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Abstract

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Full Text

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Response of Gobi Desert soil to the establishment of sea buckthorn (*Hippophae rhamnoides*) plantations

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Abstract: Vegetation restoration is a critical approach for improving soil quality in arid ecosystems, yet its effects on soil extracellular enzyme activities (EEAs), stoichiometric relationships, and nutrient dynamics in the Gobi Desert remain poorly understood. This study aimed to address this knowledge gap by analyzing a chronosequence of three stand ages (3, 11, and 14 a) of artificial sea buckthorn (*Hippophae rhamnoides* L.) plantations in the 170^th Regiment of the 9^th Agricultural Division of the Xinjiang Production and Construction Corps, China. Three 20 m(×)20 m quadrats were established for each restoration stage in early to mid-August 2024. Soil samples were collected in 0–10, 10–20, and 20–30 cm soil layers within each quadrat using a five-point method, to explore the ecological changes in Gobi Desert soil throughout the vegetation restoration. The results indicated that soil organic carbon (SOC), particulate organic carbon (POC), dissolved organic carbon (DOC), mineral-associated organic carbon (MAOC), total nitrogen (TN), and microbial biomass carbon (MBC), nitrogen (MBN), and phosphorus (MBP) all significantly increased in the 0–10 cm soil layer during vegetation restoration. In the 10–20 cm soil layer, MAOC and TN significantly increased during vegetation restoration, while in the 20–30 cm soil layer, MAOC, TN, MBN, and MBP significantly increased. Concurrently, the activities of key enzymes (β-1,4-glucosidase and β-1,4-N-acetylglucosaminidase) involved in carbon (C) and nitrogen (N) cycling were also the highest in the 14-year-old plantation in the 0–10 cm soil layer. Further analysis of enzymatic stoichiometry indicated a shift in microbial resource allocation, with significant increases in the C–N and C–phosphorus (P) ratios of EEAs, whereas the N–P ratio remained relatively stable. The drivers of these stoichiometric ratios varied with soil depth: in the 0–20 cm soil layer, the C–N and C–P ratios of EEAs were mainly influenced by soil C content, whereas the N–P ratio was not regulated by any factors. In the 20–30 cm soil layer, the C–N and C–P ratios of EEAs were mainly influenced by soil C, N, and microbial biomass content, whereas the N–P ratio was mainly affected by TP and pH. Overall, the establishment of sea buckthorn plantations, especially over a 14-a period, significantly improved Gobi Desert soil quality by enhancing nutrient content, stimulating microbial activity, and modulating extracellular enzyme strategies. These findings un-

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Keywords: vegetation restoration; soil organic carbon (SOC); microbial biomass; extracellular enzyme activities (EEAs); nutrient cycling; Gobi Desert

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1 Introduction

In arid and semi-arid areas, desertification poses a significant threat to ecosystem stability and socioeconomic development. Vegetation restoration has been widely recognized as an effective strategy to combat land degradation and improve environmental conditions (Wang et al., 2022; Li et al., 2024). In the vast Gobi deserts of Northwest China, selecting appropriate pioneer species is critical for initiating this recovery process. Sea buckthorn (*Hippophae rhamnoides* L.), a deciduous shrub renowned for its drought resistance, salt tolerance, and ability to thrive in nutrient-poor soils, is naturally distributed across the temperate regions of the Eurasian continent and has been widely introduced for this purpose (Liu et al., 2023; Yang et al., 2024; Ma et al., 2025). Beyond its economic value, sea buckthorn plays a pivotal role in controlling desertification. Its dense root system can stabilize the soil, reduce wind erosion, and enhance soil fertility, thereby creating favourable conditions for the natural succession of related plant communities and the restoration of degraded ecosystems (Tamchos and Dorjey, 2024). Different ages of sea buckthorn have a good effect on soil improvement in arid and semi-arid areas. In the sandy rock area of Dalad Banner in Inner Mongolia Autonomous Region of China, sea buckthorn plantations aged 4–7 a have a stronger soil water retention capacity than those aged 1–3 a, which is conducive to the maintenance and stability of soil moisture (Liu

et al., 2019). In plateau semi-arid desert areas, the stability of sea buckthorn communities increases with the length of fixation years, and can resist general natural threats and moderate biological disturbances (Tian et al., 2019). In addition, sea buckthorn has remarkable nitrogen (N)-fixing ability through its root nodule bacteria. The annual N fixation per hectare of mature plants (13–16 years old) is 179 kg, which is much higher than that of young plants (0–3 years old)—at only 27 kg (Zhang et al., 2020). This N-fixing ability accumulates with increasing plantation age, contributing to the long-term improvement of soil fertility and creating more favourable conditions for the growth of other plants.

The establishment of sea buckthorn plantations initiates a series of soil improvement processes. A key process is the enhancement of soil organic carbon (SOC)—a fundamental indicator of soil quality and ecosystem health (Glaser et al., 2002). It is directly related to soil fertility, water retention capacity, and greenhouse gas emissions, making SOC analysis crucial for addressing global climate change (Hartmann and Six, 2023). Afforestation increases vegetation cover and biomass, thereby promoting SOC accumulation (Sun and Chen, 2024). However, SOC accumulation is a complex process involving multiple factors and mechanisms, including the input of exogenous organic carbon (OC) and other organic materials (Jin et al., 2024; Qi et al., 2025), the physicochemical properties of plant-derived inputs (Zhang et al., 2022; Wu et al., 2025), and the pathways of soil organic matter formation (Shahbaz et al., 2017; Spohn et al., 2023) as a source of SOC (Table S1). These factors interact to promote the accumulation and stabilization of SOC, thereby improving overall soil quality. Concurrently, sea buckthorn improves soil fertility through biological N fixation and the alteration of soil microbial community structure and function (Yao et al., 2022). These changes are intimately linked to the soil extracellular enzyme activities (EEAs), which mediate the biogeochemical cycling of carbon (C), N, and phosphorus (P) (Mu et al., 2025). The response of five EEAs involved in C, N, and P cycling to drought have been studied; they were found to well reflect the activity status of soil microorganisms under different environmental stresses and their contributions to soil nutrient cycling (Rajper et al., 2024). One study investigated the changes in soil enzyme activities in arid regions under irrigation management based on enzymes such as β-glucosidase and urease, and found that soil enzyme activities are a feasible indicator of soil health (Díaz et al., 2021). The stoichiometric ratios of these EEAs provide profound insights into microbial metabolic limitations and nutrient demand, serving as sensitive bio-indicators of soil ecological processes during vegetation restoration (Abay et al., 2024). For example, during grassland restoration, the limiting nutrient for soil microorganisms gradually shifts from P to N with time (Yang et al., 2020). Further, changes in precipitation patterns significantly affect soil EEAs and stoichiometric

ratios, resulting in a dual asymmetric response to precipitation changes (Sun and Chen, 2024). Thus, soil EEAs and their stoichiometric ratios, which are influenced by various other factors, serve as important indicators of soil microbial

metabolic status and nutrient limitation (Feyissa et al., 2022).

