Effects of desert plant communities on soil enzyme activities and soil organic carbon in the proluvial fan in the eastern foothills of the Helan Mountain in Ningxia, China Postprint

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Date: 2024-05-15T00:00:00+00:00

Abstract

It is of great significance to study the effects of desert plants on soil enzyme activities and soil organic carbon (SOC) for maintaining the stability of the desert ecosystem. In this study, we studied the responses of soil enzyme activities and SOC fractions (particulate organic carbon (POC) and mineral-associated organic carbon (MAOC)) to five typical desert plant communities (Convolvulus tragacanthoides, Ephedra rhytidosperma, Stipa breviflora, Stipa tianschanica var. gobica, and Salsola laricifolia communities) in the proluvial fan in the eastern foothills of the Helan Mountain in Ningxia Hui Autonomous Region, China. We recorded the plant community information mainly including the plant coverage and herb and shrub species, and obtained the aboveground biomass and plant species diversity through sample surveys in late July 2023. Soil samples were also collected at depths of 0-10 cm (topsoil) and 10-20 cm (subsoil) to determine the soil physicochemical properties and enzyme activities. The results showed that the plant coverage and aboveground biomass of S. laricifolia community were significantly higher than those of C. tragacanthoides, S. breviflora, and S. tianschanica var. gobica communities ($P<0.05$). Soil enzyme activities varied among different plant communities. In the topsoil, the enzyme activities of alkaline phosphatase (ALP) and β-1,4-glucosidase (βG) were significantly higher in E. rhytidosperma and S. tianschanica var. gobica communities than in other plant communities ($P<0.05$). The topsoil had higher POC and MAOC contents than the subsoil. Specifically, the content of POC in the topsoil was 18.17%-42.73% higher than that in the subsoil. The structural equation model (SEM) indicated that plant species diversity, soil pH, and soil water content (SWC) were the main factors influencing POC and MAOC. The soil pH inhibited the formation of POC and promoted the formation of MAOC. Conversely, SWC stimulated POC production and hindered MAOC formation. Our study

aimed to gain insight into the effects of desert plant communities on soil enzyme activities and SOC fractions, as well as the drivers of SOC fractions in the proluvial fan in the eastern foothills of the Helan Mountain and other desert ecosystems.

Full Text

Preamble

Effects of Desert Plant Communities on Soil Enzyme Activities and Soil Organic Carbon in the Proluvial Fan of the Eastern Foothills of Helan Mountain, Ningxia, China

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Abstract: Understanding the effects of desert plants on soil enzyme activities and soil organic carbon (SOC) is crucial for maintaining the stability of desert ecosystems. This study investigated how soil enzyme activities and SOC fractions (particulate organic carbon (POC) and mineral-associated organic carbon (MAOC)) respond to five typical desert plant communities (*Convolvulus tragacanthoides*, *Ephedra rhytidosperma*, *Stipa breviflora*, *Stipa tianschanica* var. *gobica*, and *Salsola laricifolia*) in the proluvial fan of the eastern foothills of Helan Mountain in Ningxia Hui Autonomous Region, China. We recorded plant community information including plant coverage and herb/shrub species composition, and quantified aboveground biomass and plant species diversity through sample surveys conducted in late July 2023. Soil samples were collected at depths of 0–10 cm (topsoil) and 10–20 cm (subsoil) to determine soil physicochemical properties and enzyme activities. The results showed that plant coverage and aboveground biomass of the *S. laricifolia* community were significantly higher than those of the *C. tragacanthoides*, *S. breviflora*, and *S. tianschanica* var. *gobica* communities ($P<0.05$). Soil enzyme activities varied among different plant communities. In the topsoil, alkaline phosphatase (ALP) and β-1,4-glucosidase (βG) activities were significantly higher in the *E. rhytidosperma* and *S. tianschanica* var. *gobica* communities than in other plant communities ($P<0.05$). The topsoil contained higher POC and MAOC contents than the subsoil, with POC content in the topsoil being 18.17%–42.73% higher than in the subsoil. Structural equation modeling (SEM) indicated that plant species diversity, soil pH, and soil water content (SWC) were the main factors influencing POC and MAOC. Soil pH inhibited POC formation while promoting MAOC formation, whereas SWC stimulated POC production but hindered MAOC formation. This study provides insights into the effects of desert plant communities on soil enzyme activities and SOC fractions, as well as the drivers of SOC fractions in the proluvial fan of the eastern foothills of Helan Mountain and other desert ecosystems.

