass allocation, key plant traits, and their relationships with soil carbon content is essential for understanding soil carbon sequestration processes in degraded sandy grasslands, thereby supporting regional carbon budget modeling and enhancing ecosystem carbon sequestration potential.

1.1 Study Area Overview

This study was conducted in Naiman Banner, Tongliao City, Inner Mongolia (42°55 -42°57 N, 120°41 -120°45 E), located in the southern-central Horqin Sandy Land [Figure 1: see original paper]. The region features a temperate continental climate with dry winters and springs, frequent strong winds, an annual precipitation of 335 mm concentrated in summer (June–August), annual evaporation of 1500–2500 mm, and a mean annual temperature of 6.7°C. The elevation ranges from 340–350 m. The soil is primarily aeolian sandy soil, with soil carbon predominantly composed of organic carbon. Previous studies have shown that in the Horqin Sandy Land, soil carbon and nitrogen changes during desertification and restoration mainly occur in the 0–20 cm layer, with organic and inorganic carbon contents in the 0–10 cm layer of fenced grasslands being $1.04\ \mathrm{g \cdot kg^{-1}}$ and $0.07\ \mathrm{g \cdot kg^{-1}}$, respectively.

Since the mid-20th century, intense human activities (particularly grazing) have caused severe degradation, with mobile dunes covering up to 69.5% of the area. However, since the 1980s, implementation of protective policies such as seasonal grazing bans and total enclosure has facilitated vegetation recovery, creating a typical mosaic landscape of dunes and interdune lowlands comprising mobile dunes, semi-fixed dunes, fixed dunes, and grasslands enclosed for >25 years. Dominant shrubs include *Caragana microphylla*, *Salix gordejevii*, and *Artemisia halodendron*, while herbaceous species are primarily *Cleistogenes squarrosa*, *Pennisetum centrasiaticum*, *Corispermum macrocarpum*, *Salsola collina*, and *Setaria viridis*.

1.2 Experimental Design and Sampling

During the peak growing season (late August to early September), we selected mobile dunes, semi-fixed dunes, fixed dunes, and fenced grasslands (>25 years) as survey sites along the restoration gradient, based on the main desertified grassland types and their distribution patterns in the study area. Site selection followed the dune fixation evaluation criteria of Zhao et al. [2008]. A total of 32 survey plots were established across the four restoration stages (detailed vegetation information in). At each plot, three 1 m × 1 m quadrats were randomly established for biomass, litter, and soil carbon surveys.

For aboveground components, after clipping vegetation at ground level, surface litter was collected. Both samples were placed in cloth bags and transported to the laboratory. For belowground components, after aboveground biomass and litter collection, three sampling points were established along the diagonal of each quadrat. Root cores (0–10 cm and 10–20 cm layers) were collected using a root auger (100 mm diameter). Samples from the same layer were mixed and bagged. Subsequently, five sampling points were arranged in a quincunx pattern within each quadrat, and soil samples (0–10 cm and 10–20 cm layers) were collected using a soil auger (28 mm diameter), mixed by layer, and stored in sealed bags for physicochemical analysis.

1.3 Laboratory Analysis

Aboveground samples were washed with tap water, air-dried, oven-dried at 65°C for 48 hours, and weighed to determine aboveground biomass and surface litter mass. For belowground samples, root cores were washed to remove soil, and living roots were manually sorted based on shape, color, and elasticity; the remaining material was classified as underground necromass. Underground necromass was oven-dried at 65°C for 48 hours and weighed. Sorted roots were air-dried, scanned at 200 dpi using an HP G4010 scanner, and analyzed with WinRHIZO software (Régent, Canada) to obtain root length, surface area, and volume. Root tissues were then oven-dried at 65°C for 48 hours and weighed.

Soil samples were air-dried, sieved (2 mm mesh) to remove impurities, ground, and analyzed for carbon content using an elemental analyzer (Vario Macro cube, Elementar, Germany).

1.4 Data Analysis

Data analysis was performed using SPSS 20.0 and R. One-way ANOVA was used to compare dry matter allocation among restoration stages. Two-way ANOVA was applied to analyze root traits and soil carbon content across restoration stages and soil depths. Relationships between soil carbon content and vegetation dry matter allocation were examined using structural equation modeling (SEM) in the lavaan package. Data in figures and tables are presented as means ± standard error.

2.1 Changes in Vegetation Dry Matter During Restoration

Vegetation dry matter increased significantly ($P<0.05$) with restoration (Table 2). Compared to mobile dunes, surface litter, underground necromass, aboveground biomass, and root biomass in fenced grasslands increased by 361.1%, 105.5%, 252.4%, and 196.1%, respectively. During the early restoration stage (mobile to semi-fixed dunes), dry matter accumulation was relatively slow, with significant increases only in surface litter and aboveground biomass ($P<0.05$). In terms of allocation proportions, the belowground fraction (root biomass + underground necromass) decreased markedly during restoration, primarily due to reduced underground necromass, while the aboveground fraction (surface litter + aboveground biomass) increased gradually [Figure 2: see original paper].