Previous research has revealed the basic patterns by which plantation age affects soil (Mao et al., 2024). Some studies have employed a stand age sequence-based research design to examine the effects of different plantation ages on soil in *Larix principis-rupprechtii* (Guo and Tang, 2020) and *Quercus aliena* var. *acuteserrata* (Li et al., 2017) plantations. This unique plantation age gradient enables quantifications of the changes in soil C, N pools, and related EEAs from the initial stage of afforestation to the stable closure of the forest stand. Nevertheless, for sea buckthorn in the Gobi Desert, the dynamic changes in the relationships among soil physicochemical properties, nutrient availability, and the stoichiometry of soil EEAs across different plantation ages remain unclear.

To address current knowledge gaps and gain a deeper understanding of how soil dynamically responds during different developmental stages of sea buckthorn plantations, we constructed a chronosequence consisting of three stand ages (3, 11, and 14 a) (Chen et al., 2005). Our main objectives were to: (1) investigate the changes in Gobi Desert soil C and nutrient cycling over time during the restoration process of planting sea buckthorn in the Gobi Desert; and (2) explore the relationship between Gobi Desert soil C and nutrient cycling and the stoichiometric ratios of soil EEAs during the vegetation restoration process. Our findings provide key insights for future ecological restoration and C sequestration in arid regions based on nature-based solutions.

2 Materials and methods

2.1 Study area

This study selected the sea buckthorn plantations of the 170th Regiment of the 9th Agricultural Division of the Xinjiang Production and Construction Corps (Fig. 1), located in the western Junggar Basin and the edge of the Gurbantunggut Desert in Northwest China. Since 2000, the 170th Regiment of the 9th Agricultural Division of the Xinjiang Production and Construction Corps has been experimenting with sea buckthorn cultivation. The trials were successful in 2007, and large-scale planting was initiated in 2008. By 2024, the planting area has reached 3468.4 hm^2, making it the largest contiguous planting base of large-fruited sea buckthorn in China. The study area has a typical temperate continental desert climate and is characterized by high evaporation, sufficient sunlight, abundant heat, large temperature differences between day and night, and drought with minimal precipitation throughout the year. It receives an average annual precipitation of 264.4 mm and has an average annual evaporation rate of 1859.1 mm. The annual average temperature is 7.3°C, the average annual sunshine duration is 2813.3 h, and the frost-free period lasts 138 d. The accumulated temperature above 10.0°C persists over 177 d (Zhao et al., 2024). The region is characterized by a typical Gobi Desert environment with sparse vegetation cover. Specifically, the soil in the 0–30 cm layer is alkaline, with low concentrations of OC, total nitrogen (TN), total phosphorus (TP), and others

Overview of the study area based on the digital elevation model (DEM) and distribution of sampling plots for sea buckthorn plantations of three ages (3, 11, and 14 a)

Figure 1: Overview of the study area based on the digital elevation model (DEM) and distribution of sampling plots for sea buckthorn plantations of three ages (3, 11, and 14 a)

(Table S2), indicating low overall soil fertility.

2.2 Experimental design and soil sampling

This study employed the chronosequence approach. We selected sea buckthorn plantations of different ages (3, 11, and 14 a) with comparable site conditions as sampling plots. Table 1 lists the basic characteristics of the plots. Information on the plantations of the sampling plots was collected from relevant land management personnel, which confirmed that the plantation management practices across the plots were largely consistent.

The experiment began in early to mid-August 2024, during the beginning of the most vigorous season of plant growth. Soil samples from sea buckthorn plantations of different ages were collected from an artificial sea buckthorn planting area in each selected plot. Three 20 m(×)20 m quadrats were set up in each plot, and the height, plant spacing, and row spacing of the trees in the

Fig. 1 Overview of the study area based on the digital elevation model (DEM) and distribution of sampling plots for sea buckthorn plantations of three ages (3, 11, and 14 a)

Table 1 Details of the sampling plots

Plantation age (a)	Average plant height (cm)	Spacing between plants (m)	Row spacing (m)	Stand density (trees/hm^2)
3	162.54 ± 1.62	1.5	4	1666.67
11	240.45 ± 3.19	1.5	4	1666.67
14	255.95 ± 3.72	1.5	4	1666.67

Note: Mean±SD.

quadrats were recorded. The three 20 m(×)20 m quadrats were located in proximity to each other, ensuring replicability. In each quadrat, three sampling points were established, and soil samples were collected at each point following the five-point sampling method. Soil samples were collected from three depth layers: 0–10, 10–20, and 20–30 cm. After removing litter, gravel, and other debris through a 2-mm sieve, the soil was split into two portions. One portion

was used for analyzing soil physicochemical properties, whereas the other was stored in a refrigerator at 4.0°C in the laboratory for subsequent analyses of soil microbial biomass and EEAs. The samples designated for EEA analysis were processed within 24 h of collection.

2.3 Assessment of soil physicochemical characteristics and microbial biomass

A portion of the naturally air-dried soil samples was used to determine SOC (g/kg), dissolved organic carbon (DOC; mg/kg), particulate organic carbon (POC; g/kg), mineral-associated organic carbon (MAOC; g/kg), TN (g/kg), and TP (g/kg). The remaining samples were used to determine soil microbial biomass carbon (MBC; mg/kg), nitrogen (MBN; mg/kg), and phosphorus (MBP; mg/kg). SOC and TN were measured using an elemental analyzer (FlashSMART, Thermo Fisher Scientific, Waltham, USA) after acidification to remove inorganic C, and excess acid was neutralized with NaOH (Zhu et al., 2020). TP was determined using the alkali fusion-molybdenum blue spectrophotometric method. TP content was then obtained using a spectrophotometer (UV-1900i, Shimadzu, Kyoto, Japan) at a wavelength of 880 nm (Yang et al., 2018). Soil pH was determined by an acidimeter (PB-10, Sartorius, Beijing, China) using a soil:water mixture with a ratio of 1:2.5 (Zhu et al., 2020). DOC was extracted from the treated soil using 0.5 mol/L K_2SO_4 solution and shaken at 180 r/min for 30 min. The suspension was centrifuged at 4000 r/min for 10 min, and the supernatant was decanted and vacuum filtered through a 0.45 micron nitrocellulose membrane filter. DOC content was measured using a total organic carbon (TOC) analyzer (TOC-VCPH, Shimadzu, Kyoto, Japan) (Dong et al., 2026). POC was extracted and quantified using the sodium hexametaphosphate extraction method. Approximately 10 g of soil was placed in a 50-mL plastic bottle, and 30 mL of a 5 g/L sodium

hexametaphosphate solution was added. The mixture was shaken for 18 h and sieved through 53-μm and 250-μm meshes. The soil was washed with water until the filtrate ran clear and free of fine soil particles. Soil particles larger than 53 μm were transferred to a well-weighed aluminium box, oven dried at 60.0°C, and weighed. The ratio of the dried soil sample to the total soil sample weight was calculated to determine the proportion of soil particle components (Zhu et al., 2024). In the process of measuring POC, the organic matter under the sieve (<53 μm) was dried at 60.0°C, weighed, and the OC content (g/kg) was measured. The MAOC content was calculated by multiplying the percentage of each particle fraction in the soil (Cambardella and Elliott, 1993). MBC, MBN, and MBP were measured using the chloroform fumigation-extraction technique. First, the soil samples were fumigated with chloroform to kill the microorganisms. Subsequently, nutrients were extracted from the microorganisms. MBC was determined using a TOC analyzer (TOC-VCPH, Shimadzu, Kyoto, Japan); MBN was determined using an Auto Analyzer (Auto Analyzer 3, SEAL Analytical, Norderstedt, Germany); and MBP was determined using ultraviolet

spectrophotometer (UV-1900i, Shimadzu, Kyoto, Japan) (Yang et al., 2018).