Keywords: proluvial fan; desert plant community; soil enzyme activity; particulate organic carbon; mineral-associated organic carbon; Helan Mountain

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Received 2024-01-21; revised 2024-04-26; accepted 2024-04-29

Citation: SHEN Aihong, SHI Yun, MI Wenbao, YUE Shaoli, SHE Jie, ZHANG Fenghong, GUO Rui, HE Hongyuan, WU Tao, LI Hongxia, ZHAO Na. 2024. Effects of desert plant communities on soil enzyme activities and soil organic carbon in the proluvial fan in the eastern foothills of the Helan Mountain in Ningxia, China. *Journal of Arid Land*, 16(5): 725-737. https://doi.org/10.1007/s40333-024-0076-1

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1 Introduction

Soil represents the largest carbon pool in terrestrial ecosystems, containing approximately 1550 Pg of soil organic carbon (SOC), which accounts for two-thirds of the global soil carbon pool (Scharlemann et al., 2014; Lehmann and Kleber, 2015). Soil plays a critical role in global climate change responses and carbon cycling processes, as even minor changes in soil properties can significantly affect the soil carbon balance (Hicks et al., 2017; Cotrufo et al., 2019). An increasing number of researchers advocate classifying SOC into two fractions: particulate organic carbon (POC) and mineral-associated organic carbon (MAOC) (Lavallee et al., 2020; Yu et al., 2022). These SOC fractions differ in their formation pathways, turnover times, and functions (Cotrufo et al., 2019; Sokol et al., 2019b; Lavallee et al., 2020). POC is dominated by plant macromolecules with higher carbon-to-nitrogen (C:N) ratios and faster turnover rates, whereas MAOC is dominated by microbially derived fractions with lower C:N ratios and slower turnover rates (Lavallee et al., 2020). Cotrufo et al. (2019) reported significant differences in POC across European grasslands. MAOC accounts for more than 50% of total SOC in forest ecosystems, with the primary source of SOC molecules adsorbed by MAOC being microbial products and their residual materials (Sokol et al., 2019b). However, insufficient research supports these turnover processes, and how they vary with ecosystem type remains unclear.

The relationship between plant communities and soil environment has become a prominent topic in ecology (Atwood and Hammill, 2018; Hu et al., 2018; Xu et al., 2023). Desert plant communities serve critical functions such as windbreak and sand fixation, maintaining ecosystem stability as core components of desert ecosystems (Token et al., 2022). Soil, as an important nutrient reservoir and fundamental indicator of human activity, provides nutrients to desert plants, thereby affecting their long-term growth (Li et al., 2018). Plant community diversity can also influence soil multifunctionality (Singh et al., 2018; Yang et al., 2022). Diverse plant communities secrete different types and quantities of root exudates during growth, which promote the growth and metabolism of soil microorganisms, thereby increasing SOC input rates (Chen et al., 2022a). Additionally, different plant species and combinations provide various types and qualities of litter and dead roots that can be degraded by microorganisms and converted into more stable SOC forms (Sokol et al., 2019a; Wei et al., 2021). Studies have shown that diverse plant communities promote soil microbial diversity, thereby increasing SOC stability and long-term storage (Breulmann et al., 2012; Lange et al., 2015). Plant community diversity also influences soil physical properties such as structure, aeration, and water retention, which affect SOC distribution and stability (Spohn et al., 2023; Xie et al., 2023). For example, diverse plant communities can promote root growth and soil aggregate formation, increasing soil porosity and aeration, thereby improving SOC distribution and stability (Erktan et al., 2016).

Desert plants, as important vegetation types affecting desert soils in arid and semi-arid regions, have been shown to influence SOC and enzyme activities to varying degrees (Chen et al., 2022b). However, due to complex landforms in these regions, the effects of desert plants on soil nutrients and enzyme activities have rarely been reported, particularly in proluvial fan areas. Helan Mountain serves as an important ecological security barrier in Northwest China and a significant natural geographic boundary. The proluvial fan represents a fundamental geomorphological unit in the eastern foothills of Helan Mountain (Wei et al., 2023). Rapid ecotourism development along Helan Mountain, continuous vineyard expansion in the eastern foothills, and frequent seasonal flash floods have substantially disturbed the original ecological environment of desert grassland in the proluvial fan, leading to a series of soil environmental problems (Zhang et al., 2022a). Current soil ecology research in Helan Mountain primarily focuses on soil physicochemical properties and vegetation at different altitudes (Zhang et al., 2022b; Wei et al., 2023; Zhang et al., 2023). However, few studies have examined the chemical properties of soils in Helan Mountain’ s desert plant communities, particularly comprehensive investigations of soil enzyme activities and SOC fractions in proluvial fan areas. Therefore, studying the effects of desert plants on soil enzyme activities and SOC fractions is essential for maintaining desert ecosystem stability.