2.2 Root Traits

Root trait analysis revealed differential changes among traits and soil depths during restoration [Figure 3: see original paper]. Root diameter showed no significant differences among restoration stages ($P>0.05$). Root length and surface area increased significantly along the restoration gradient ($P<0.05$), though differences among semi-fixed dunes, fixed dunes, and fenced grasslands were not significant ($P>0.05$). Root volume increased significantly with restoration in both layers ($P<0.05$), with greater increases in the 0–10 cm layer. Significant vertical differences ($P<0.05$) were observed for all traits except root diameter. Specific root length and specific surface area were significantly higher in fixed dunes than in other stages ($P<0.05$), with no significant differences among mobile dunes, semi-fixed dunes, and fenced grasslands ($P>0.05$).

2.3 Changes in Soil Carbon Content During Restoration

Soil carbon content increased significantly with restoration ($P<0.01$), with more pronounced increases in the 0–10 cm layer (Table 3). Compared to mobile dunes, soil carbon in the 0–10 cm layer increased by 33.3%, 62.0%, and 339.3% in semi-fixed dunes, fixed dunes, and fenced grasslands, respectively. In the 10–20 cm layer, soil carbon was 16.7%, 119.4%, and 208.3% higher in semi-fixed dunes, fixed dunes, and fenced grasslands, respectively. Significant vertical differences existed, with higher carbon content in the 0–10 cm layer than in the 10–20 cm layer.

2.4 Relationships Between Soil Carbon and Vegetation

Structural equation modeling revealed that aboveground biomass had no significant direct or indirect effects (via litter or root biomass) on soil carbon content [Figure 4: see original paper]. Root biomass influenced soil carbon only indirectly through underground necromass and root surface area. The response relationships differed between soil layers: 0–10 cm soil carbon was affected by surface litter, underground necromass, and root surface area, whereas 10–20 cm soil carbon was influenced only by underground necromass and root surface area. Path coefficients indicated that litter input contributed more to 0–10 cm soil carbon, while root surface area contributed relatively more to 10–20 cm soil carbon.

3.1 Restoration Process and Significance

Human activities are primary drivers of desertification in the Horqin Sandy Land. Since the mid-20th century, overgrazing, fuelwood collection, and unsustainable land use changes have caused severe degradation. However, the region' s favorable water and heat resources enable rapid recovery under effective protection. Grazing exclusion is a primary restoration measure and the most effective approach for ecological rehabilitation in the Horqin Sandy Land. Long-term monitoring demonstrates that enclosure for >25 years significantly increases vegetation cover and stability in both mobile and fixed dunes. Our results show that seasonal grazing bans (semi-fixed and fixed dunes) and long-term enclosure (fenced grasslands) significantly enhanced aboveground biomass, belowground biomass, and litter compared to mobile dunes (Table 2). Soil carbon content also increased significantly with restoration (Table 3), confirming the effectiveness of grazing exclusion and enclosure measures.

3.2 Factors Influencing Soil Carbon

Litter is the primary source of soil organic carbon, and its production is influenced by vegetation productivity. Consequently, aboveground biomass is often considered the most important factor explaining soil carbon storage, a relationship well-documented in forests and grasslands. However, this study found no significant relationship between aboveground biomass and soil carbon content in either the 0–10 cm or 10–20 cm layers [Figure 4: see original paper]. This may be attributed to litter redistribution processes. Litter serves as a direct source of soil organic matter, forming particulate organic carbon through decomposition and mineral-associated organic carbon via microbial processing. Litter also influences microbial carbon use efficiency and microbial necromass carbon content. Consequently, litter mass is significantly positively correlated with soil carbon content, as confirmed in this study [Figure 4: see original paper].

In our study area, intense wind activity affects litter redistribution, and differences in litter interception capacity among restoration stages create distinct source-sink dynamics. This litter redistribution and source-sink relationship may be the primary reason for the weak correlation between aboveground biomass and soil carbon content. Therefore, future research and regional carbon budget assessments should account for this process.

Beyond litter input, root surface area exhibited significant positive effects on soil carbon content [Figure 4: see original paper]. Root surface area directly influences root exudation and rhizosphere microbial activities. Studies suggest that root contributions to soil carbon may exceed those of aboveground parts, as root growth produces exudates that serve as carbon sources for microbes and regulate rhizosphere microenvironments (e.g., pH, moisture), thereby influencing microbial necromass carbon and mineral-associated carbon. Our findings indicate that root activity significantly contributes to soil carbon accumulation in degraded sandy grasslands. Future research should therefore consider root traits such as surface area and length in assessments of soil carbon accumulation and regional carbon budgets.

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4 Conclusion

Based on our analysis of vegetation biomass changes and their relationships with soil carbon during ecological restoration in the Horqin Sandy Land, we conclude:

1) Enclosure is an effective restoration measure for the Horqin Sandy Land, as evidenced by significant increases in aboveground biomass, belowground biomass, surface litter, underground necromass, and soil carbon content during restoration.
2) Soil carbon content in both the 0–10 cm and 10–20 cm layers is not significantly related to aboveground biomass. Instead, litter input and root growth processes significantly influence soil carbon content, with root surface area and underground necromass being key factors affecting soil carbon accumulation.

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