2.4 Measurement of soil EEAs

This study determined the β-1,4-glucosidase (BG), β-1,4-N-acetylglucosaminidase (NAG), L-leucine aminopeptidase (LAP), and phosphatase (AP) activities using a microplate fluorescence method and a multimode microplate reader for fluorescence excitation and detection. Each sample was analyzed in triplicate in the wells of a microplate. Specifically, 1 g of fresh soil sample was weighed and mixed with 125 mL of 50 mmol/L sodium acetate buffer solution, with the pH adjusted to 5.0 (the pH for AP was adjusted to 8.0). The sample was vortexed for 1 min, and 200 mL of the soil suspension and 50 mL of the corresponding substrate were added to the sample wells. For the standard wells, the soil suspension was mixed with 50 mL of 10 mmol/L standard buffer solution and 200 mL of sodium acetate buffer solution to determine soil EEAs (Cheng et al., 2023).

2.5 Measurement of stoichiometric ratios of soil EEAs

We calculated the stoichiometric ratios of soil EEAs to reflect the balance between microbial nutrient demand and soil resource availability in terms of biogeochemistry. These ratios indicate the elemental limitations experienced by soil microorganisms under varying nutrient conditions. The relevant formulas are as follows (Yang et al., 2023):

$$\mathrm{EEA_{C:N}} = \ln(\mathrm{BG}) / \ln(\mathrm{LAP} + \mathrm{NAG}), \qquad (1)$$

$$\mathrm{EEA_{C:P}} = \ln(\mathrm{BG}) / \ln(\mathrm{AP}), \qquad (2)$$

$$\mathrm{EEA_{N:P}} = \ln(\mathrm{LAP} + \mathrm{NAG}) / \ln(\mathrm{AP}), \qquad (3)$$

$$\mathrm{VL} = \sqrt{\left(\mathrm{EEA_{C:P}^2} + \mathrm{EEA_{C:N}^2}\right)}, \qquad (4)$$

$$\mathrm{VA} = \mathrm{ATAN2}(\mathrm{EEA_{C:P}}, \mathrm{EEA_{C:N}}) \times (180/\pi), \qquad (5)$$

where $\mathrm{EEA_{C:N}}$ is the C–N stoichiometric ratio of EEAs; $\mathrm{EEA_{C:P}}$ is the C–P stoichiometric ratio of EEAs; $\mathrm{EEA_{N:P}}$ is the N–P stoichiometric ratio of EEAs; VL signifies the extent of soil microbial C limitation, with a greater value indicating a higher degree of microbial C limitation; and VA (°) indicates soil microbial N or P limitation. A VA value greater than 45° suggests that microorganisms are limited by P, whereas a VA value less than 45° indicates N limitation (Bi et al., 2024).

Fig. 2

Figure 2: Fig. 2

2.6 Data processing and analyses

Data were compiled using Excel 2021, and statistical analyses were conducted using SPSS 26.0 software. One-way analysis of variance and Tukey' s test were employed to assess differences in soil EEAs and physicochemical properties among plantations of different ages within the same soil depth. Pearson' s correlation analysis was utilized to examine the relationships between soil EEA stoichiometric ratios and soil physicochemical properties. All figures were created using OriginPro 2021.

3 Results

3.1 Variations in soil physicochemical properties and microbial biomass during vegetation restoration in the Gobi Desert

In the three soil layers, most parameters did not significantly differ between the 3- and 11-year-old plantations, while significant increases were observed in the 14-year-old plantation (Fig. 2). Specifically, significant differences in soil pH were observed at the same depths across the three plantation ages. The 0–10 cm topsoil layer exhibited significant changes as plantation age increased. The pH values in all three soil layers initially rose and subsequently declined with plantation age (Fig. 2a). The contents of DOC and POC significantly increased with plantation age in the 0–10 cm soil layer (Fig. 2b and d). In contrast, no significant differences were found in the 10–20 and 20–30 cm soil layers across the three stand ages. The SOC content showed significant differences in the 0–10 cm soil layer, with no significant differences in the 10–20 and

Fig. 2 Variations in soil physicochemical properties and microbial biomass across soil layers along a sea buckthorn plantation age gradient. (a), pH; (b), dissolved organic carbon (DOC); (c), soil organic carbon (SOC); (d), particulate organic carbon (POC); (e), mineral-associated organic carbon (MAOC); (f), total nitrogen (TN); (g), total phosphorus (TP); (h), microbial biomass carbon (MBC); (i), microbial biomass nitrogen (MBN); (j), microbial biomass phosphorus (MBP). ***, ***, and*** indicate significant differences among plantation ages at $P<0.050$, $P<0.010$, and $P<0.001$ levels, respectively; ns indicates that the observed differences are not statistically significant among plantation ages. Different lowercase letters on the bar chart within the same soil depth layer indicate significant differences among plantation ages. Error bars indicate standard errors.

20–30 cm soil layers (Fig. 2c). However, multiple comparisons revealed that the SOC content in the 20–30 cm soil layer significantly increased in the 14-year-old plantation compared with that in the 3-year-old plantation. MAOC

Fig. 3. Variations in the activities of β-1,4-glucosidase (BG; a), β-1,4-N-acetylglucosaminidase (NAG; b), L-leucine aminopeptidase (LAP; c), and phosphatase (AP; d) across soil layers along a sea buckthorn plantation age gradient.

Figure 3: Fig. 3. Variations in the activities of β-1,4-glucosidase (BG; a), β-1,4-N-acetylglucosaminidase (NAG; b), L-leucine aminopeptidase (LAP; c), and phosphatase (AP; d) across soil layers along a sea buckthorn plantation age gradient.

content within the same layer also increased with plantation age (Fig. 2e). MAOC content significantly increased with plantation age in the 0–10 and 10–20 cm soil layers (P<0.010). Particularly, this increase was highly significant in the 20–30 cm soil layer (P<0.001). TN differed highly significantly in the 0–10 cm topsoil layer (P<0.001) and significantly in the 10–20 cm and 20–30 cm soil layers (P<0.050). Although TN content between the 3- and 11-year-old plantations did not differ in any soil layer, both differed significantly from the 14-year-old plantation (Fig. 2f). The TP content within the same soil layers did not significantly increase with plantation age (Fig. 2g). In the 0–10 cm topsoil layer, MBC, MBN, and MBP contents significantly increased with plantation age (Fig. 2h–j). In the 10–20 cm soil layer, the increase was not significant and multiple comparisons revealed that the MBP content in the 14-year-old plantation significantly increased compared with the 3-year-old plantation. In the 20–30 cm soil layer, MBN and MBP contents significantly increased with plantation age, whereas MBC content did not show a significant increase; multiple comparisons revealed that the MBC content in the 14-year-old plantation significantly increased compared with the 3-year-old plantation.