In this study, we selected five different desert plant communities from the proluvial fan in the eastern foothills of Helan Mountain to investigate their effects on soil enzyme activities and SOC fractions. We hypothesized that: (1) soil enzyme activities in different desert plant communities are primarily influenced by vegetation biomass and soil nutrients, with enzyme activities decreasing to adapt to the environment when soil nutrients cannot meet microbial metabolic demands; and (2) SOC fractions are positively correlated with aboveground biomass of desert plant communities, with plant residual carbon being converted into stable SOC through microbial decomposition and stored in the soil carbon pool. Our results provide a foundation for soil biological restoration and the construction mechanisms of desert plant communities, offering important scientific support for ecological restoration projects aimed at maintaining biodiversity and ecological barrier functions of Helan Mountain.

2.1 Study Area

The study area (38°34 15 -38°49 40 N, 105°55 25 -106°10 16 E) is located in Helan Mountain, northwestern Ningxia Hui Autonomous Region, China. Helan Mountain extends in a southwest-northeast direction with an average altitude of 2000 m. The topography of the eastern foothills is high in the west and low in the east, forming a proluvial fan created by alluvial accumulation. Sampling altitudes ranged between 1226 and 1506 m. The region has a continental monsoon climate characterized by drought, low rainfall, abundant sunshine, and large diurnal temperature variations (Chao et al., 2023). The average annual temperature is 8.5°C, the average daily temperature difference is 10.3°C-15.7°C, annual precipitation is 180-250 mm (with 60%-80% concentrated from June to August), and average annual evaporation is 2000 mm (Zhao et al., 2024).

2.2 Experimental Design and Sampling

In late July 2023, we investigated five desert plant communities: *Convolvulus tragacanthoides*, *Ephedra rhytidosperma*, *Stipa breviflora*, *Stipa tianschanica* var. *gobica*, and *Salsola laricifolia* in the proluvial fan of the eastern foothills of Helan Mountain. During field surveys, we randomly selected four 10 m × 10 m plots in each plant community for vegetation investigation, recording community name, plant coverage, and herb and shrub species (name and individual count). Simultaneously, a 1 m × 1 m quadrat was randomly established in each 10 m × 10 m plot to determine aboveground biomass and plant species diversity. After investigation, aboveground plants were harvested, transported to the laboratory, washed with distilled water, heated at 105°C for 0.5 h, then dried at 65°C to constant weight to obtain aboveground biomass. Soil types in each plant community were investigated separately and identified as sierozem, brown calcic soil, and chestnut soil with coarse texture and gravel content (International Union of Soil Sciences Working Group World Reference Base, 2014). Soil samples from each plant community were collected after removing surface litter and the O-horizon using a five-point sampling method. Soils were collected at depths of 0–10 cm (topsoil) and 10–20 cm (subsoil) using a 5 cm diameter soil auger. Soils from the five points were thoroughly mixed, stones and roots removed, transported to the laboratory, and passed through a 2.00 mm sieve. Each soil sample was divided into two portions: one for determining soil pH, SOC, total nitrogen (TN), available phosphorus (AP), total phosphorus (TP), available potassium (AK), total potassium (TK), POC, and MAOC; the other stored at -20°C for enzyme activity determination.

2.3 Laboratory Analyses

2.3.1 Soil Physicochemical Properties and Enzyme Activities

Soil pH was determined using a PHS-3G pH meter (soil-to-water ratio 1.0:2.5), and soil water content (SWC, %) was measured using the classical drying method. SOC (g/kg) was determined by the potassium dichromate external heating volumetric method (Walkley and Black, 1934). TP and TN contents (g/kg) were determined by molybdenum-antimony anti-colorimetry and the Kjeldahl method, respectively. TK (g/kg) was measured by flame photometry, AP (g/kg) by $NaHCO_3$ extraction, and AK (g/kg) by NH_4OAc extraction and flame spectrophotometry. $NO_3{}^-$-N and $NH_4{}^+$-N (mg/kg) were extracted with 0.01 mol/L $CaCl_2$ solution, and filtrates were analyzed using a flow injection automatic analyzer (FIA-Compact, Braun and Lübbe, Norderstedt, Germany). Soil extracellular enzymes were extracted and cultured according to Zhang et al. (2018). Soil enzyme activities (mol/(d · g)) of alkaline phosphatase (ALP), β-1,4-glucosidase (βG), cellobiohydrolase (CBH), β-xylosidase (βX), leucine aminopeptidase (LAP), β-1,4-N-acetylglucosaminidase (NAG), and cellulase (βD) were measured using 96-well enzyme plate fluorescence analysis (Stone et al., 2014).