3.2 Variations in soil EEAs during vegetation restoration

In the 0–10 cm soil layer, BG activity did not significantly increase with plantation age; in the 10–20 cm soil layer, single-factor analysis showed no differences, while multiple comparisons revealed that the 14-year-old plantation significantly increased compared with the 3-year-old plantation; in the 20–30 cm soil layer, BG activity increased significantly (Fig. 3a). NAG activity increased significantly with plantation age in the 0–10 and 20–30 cm soil layers but not in the 10–20 cm soil layer (Fig. 3b). In the 20–30 cm soil layer, LAP activity first increased and then decreased with plantation age (Fig. 3c). No significant differences in AP activity were observed in the same soil layers across plantation ages (Fig. 3d). Overall, during the stand development of sea buckthorn plantations, BG activity increased significantly, the NAG activity first decreased and then increased, while the activities of LAP and AP first increased and then decreased.

Fig. 3 Variations in the activities of β-1,4-glucosidase (BG; a), β-1,4-N-acetylglucosaminidase (NAG; b), L-leucine aminopeptidase (LAP; c), and

Fig. 4. Variations in the carbon and nitrogen stoichiometric ratio (EEA_C:N; a), carbon and phosphorous stoichiometric ratio (EEA_C:P; b), and nitrogen and phosphorous stoichiometric ratio (EEA_N:P; c) of soil extracellular enzyme activities (EEAs) across soil layers along a sea buckthorn plantation age gradient.

Figure 4: Fig. 4. Variations in the carbon and nitrogen stoichiometric ratio (EEA_C:N; a), carbon and phosphorous stoichiometric ratio (EEA_C:P; b), and nitrogen and phosphorous stoichiometric ratio (EEA_N:P; c) of soil extracellular enzyme activities (EEAs) across soil layers along a sea buckthorn plantation age gradient.

phosphatase (AP; d) across soil layers along a sea buckthorn plantation age gradient. * indicates that there are significant differences among plantation ages at $P<0.050$ level; ns indicates that the observed differences are not statistically significant among plantation ages. Different lowercase letters on the bar chart within the same soil depth layer indicate significant differences among plantation ages. Error bars indicate standard errors.

3.3 Variations in soil EEA stoichiometric ratios and microbial nutrient limitation

Based on the results of soil EEAs (Fig. 3), we calculated and analyzed the soil EEA stoichiometric ratios and the indicators for quantifying soil nutrient limitations. With increasing plantation age, the $EEA_{C:N}$ ratio significantly increased in the 0–10 cm (P=0.035), 10–20 cm (P=0.007), and 20–30 cm (P=0.013) soil layers (Fig. 4a). The $EEA_{C:P}$ ratio did not change significantly in the 0–10 cm soil layer but increased significantly with plantation age in the 20–30 cm soil layer (Fig. 4b). Multiple comparisons showed that in the 10–20 cm soil layer, $EEA_{C:P}$ ratio in both the 11- and 14-year-old plantations significantly increased compared with that of the 3-year-old plantation ($P<0.050$). No significant change was noted in the $EEA_{N:P}$ ratio with increasing plantation age in 0–10 and 10–20 cm soil layers. However, in the 20–30 cm soil layer, the $EEA_{N:P}$ ratio initially increased and then significantly decreased with plantation age (P=0.026; Fig. 4c). Overall, $EEA_{C:N}$ and $EEA_{C:P}$ increased significantly with plantation age, whereas $EEA_{N:P}$ remained almost unchanged (Fig. 4). Vector analysis revealed that the VL of soil EEA stoichiometric ratios increased with plantation age in all soil layers (Fig. 5a). VA was less than 45° in all soil layers (Fig. 5b). Variations in VL and VA were not significant in the 0–10 cm layer. Variation in VL was significant in the 10–20 cm (P=0.025) and 20–30 cm (P=0.018) soil layers, whereas variation in VA was not significant in the 10–20 cm layer but was significant in the 20–30 cm layer (P=0.028).

Fig. 4 Variations in the carbon and nitrogen stoichiometric ratio ($EEA_{C:N}$; a), carbon and phosphorous stoichiometric ratio ($EEA_{C:P}$; b), and nitrogen

Fig. 5. Variations in vector length (VL; a) and vector angle (VA; b) across soil layers along a sea buckthorn plantation age gradient.

Figure 5: Fig. 5. Variations in vector length (VL; a) and vector angle (VA; b) across soil layers along a sea buckthorn plantation age gradient.

and phosphorous stoichiometric ratio ($EEA_{N:P}$; c) of soil extracellular enzyme activities (EEAs) across soil layers along a sea buckthorn plantation age gradient. * and ** indicate there are significant differences among plantation ages at $P<0.050$ and $P<0.010$ levels, respectively; ns indicates that the observed differences are not statistically significant among plantation ages. Different lowercase letters on the bar chart within the same soil depth layer indicate significant differences among plantation ages. Error bars indicate standard errors.

Fig. 5 Variations in vector length (VL; a) and vector angle (VA; b) across soil layers along a sea buckthorn plantation age gradient. * indicates there are significant differences among plantation ages at $P<0.050$ level; ns indicates that the observed differences are not statistically significant among plantation ages. Different lowercase letters on the bar chart within the same soil depth layer indicate significant differences among plantation ages. Error bars indicate standard errors.

3.4 Relationship between soil physicochemical properties and EEA stoichiometric ratios during vegetation restoration

The ratio of $EEA_{C:N}$ showed a significant negative correlation with MAOC content across all three soil layers ($P<0.050$; Fig. 6). For $EEA_{C:P}$, a significant negative correlation with MAOC content was observed in the 10–20 cm ($P=0.019$) and 20–30 cm ($P=0.030$) soil layers. However, neither $EEA_{C:P}$ nor $EEA_{N:P}$ exhibited significant correlations with any other soil physicochemical properties in the 0–10 cm layer (Fig. 6a). $EEA_{N:P}$ did not exhibited significant correlations with any other soil physicochemical properties in the 10–20 cm soil layer (Fig. 6b). In the 0–10 cm soil layer, $EEA_{C:N}$ was significantly positively correlated with DOC and POC ($P<0.050$; Fig. 6a). In the 10–20 cm soil layer, $EEA_{C:N}$ was significantly positively correlated with TN ($P=0.042$; Fig. 6b). In the 20–30 cm soil layer, both $EEA_{C:N}$ and $EEA_{C:P}$ were significantly positively correlated with POC ($P<0.050$) and highly significantly positively correlated with SOC, MBC, and MBN ($P<0.010$). $EEA_{C:N}$ was highly significantly positively correlated with MBP and TN ($P<0.010$), whereas $EEA_{C:P}$ showed significant positive correlations with MBP and TN ($P<0.050$). $EEA_{N:P}$ was highly significantly positively correlated with pH ($P<0.010$) but significantly negatively correlated with TP ($P<0.050$). No significant relationships were found between $EEA_{N:P}$ and other soil physicochemical properties (Fig. 6c).

Fig. 6 Correlation analysis between the soil EEA stoichiometric ratios and soil physicochemical properties in the 0–10 cm (a), 10–20 cm (b), and 20–30 cm (c) soil layers. *, significance at P<0.050 level;* ***, significance at P<0.010 level;***

Fig. 6 correlation analysis between soil EEA stoichiometric ratios and soil physicochemical properties in three soil layers

Figure 6: Fig. 6 correlation analysis between soil EEA stoichiometric ratios and soil physicochemical properties in three soil layers

, significance at $P<0.001$ level.

4 Discussion

4.1 Impact of sea buckthorn plantation age on soil C and nutrient content

This study revealed that artificial cultivation of sea buckthorn can effectively improve soil properties and particularly enhance soil C content in the arid areas of the Gobi Desert. In the 0–10 cm topsoil layer, SOC and TN contents significantly increased with plantation age. Planting sea buckthorn did not significantly boost P content in any of the three soil layers. This may be because the surface soil receives more organic matter than inorganic matter, and the C- and N-related microbial activities, which promote the accumulation of C and N, are high (Hartmann and Six, 2023). In addition, litter in the topsoil layer affects the formation and stability of soil organic matter through microbial transformation products during decomposition, thereby increasing soil C content (Spohn et al., 2023). DOC and MBC also tended to increase with plantation age in the surface soil; however, the increase in deep soil was minimal, suggesting that

advancing plantation age could primarily enhance microbial activity in the surface soil. In contrast, microbial activity in deep soil remained unaffected by plantation age.

During the stand development of sea buckthorn plantations, the diversity of microbial communities in the surface soil was improved by increasing the species and quantity of microorganisms, thereby promoting the health and stability of the soil ecosystem, while having a relatively minor impact on deep soil (Zhang et al., 2022). MAOC is generally more stable than POC and is the most stable component of the mineral soil C pool (Cong et al., 2025). In our study, as the sea buckthorn plantation developed, the proportion of POC in the total C pool was greater than that of MAOC, and its content was relatively stable compared to that in mineral soil. This indicated that POC may be the most important stable component in the soil C pool of Gobi Desert. We also found that as the sea buckthorn plantation aged, the contents of soil C and N both increased significantly. This may be attributed to the greater input of organic matter from sea buckthorn into the soil during the stand development, which enhances microbial activity and intensifies the decomposition of organic matter, thereby increasing the content of soil C and N and improving the fertility of Gobi Desert soil (Zeng et al., 2024).

4.2 Impact of sea buckthorn plantation age on soil EEAs

Soil EEAs serve as a vital marker for soil biochemical processes and indicate shifts in nutrient cycling and microbial activity within the soil (Daunoras et al., 2024). We found that during the stand development of sea buckthorn plantations from 3 to 14 a, the activities of soil enzymes (such as BG and NAG) increased. These enzymes are crucial in breaking down soil organic matter and facilitating the cycling of nutrient elements (Mu et al., 2025), thereby increasing the related soil C and N content and promoting soil C circulation. This may be attributed to the root growth of sea buckthorn and the associated increase in root exudates (Liu et al., 2023). The increase in SOC promoted exudate release and enhanced soil EEAs (Zhou et al., 2025). BG and NAG were the most active enzymes in the 14-year-old plantation, whereas LAP and AP were the most active in the 11-year-old plantation. Thus, during the stand development of sea buckthorn plantations, the residues and root systems of ground vegetation in the soil are the main sources of soil organic matter, leading to changes in the activity of various soil enzymes (Yang et al., 2020). C and N are essential nutrients for plant growth and key limiting factors for soil microbial metabolic activity (Keenan et al., 2023). Soil microorganisms obtain nutrients by secreting extracellular enzymes (Bi et al., 2024). The stoichiometric ratios of EEAs reflect the demand and limitations of microorganisms for different nutrients (Moreno et al., 2022). Under C limitation, microorganisms increase the secretion of C-acquiring enzymes, such as BG. Conversely, when they are limited by N or P, enzymes, such as NAG or AP, are secreted in high amounts (Abay et al., 2024). Our study supports these findings (Figs. 3 and 5). The SOC, POC, MAOC, DOC, and TN contents in the soil of sea buckthorn plantations increased with plantation age, possibly because planting sea buckthorn improved soil quality, supplied energy and nutrients to soil microorganisms, and promoted microbial growth and metabolism, thereby enhancing soil EEAs (Moreno et al., 2022; Yang et al., 2024). A significant negative correlation was observed between $EEA_{C:N}$ and MAOC content. Therefore, the increase in MAOC content in Gobi Desert soil with plantation age may indicate a relative N deficiency, prompting microorganisms to allocate resources for N acquisition, which is reflected in the high activity of N-decomposing enzymes (Fig. 3).

Soil pH within the same layer initially increased and then decreased with plantation age, mirroring the trends in LAP and AP activities. This observation indicated that the EEAs related to soil N and P cycling may be affected by soil pH. The correlation analysis indicated that $EEA_{N:P}$ was highly significantly positively associated with pH. An appropriate pH range promotes enzyme activity, whereas extremely high or low pH inhibits it (Nannipieri et al., 2018). Soil microbial communities can also alter soil pH and OC content through EEAs (Li et al., 2021). In this study, MBC, MBN, and MBP contents in the same soil layer increased with plantation age, indicating microbial C, N, and P accumulation. Soil BG and NAG activities in the same soil layer

increased with plantation age, indicating a positive impact of sea buckthorn

plantations on the soil ecosystem. This is because soil EEAs rise as microbial diversity and activity increase, thereby enhancing ecosystem stability (Williams et al., 2025). Therefore, over time, sea buckthorn plantations may contribute to soil nutrient cycling and ecosystem health.

4.3 Effects of sea buckthorn plantation age on ecological stoichiometry and nutrient limitation

The soil EEA stoichiometric ratios can reflect the relative demand and limitations of soil microorganisms for C, N, and P (Abay et al., 2024). $EEA_{C:N}$ and $EEA_{C:P}$ increased with plantation age across different soil layers, indicating that a rise in soil C content enhanced C availability for microorganisms and altered the soil C–N and C–P stoichiometry (Wang et al., 2024). Further correlation analysis revealed that increases in SOC, DOC, and POC contents significantly increased $EEA_{C:N}$ and $EEA_{C:P}$. This observation indicated that the rise in soil C content boosts microbial C demand, leading to higher $EEA_{C:N}$ and $EEA_{C:P}$. In contrast, $EEA_{N:P}$ was primarily affected by pH and P content, showing only weak correlations with C components. The stoichiometric ratios of C, N, and P in ecosystems are close to 1:1:1 and are influenced by climate and pH (Xu et al., 2017). In the 10–20 and 20–30 cm soil layers, the $EEA_{N:P}$ ratio initially rose and then declined with plantation age. This indicated that the growth of sea buckthorn plantations can improve soil EEAs. Such changes in enzyme stoichiometry indicated shifts in metabolic state and nutrient limitations (Abay et al., 2024). In this study, the $EEA_{C:N}$ and $EEA_{C:P}$ ratios were positively correlated with MBC, MBN, and MBP. Microbial community structure significantly influences MBC, MBN, and MBP concentrations, thereby regulating the cycling and availability of C, N, and P in soil, which in turn affects soil enzyme activity and its stoichiometry (Williams et al., 2025).

Soil nutrient limitation is reflected in enzyme stoichiometry, which indicates the ability of microorganisms to obtain and utilize soil nutrients (Yi et al., 2022). During the process of vegetation restoration, the nutrient limitation characteristics of soil microorganisms change with increasing years of restoration (Moreno et al., 2022). This variation might stem from differences in the availability of key nutrients such as C, N, and P in the soil, which can lead to C and P limitations (You et al., 2025). SOC content in the study area increased with plantation age, providing a rich C source for microorganisms. Theoretically, this should alleviate microbial C limitation (You et al., 2025). However, the VL values in all three soil layers increased across the three stand ages, indicating a persistent and increasing C limitation. This may be due to the degradation of the 14-year-old sea buckthorn plantation, where, despite the absorption of large amounts of C, the C is not converted into its non-structural form or is transported belowground as energy for soil microbes. The VA values in all three soil layers across the three stand ages were less than 45°, indicating that N limitation persists regardless of the soil layer. Despite the decrease in soil N limitation with increasing plantation age, unlike bare soil, planted vegetation can enhance mi-

Fig. 7 Model diagram of variations in soil properties and EEAs along a sea buckthorn plantation age gradient.