2.3.2 SOC Fractions

Sodium hexametaphosphate was used to separate the two SOC fractions (POC and MAOC) (Bradford et al., 2008; Sokol et al., 2019a). Specifically, 20 g of air-dried soil samples were placed in a triangular flask, 60 mL of 5% sodium hexametaphosphate solution was added, and the mixture was shaken (180 r/min, 18 h) on a shaker (BSD-YF2600, Qingdao Mingbo Environmental Protection Technology Co., Ltd., Qingdao, China) to disperse aggregates. The suspension was then washed with distilled water through a 53 m sieve to separate the POC fraction ($ $53 m) and MAOC fraction (<53 m). After drying at 65°C to constant weight, the fractions collected in beakers were weighed to obtain the separation ratio. The contents of the two separated SOC fractions (POC and MAOC) were determined by the potassium dichromate external heating volumetric method after passing through a 0.15 mm sieve.

2.4 Calculation of Plant Species Diversity

Based on field survey data, plant species diversity in each community was calculated using the Shannon-Wiener index (Zhang et al., 2015):

$$W = -\sum_{i=1}^{S} P_i \ln(P_i)$$

where W is the Shannon-Wiener index, S is the total number of species, and P is the proportion of individuals of species i relative to the total number of individuals.

2.5 Data Analysis

All experimental data were compiled in Microsoft Excel 2013 and tested for homogeneity of variance and normality prior to analysis. Statistical significance ($P<0.05$ or $P<0.01$) was determined using one-way analysis of variance (ANOVA). Plots were constructed using OriginPro 2021 software (OriginLab, Massachusetts, USA). Structural equation modeling (SEM) was performed using the lavaan package in R 3.6.0 (R Core Team, 2019) to analyze potential direct and indirect effects of plant characteristics (plant coverage and species diversity) and soil characteristics (physicochemical properties and enzyme activities) on POC and MAOC. Path coefficients indicated the direction and strength of direct influence between variables. Additionally, a partial least squares path model (PLS-PM) was employed to explain these complex effects on POC and MAOC accumulation.

3.1 Plant Species Diversity

Five different plant communities were investigated. The results showed that plant coverage, aboveground biomass, and Shannon-Wiener index of the *S. breviflora* community were significantly lower than those of other communities (Fig. 1 [Figure 1: see original paper]). The plant coverage and aboveground biomass of the *S. laricifolia* community were significantly higher than those of the *C. tragacanthoides*, *S. breviflora*, and *S. tianschanica* var. *gobica* communities ($P<0.05$), exceeding the other four communities by 25.84%-37.31% and 48.87%-92.10%, respectively (Fig. 1a and b). The Shannon-Wiener index of the *S. breviflora* community (0.85$±$0.08) was significantly lower by 23.06%-33.10% compared to other plant communities (Fig. 1c).

3.2 Soil Physicochemical Properties and Enzyme Activities

Soil physicochemical properties differed among plant communities (Table 1). SWC was significantly higher in the *C. tragacanthoides* community than in other communities. Soil pH and AK content were significantly lower in the topsoil of the *E. rhytidosperma* community than in other communities ($P<0.05$), whereas soil TP showed the opposite trend. Soil TN content and NH_4^+-N concentration were significantly higher in the *S. tianschanica* var. *gobica* community than in other communities ($P<0.05$), while NO_3^--N concentration showed the reverse pattern. Soil TK content in the *S. tianschanica* var. *gobica* community was significantly higher ($P<0.05$) than in other communities.

Soil enzyme activities involved in carbon (C), nitrogen (N), and phosphorus (P) transformations varied among plant communities (Fig. 2 [Figure 2: see original paper]). ALP, βG, βX, and βD activities were higher in topsoil than subsoil. βG and ALP activities were significantly higher in the topsoil of *E. rhytidosperma* and *S. tianschanica* var. *gobica* communities than in other communities ($P<0.05$; Fig. 2a and b). LAP and βD activities were highest in the *S. laricifolia* community soils, while NAG activity was highest in the topsoil of the *S. laricifolia* community (Fig. 2f).