Figure 7: Fig. 7 Model diagram of variations in soil properties and EEAs along a sea buckthorn plantation age gradient.

crobial C and N limitations (Ling et al., 2025). This may be attributed to the application of fertilizers or increased nodule-forming N-fixing bacteria, which enhance N-fixing capacity (Wu et al., 2022). These results further highlighted the complexity of soil nutrient limitations at different developmental stages of sea buckthorn plantations.

4.4 Pattern of soil property improvement across different plantation ages of sea buckthorn

Vegetation restoration is a key factor influencing natural ecosystems because it reflects how vegetation affects ecosystem characteristics and dynamics at different developmental stages (Heidrich et al., 2020). In this study, we found that the soil C and N contents, soil microbial biomass, and related EEAs in the Gobi Desert tended to increase with plantation age. This is because vegetation restoration significantly improves the physical, chemical, and biological properties of the soil by increasing SOC and TN content, enhancing microbial activity, and alleviating soil N limitation. However, C limitation may also occur during restoration, necessitating appropriate management measures such as fertilization and selection of suitable vegetation types to optimize soil fertility and ecosystem functions. Despite constraints in both C

and N, N limitation was gradually alleviated with plantation age (Fig. 7), indicating that enhancing EEAs for acquiring soil C and N is a key mechanism driving soil property improvement in sea buckthorn plantations.

Fig. 7 Model diagram of variations in soil properties and EEAs along a sea buckthorn plantation age gradient. The blue arrow indicates an increase in the content and the orange arrow indicates no change in the content; the yellow arrow indicates the process of action of organic carbon (OC), TN, and TP; and the green arrow indicates the process of action of MBC, MBN, and MBP.

This study provides a phased understanding of the ecological restoration role of sea buckthorn plantations in the Gobi Desert, highlighting their importance in improving soil properties and ecosystem functions. However, the absence of bare land controls limits the accurate quantification of sea buckthorn' s net contribution to restoration. To further enhance the applicability and mechanistic insight of these findings, few aspects warrant further investigation. Future work should include long-term observations across multiple growing seasons and years to assess the stability of key ecological processes in sea buckthorn plantations at different ages, along with the incorporation of bare land baselines to better distinguish plantation-induced effects. Expanding the spatial scope of

the study would also improve the generalizability of the results. In addition, quantifying the N-fixation capacity of sea buckthorn across varying plantation ages could help clarify its role in regulating soil fertility and EEAs. Further research into microbial community composition is also needed to better reveal the underlying mechanisms of ecological restoration. Addressing these aspects will contribute to a more comprehensive understanding of the ecological functions of sea buckthorn in arid land restoration.

5 Conclusions

This study elucidated the impacts of sea buckthorn plantation age on soil C sequestration, EEAs, and microbial metabolic constraints in the Gobi Desert. SOC, MBC, MBN, MBP, and activities of enzymes (such as BG and NAG) significantly increased with the duration of sea buckthorn vegetation restoration, suggesting that the decomposition of sea buckthorn litter, root exudates, and N-fixing symbiosis enhance soil C and nutrient accumulation and enzyme-mediated nutrient cycling. Although N limitation was alleviated with stand age of sea buckthorn, C limitation

persisted and tended to intensify because of the low energy conversion efficiency of soil microbial metabolism. Balancing C and N inputs is essential for optimizing soil health and microbial activity, which in turn is vital for a comprehensive understanding of the age-driven soil–microbe interactions for effective desert restoration, particularly regarding C sequestration and ecosystem stability improvement. Future management strategies for sea buckthorn vegetation should be tailored to specific climatic and edaphic conditions to sustainably increase SOC content and enhance C sequestration capacity in Gobi Desert soils.

Conflict of interest

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

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References

Abay P, Gong L, Luo Y, et al. 2024. Soil extracellular enzyme stoichiometry reveals the nutrient limitations in soil microbial metabolism under different carbon input manipulations. Science of The Total Environment, 913: 169793, doi: 10.1016/j.scitotenv.2023.169793.

Bi Y L, Guo N, Zhang Y X, et al. 2024. Responses of soil stoichiometry and soil enzyme activities in the different distance around opencast coal mine of the Hulun Buir Grassland of China. International Journal of Coal Science and Technology, 11(1): 221–231.

Cambardella C A, Elliott E T. 1993. Methods for physical separation and characterization of soil organic matter fractions. Geoderma, 56(1–4): 449–457.

Chen Y M, Liu G B, Xu B C. 2005. Effects of artificial seabuckthorn forest on soil and water conservation in loess hilly region. Chinese Journal of Applied Ecology, 16(4): 595–599. (in Chinese)

Cheng Y J, Du A P, Wang Z C, et al. 2023. Soil enzyme activity differs among native species and continuously planted eucalyptus plantations. Forests, 14(11): 2210, doi: 10.3390/f14112210.

Cong J X, Li G X, Han D X, et al. 2025. Historical variation in carbon fractions in permafrost peatland and its effects on peatland carbon pool. Land Degradation and Development, 36(7): 2303–2314.

Daunoras J, Kačergius A, Gudiukaitė R. 2024. Role of soil microbiota enzymes in soil health and activity changes depending on climate change and the type of soil ecosystem. Biology, 13(2): 85, doi: 10.3390/biology13020085.

Díaz F J, Sanchez-Hernandez J C, Notario J S. 2021. Effects of irrigation management on arid soils enzyme activities. Journal of Arid Environments, 185: 104330, doi: 10.1016/j.jaridenv.2020.104330.

Dong X G, Zhang Z Y, Liu Z W, et al. 2026. Litter mixture decomposition enhances the accumulation of soil active carbon and nitrogen in an alpine grassland. Frontiers in Microbiology, 17: 1801190, doi: 10.3389/fmicb.2026.1801190.

Feyissa A, Gurmesa G A, Yang F, et al. 2022. Soil enzyme activity and stoichiometry in secondary grasslands along a climatic gradient of subtropical China. Science of The Total Environment, 825: 154019, doi: 10.1016/j.scitotenv.2022.154019.

Galiano L, Timofeeva G, Saurer M, et al. 2017. The fate of recently fixed carbon after drought release: towards unravelling C storage regulation in *Tilia platyphyllos* and *Pinus sylvestris*. Plant, Cell & Environment, 40(9): 1711–1724.

Glaser B, Lehmann J, Zech W. 2002. Ameliorating physical and chemical properties of highly weathered soils in the tropics with charcoal—a review. Biology and Fertility of Soils, 35(4): 219–230.

Guo H, Tang W P. 2020. Enzyme activity and microbial community diversity in rhizosphere and non-rhizosphere of *Larix principis-rupprechtii*. Ecology and Environmental Sciences, 29(11): 2163–2170. (in Chinese)

Hartmann M, Six J. 2023. Soil structure and microbiome functions in agroecosystems. Nature Reviews Earth and Environment, 4(1): 4–18.

Heidrich L, Bae S, Levick S, et al. 2020. Heterogeneity-diversity relationships differ between and within trophic levels in temperate forests. Nature Ecology and Evolution, 4(9): 1204–1212.

Jin W, Liu Z T, Cheng Z R, et al. 2024. External carbon addition alters soil photosynthetic carbon accumulation and rhizosphere processes of carbon. Applied Soil Ecology, 201: 105478, doi: 10.1016/j.apsoil.2024.105478.

Keenan S W, Emmons A L, DeBruyn J M. 2023. Microbial community coalescence and nitrogen cycling in simulated mortality decomposition hotspots. Ecological Processes, 12(1): 45, doi: 10.1186/s13717-023-00451-y.

Li T P, Wang R Z, Cai J P, et al. 2021. Enhanced carbon acquisition and use efficiency alleviate microbial carbon relative to nitrogen limitation under soil acidification. Ecological Processes, 10(1): 32, doi: 10.1186/s13717-021-00309-1.

Li X T, Xia K, Wu T X, et al. 2024. Increased precipitation has not enhanced the carbon sequestration of afforestation in Northwest China. Communications Earth and Environment, 5(1): 619, doi: 10.1038/s43247-024-01733-9.

Li Z, Dong N N, Hou L, et al. 2017. Characteristics of soil and litter organic carbon and total nitrogen in different age groups of *Quercus aliena* var. *acuteserrata* forests in the Qinling Mountains. Journal of Central South University of Forestry and Technology, 37(12): 127–132, 138. (in Chinese)

Ling J, Dungait J A J, Delgado-Baquerizo M, et al. 2025. Soil organic carbon thresholds control fertilizer effects on carbon accrual in croplands worldwide. Nature Communications, 16(1): 3009, doi: 10.1038/s41467-025-57981-6.

Liu J, Li H, Guo J Y, et al. 2019. Soil improvement of *Hippophae rhamnoides* under different forest ages in sandstone area based on gray correlation analysis. Bulletin of Soil and Water Conservation, 39(4): 127–133. (in Chinese)

Liu L, Guo Y F, Liu X Y, et al. 2023. Relationship between the roots of *Hippophae rhamnoides* at different stump heights and the root microenvironment in feldspathic sandstone areas. PeerJ, 11: e14819, doi: 10.7717/peerj.14819.

Ma F Y, He M Y, Wang M, et al. 2025. Assessing habitat suitability for *Hippophae rhamnoides* subsp. *turkestanica* amid climate change using the MaxEnt model. Forests, 16(3): 468, doi: 10.3390/f16030468.

Mao L, Miao Y G, Ge Y R, et al. 2024. Effects of different afforestation years on soil moisture and nutrient content in Maxian Mountain of the Loess Plateau. Scientific Reports, 14(1): 16194, doi: 10.1038/s41598-024-66408-z.

Moreno J L, Bastida F, Díaz-López M, et al. 2022. Response of soil chemical properties, enzyme activities and microbial communities to biochar application and climate change in a Mediterranean agroecosystem. Geoderma, 407: 115536, doi: 10.1016/j.geoderma.2021.115536.

Mu C H, Li J Q, Huang F C, et al. 2025. Response of extracellular enzyme stoichiometric properties and microbial metabolic limitations to the ecosystem transition mode employed in red jujube economic forests on the Loess Plateau. Microorganisms, 13(4): 729, doi: 10.3390/microorganisms13040729.

Nannipieri P, Trasar-Cepeda C, Dick R P. 2018. Soil enzyme activity: a brief history and biochemistry as a basis for appropriate interpretations and meta-analysis. Biology and Fertility of Soils, 54: 11–19.

Qi H J, Lei J Y, He J Q, et al. 2025. Exogenous carbon type determines the structure and stability of soil organic carbon in dryland farmlands under a continental semi-arid climate. Agronomy, 15(6): 1425, doi: 10.3390/agronomy15061425.

Rajper A M, Willing B P, Cahill J F, et al. 2024. Drought and defoliation affect soil extracellular enzyme activity in northern temperate grasslands. Journal of Arid Environments, 223: 105197, doi: 10.1016/j.jaridenv.2024.105197.

Shahbaz M, Kuzyakov Y, Sanaullah M, et al. 2017. Microbial decomposition of soil organic matter is mediated by quality and quantity of crop residues: mechanisms and thresholds. Biology and Fertility of Soils, 53: 287–301.

Spohn M, Bagchi S, Biederman L A, et al. 2023. The positive effect of plant diversity on soil carbon depends on climate. Nature Communications, 14(1): 6624, doi: 10.1038/s41467-023-42340-0.

Sun Y, Chen X L. 2024. Differential responses of soil extracellular enzyme activity and stoichiometry to precipitation changes in a poplar plantation. Environmental Research, 241: 117565, doi: 10.1016/j.envres.2023.117565.

Tamchos S, Dorjey K. 2024. *Hippophae rhamnoides* subsp. *turkestanica*: a potential species for sustainable propagation in the cold desert of Ladakh. National Academy Science Letters, 48: 89–94.

Tian L H, Wu W Y, Zhou X, et al. 2019. The ecosystem effects of sand-binding shrub *Hippophae rhamnoides* in alpine semi-arid Desert in the northeastern Qinghai–Tibet Plateau. Land, 8(12): 183, doi: 10.3390/land8120183.

Wang C, Zhang W W, Li X N, et al. 2022. A global meta-analysis of the impacts of tree plantations on biodiversity. Global Ecology and Biogeography, 31(3): 576–587.

Wang K, Mao X P, Yang J J, et al. 2024. Soil extracellular enzyme activity and microbial resource limitation exhibited close relationships with groundwater table decline in desert wetlands. CATENA, 236: 107754, doi: 10.1016/j.catena.2023.107754.

Williams G, Miller R, Deng S P. 2025. Dynamic relationships between microbial community, enzyme activity, and soil properties across global ecosystems. Applied Soil Ecology, 206: 105843, doi: 10.1016/j.apsoil.2024.105843.

Wu T, Guo J, Li G, et al. 2025. Soil organic carbon contents and their major influencing factors in mangrove tidal flats: a comparison between estuarine and non-estuarine areas. Ecological Processes, 14(1): 15, doi: 10.1186/s13717-025-00581-5.

Wu Z F, Chen H Y, Pan Y, et al. 2022. Genome of *Hippophae rhamnoides* provides insights into a conserved molecular mechanism in actinorhizal and rhizobial symbioses. New Phytologist, 235(1): 276–291.

Xu Z W, Yu G R, Zhang X Y, et al. 2017. Soil enzyme activity and stoichiometry in forest ecosystems along the North-South Transect in eastern China (NSTEC). Soil Biology and Biochemistry, 104: 152–163.

Yang K Q, Zhang Z A, Tang M, et al. 2024. Seabuckthorn (*Hippophae rhamnoides* L.) plantation degradation aggravates microbial metabolic C and P limitations on the Northern Loess Plateau in China. Science of The Total Environment, 945: 174088, doi: 10.1016/j.scitotenv.2024.174088.

Yang T, Zhang H R, Zheng C H, et al. 2023. Bacteria life-history strategies and the linkage of soil C-N-P stoichiometry to microbial resource limitation differed in karst and non-karst plantation forests in southwest China. CATENA, 231: 107341, doi: 10.1016/j.catena.2023.107341.