3.3 SOC Fractions

POC and MAOC contents were higher in topsoil than subsoil across all plant communities, with topsoil POC contents being 18.17%–42.73% higher than subsoil contents (Fig. 3a [Figure 3: see original paper] and b). The highest contents were observed in the *S. breviflora* community: POC (4.90\$$\pm 0.55 g/kg), MAOC(8.83\pm 0.34 g/kg), andSOC(15.31\pm 1.20 g/kg).Comparedtoothercommunities, the* S.breviflora*communitytopsoilcontained7.77\pm 0.49 g/kg; subsoil: 11.22\pm$\$0.76 g/kg), significantly lower than other communities ($P<0.05$; Fig. 3c).

3.4 Influencing Factors of POC and MAOC

Factors affecting the two functional SOC fractions (POC and MAOC) were combined to examine their effects (Fig. 4 [Figure 4: see original paper]). According to SEM, the main factors influencing POC and MAOC included plant species diversity, plant coverage, soil pH, SWC, and soil enzyme activities related to SOC cycling. Soil pH and SWC had opposite effects on POC and MAOC formation: pH inhibited POC formation while promoting MAOC formation, whereas SWC had the opposite effect ($P<0.05$).

4.1 Effects of Desert Plant Communities on Soil Enzyme Activities

Soil enzyme activities reflect changes in soil physicochemical properties and participate in soil biochemical processes (Li et al., 2020a; Sheng et al., 2020; Wen et al., 2023). Our results showed that ALP and βG activities were significantly higher in the *E. rhytidosperma* community than in other communities, likely due to the strong soil and water conservation capacity of *E. rhytidosperma* in the proluvial fan, attributed to its well-developed primary root. During vegetation restoration, plant community species diversity is closely related to soil enzyme activities (Xiao et al., 2020; Xu et al., 2021). Plant species diversity promotes soil microbial community structure and abundance, which in turn affects microbial metabolite and related protein production (Zhang et al., 2018). Conversely, plant communities influence nutrient inputs to soil and regulate enzyme activities by affecting soil physicochemical properties (Deng et al., 2019; Li et al., 2020b). However, in areas affected by soil erosion, erosion processes (raindrop splash and surface runoff) cause nutrient loss from topsoil and reduce soil enzyme activities (Wang et al., 2011; Costantini et al., 2018; Du et al., 2021).

We found that soil βX activities in four plant communities (except *C. tragacanthoides*) decreased with soil depth. This may relate to soil formation and development processes in the proluvial fan of Helan Mountain' s eastern foothills. With increasing soil depth, nutrient and aeration conditions deteriorated, inhibiting microbial community metabolic capacity and making subsoil enzyme activities significantly lower than topsoil activities. βX promotes oxidation of soil organic substances (e.g., phenols, amines) to produce quinone, which is essential for microbial community development (Liu and Zhang, 2019; Zhang et al., 2022a; Yang et al., 2023). Soil enzyme activity changes are regulated by multiple factors including climate, soil properties, and plant age (Cao et al., 2021; Jin et al., 2022). The study area has experienced significant human disturbance, and industrial development such as grape cultivation likely contributes to soil enzyme activity instability. Additionally, due to differences in soil nutrients and matrices among plant communities, extracellular enzyme activities vary (Cui et al., 2021). βG and CBH activities play important roles in the SOC cycle, primarily involved in cellulose degradation (Fan et al., 2021). High CBH activity in the *S. laricifolia* community may relate to soil nutrients (NO_3^--N and NH_4^+-N) and pH. Li et al. (2020a) demonstrated that soil N forms and pH simultaneously affect enzyme activities.

4.2 Effects of Desert Plant Communities on POC and MAOC

Except for the *C. tragacanthoides* community, the two SOC fractions showed consistent patterns across other plant communities: POC and MAOC contents in topsoil were significantly higher than in subsoil (Fig. 3a and b). This occurs primarily because surface litter preferentially enters the topsoil, where microbial decomposition transforms it into SOC (Almeida et al., 2021; Ridgeway et al., 2022; Bourget et al., 2023). Microbial decomposition of exogenous SOC is limited by nutrient availability to soil microorganisms in subsoil (Liu et al., 2023). As the main product of plant-derived C formation, POC is produced primarily through decomposition of plant components (e.g., lignin phenols) by soil microorganisms (Jia et al., 2021; Hansen et al., 2024). MAOC is mainly produced from microbial-derived C (Sokol and Bradford, 2019; Yu et al., 2022). Microorganisms participate in SOC production both as decomposers and through the synergistic action of "ex vivo modification" and "in vivo turnover" via the microbial carbon pump (Liang et al., 2017; Zhu et al., 2020). Microbial necromass

C contributes 35%-51% to SOC (Wang et al., 2021), and microbial residue C is the main source in MAOC formation (Sokol and Bradford, 2019; Guo et al., 2022; Zhao et al., 2023).