Yang Y, Liang C, Wang Y Q, et al. 2020. Soil extracellular enzyme stoichiometry reflects the shift from P- to N-limitation of microorganisms with grassland restoration. Soil Biology and Biochemistry, 149(1): 107928, doi: 10.1016/j.soilbio.2020.107928.

Yang Z A, Zhu Q A, Zhan W, et al. 2018. The linkage between vegetation and soil nutrients and their variation under different grazing intensities in an alpine meadow on the eastern Qinghai-Tibetan Plateau. Ecological Engineering, 110: 128–136.

Yao Y, Dong L J, Fu X H, et al. 2022. *HrTCP20* dramatically enhance drought tolerance of sea buckthorn (*Hippophae rhamnoides* L.) by mediating the JA signaling pathway. Plant Physiology and Biochemistry, 174: 51–62.

Yi J, Zeng Q C, Mei T Y Z, et al. 2022. Disentangling drivers of soil microbial

nutrient limitation in intensive agricultural and natural ecosystems. Science of The Total Environment, 806: 150555, doi: 10.1016/j.scitotenv.2021.150555.

You M Y, Guo D K, Shi H A, et al. 2025. Microbial nutrient limitations and chemical composition of soil organic carbon regulate the organic carbon mineralization and temperature sensitivity in forest and grassland soils. Plant and Soil, 514(1): 459–476.

Zeng J, Li X Y, Jian J N, et al. 2024. Differences in the regulation of soil carbon pool quality and stability by leaf-litter and root-litter decomposition. Environmental Research, 263: 120285, doi: 10.1016/j.envres.2024.120285.

Zhang A M, Yin Y R, Sun K. 2020. Research progress in *Frankia* spp. associated with *Hippophae* L. Microbiology China, 47(11): 3933–3944. (in Chinese)

Zhang C, Zhou X H, Wang X Y, et al. 2022. *Elaeagnus angustifolia* can improve salt-alkali soil and the health level of soil: emphasizing the driving role of core microbial communities. Journal of Environmental Management, 305: 114401, doi: 10.1016/j.jenvman.2021.114401.

Zhao Y Y, Zhu Y M, Feng S L, et al. 2024. The impact of temperature on cotton yield and production in Xinjiang, China. npj Sustainable Agriculture, 2: 33, doi: 10.1038/s44264-024-00043-z.

Zhou J, Loeppmann S, Yang H S, et al. 2025. Linking microbial community dynamics to rhizosphere carbon flow depend on arbuscular mycorrhizae and nitrogen fertilization. Biology and Fertility of Soils, 61: 791–804.

Zhu E X, Liu T, Zhou L, et al. 2020. Leaching of organic carbon from grassland soils under anaerobiosis. Soil Biology and Biochemistry, 141: 107684, doi: 10.1016/j.soilbio.2019.107684.

Zhu E X, Liu Z G, Ma L X, et al. 2024. Enhanced mineral preservation rather than microbial residue production dictates the accrual of mineral-associated organic carbon along a weathering gradient. Geophysical Research Letters, 51(6): e2024GL108466, doi: 10.1029/2024GL108466.

Appendix

Table S1 Studies on the sources of organic carbon

Organic carbon accumulation type	Study area	Mechanism	Reference
Input of exogenous organic carbon and other organic materials	Jiangsu Province, China	Enhancing soil carbon sequestration potential through the input of exogenous organic carbon	Jin et al. (2024)
Input of exogenous organic carbon and other organic materials	Xiji County, China	Improving SOC stability via exogenous carbon-enhanced enzyme activities	Qi et al. (2025)
Physicochemical properties of plant inputs	Southern China	Increasing significantly SOC content through the addition of soil nutrients	Wu et al. (2025)
Physicochemical properties of plant inputs	Heilongjiang Province, China	Improving SOC through the release of root exudates into the soil	Zhang et al. (2022)
Pathways of soil organic matter formation	Africa, Asia, Australia, Europe, North America, and South America	Restoring plant diversity enhances soil carbon sequestration	Spohn et al. (2023)
Pathways of soil organic matter formation	Northwest Germany	Contributing to soil organic matter formation via microbial necrotic biomass inputs	Shahbaz et al. (2017)

Note: SOC, soil organic carbon.

Table S2 Physicochemical properties of the 0–30 cm soil layer in the Gobi Desert

Indicator	0–10 cm soil layer	10–20 cm soil layer	20–30 cm soil layer
pH	8.68 ± 0.45	8.92 ± 0.45	8.92 ± 0.27

Indicator	0–10 cm soil layer	10–20 cm soil layer	20–30 cm soil layer
DOC (mg/kg)	26.31 ± 0.61	23.64 ± 3.33	20.47 ± 0.82
SOC (g/kg)	2.85 ± 0.30	2.22 ± 0.17	2.39 ± 0.64
POC (g/kg)	1.86 ± 0.09	1.64 ± 0.18	1.68 ± 0.27
MAOC (g/kg)	0.94 ± 0.06	0.59 ± 0.07	0.72 ± 0.11
TN (g/kg)	0.23 ± 0.01	0.21 ± 0.05	0.24 ± 0.08
TP (g/kg)	0.82 ± 0.02	0.68 ± 0.04	0.67 ± 0.05
MBC (mg/kg)	51.21 ± 3.92	35.84 ± 3.40	34.41 ± 3.58
MBN (mg/kg)	3.67 ± 0.24	2.50 ± 0.35	2.28 ± 0.26
MBP (mg/kg)	1.83 ± 0.20	1.22 ± 0.17	1.16 ± 0.13

Note: DOC, dissolved organic carbon; POC, particulate organic carbon; MAOC, mineral-associated organic carbon; TN, total nitrogen; TP, total phosphorus; MBC, microbial biomass carbon; MBN, microbial biomass nitrogen; MBP, microbial biomass phosphorus.

References

Jin W, Liu Z T, Cheng Z R, et al. 2024. External carbon addition alters soil photosynthetic carbon accumulation and rhizosphere processes of carbon. Applied Soil Ecology, 201: 105478, doi: 10.1016/j.apsoil.2024.105478.

Qi H J, Lei J Y, He J Q, et al. 2025. Exogenous carbon type determines the structure and stability of soil organic carbon in dryland farmlands under a continental semi-arid climate. Agronomy, 15(6): 1425, doi: 10.3390/agronomy15061425.

Wu T, Guo J, Li G, et al. 2025. Soil organic carbon contents and their major influencing factors in mangrove tidal flats: a comparison between estuarine and non-estuarine areas. Ecological Processes, 14(1): 15, doi: 10.1186/s13717-025-00581-5.

Zhang C, Zhou X H, Wang X Y, et al. 2022. *Elaeagnus angustifolia* can improve salt-alkali soil and the health level of soil: emphasizing the driving role of core microbial communities. Journal of Environmental Management, 305: 114401, doi: 10.1016/j.jenvman.2021.114401.

Spohn M, Bagchi S, Biederman L A, et al. 2023. The positive effect of plant diversity on soil carbon depends on climate. Nature Communications, 14(1): 6624, doi: 10.1038/s41467-023-42340-0.

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Shahbaz M, Kuzyakov Y, Sanaullah M, et al. 2017. Microbial decomposition of soil organic matter is mediated by quality and quantity of crop residues: mechanisms and thresholds. Biology and Fertility of Soils, 53: 287–301.

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

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