Consistent with our second hypothesis, plant species diversity promoted POC and MAOC production in soil (Fig. 4). Plant species diversity affects SOC accumulation by stimulating SOC formation during vegetation restoration and increasing exogenous C input during microbial decomposition (Wang et al., 2022; Spohn et al., 2023). The *S. breviflora* community had a significantly lower Shannon-Wiener index than the *S. laricifolia* community, yet higher POC, MAOC, and SOC contents in topsoil than subsoil (Figs. 1 and 3). After litter enters soil, it consumes soil N sources, reducing the soil C:N ratio (Cheng et al., 2023). Plants with low C:N ratios can rapidly decompose to form POC after entering soil, whereas plant sources with high C:N ratios cannot be quickly utilized due to the presence of recalcitrant macromolecules, resulting in lower POC, MAOC, and SOC levels in the *S. laricifolia* community (Wei et al., 2021; Ridgeway et al., 2022). Furthermore, changes in plant species diversity enrich SOC sources and promote POC and MAOC formation in soil (Hu et al., 2023). SWC indirectly affects SOC formation and accumulation by influencing soil microbial community composition (Zhang et al., 2020; Deng et al., 2023; Liu et al., 2023). Due to SWC and aeration limitations in subsoil, microbial community activity and composition are lower than in topsoil (Li et al., 2021; Püschel et al., 2023). Additionally, abundant plant litter on the surface increases soil nutrients, promoting microbial community propagation (Bourget et al., 2023; Cheng et al., 2023). Microorganisms promote litter decomposition, allowing plant-derived C to enter the soil carbon pool (Ridgeway et al., 2022).

5 Conclusions

Our study experimentally demonstrated that soil physicochemical properties and enzyme activities differed among plant communities in the proluvial fan of Helan Mountain' s eastern foothills due to community variations. SOC content ranked as: *S. tianschanica* var. *gobica* > *E. rhytidosperma* > *C. tragacanthoides* > *S. laricifolia* > *S. breviflora*. Soil enzyme activities of ALP, βG, βX, and βD changed significantly with soil depth. Additionally, soil enzyme activities were closely related to soil physicochemical properties and were affected by them to varying degrees, forming a complex network relationship. This study only investigated changes in soil enzyme activities and two SOC fractions among different plant communities, while the mechanisms of SOC formation and stabilization mediated by soil microorganisms in different plant communities remain unclear. Furthermore, studies on SOC formation and stabilization mechanisms in the study area are limited, primarily due to the complexity of soil microbial communities and the multidimensional nature of SOC dynamics. Future research should employ comprehensive approaches combining soil chemical analyses, microbial community structure and function analyses, and long-term positioning experiments to reveal SOC formation and stabilization mechanisms mediated by soil microorganisms in different plant communities. Stable isotope tracer techniques and molecular biology methods can be used to better understand the role of microorganisms in the SOC cycle and provide a scientific basis for soil carbon management.

Conflict of Interest: The authors declare no known competing financial interests or personal relationships that could have influenced the work reported in this paper.

Acknowledgements: This study was supported by the Key Project of the Natural Science Foundation of Ningxia Hui Autonomous Region, China (2022AAC02020), the Major Strategic Research Project of the Chinese Academy of Engineering and Local Cooperation (2021NXZD8), and the Key Research and Development Plan Project of Ningxia Hui Autonomous Region, China (2022004129003). We are grateful to the editors and anonymous reviewers for their insightful comments and suggestions that improved this manuscript.

Author Contributions: Conceptualization: SHEN Aihong, SHI Yun, MI Wenbao; Methodology: YUE Shaoli, SHE Jie; Formal Analysis: ZHANG Fenghong, GUO Rui; Writing - Original Draft Preparation: SHEN Aihong, HE Hongyuan, LI Hongxia, ZHAO Na; Writing - Review and Editing: SHEN Aihong, SHI Yun, MI Wenbao, WU Tao; Funding Acquisition: SHI Yun; Resources: SHEN Aihong; Supervision: SHI Yun, MI Wenbao. All authors approved the manuscript.

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Note: Figure translations are in progress. See original paper for figures.