

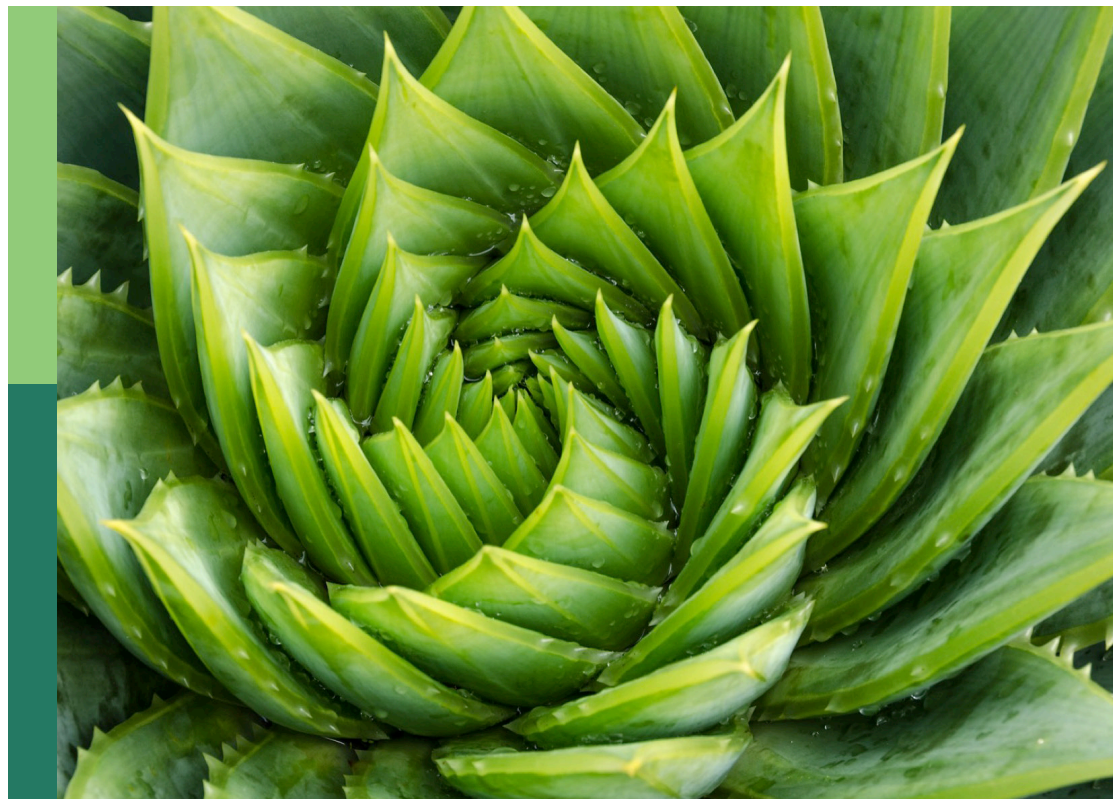
Response and adaptation of terrestrial ecosystem carbon, nitrogen, and water cycles to climate change in arid desert regions

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and Dafeng Hui

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Response and adaptation of terrestrial ecosystem carbon, nitrogen, and water cycles to climate change in arid desert regions

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Coordination and adaptation of water processes in *Populus euphratica* in response to salinity

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Water processes secure plant survival and maintain their ecosystem function. Salinity affects water processes, but the mechanisms remain unclear and may depend on the degree of salinity stress. To improve the understanding of the cooperation of plant organs involved in water processes under salinity stress, we determined hydraulic, gas exchange, and physiological and biochemical parameters in *Populus euphratica* Oliv. under different salinity stresses. The results suggested that *P. euphratica* enhanced water transport efficiency in a salinity-stress environment, and the strengthening effect of roots in the water transfer process was greater than that of the aboveground parts. *P. euphratica* also increased water use efficiency and water transport efficiency in mild and moderate salinity stress (less than 200 mmol/L NaCl) but was adversely affected by heavy salinity stress (more than 300 mmol/L NaCl). Furthermore, *P. euphratica* increased its water storage by regulating antioxidant enzyme scavenging capacity and osmoregulation, which resulted in coordinated greater water utilization and enhanced water transport among plant organs and indicated that the adverse effects on water processes triggered by salinity stress depended on the extent of salt stress. *P. euphratica* lessened stress-induced damage and maintained plant productivity by coordination and cooperation of water processes under certain levels of salinity. Research on the coordination and cooperation involving water processes in riparian forests in saline areas provides the scientific basis for riparian plant protection and restoration.

KEYWORDS

Populus euphratica, leaf-specific hydraulic conductance, water transport, water utilization, water storage, salt stress

1 Introduction

Salinized soils constitute 7.6% of the world's total landmass, with significant extents of these soils in the arid northwestern regions in China. Salinity, one of the major agents of environmental disturbance, interferes with the productivity and growth of plants, especially in arid and semi-arid areas (Deinlein et al., 2014; Yang et al., 2021). Further expansion of salinized soil areas is inevitable due to continued high irrigation levels.

The arid northwestern regions of China feature downstream river basins that are well-known for expanses of riparian forests growing in oases in the desert (Chen et al., 2011; Zhang Y. et al., 2014). *Populus euphratica*, a constructive species in oases, plays a vital role in maintaining vulnerable ecological functions in riparian areas (Chen et al., 2012). *P. euphratica* exhibits strong stress resistance and grows under adverse conditions, where it has existed for thousands of years in environments with high salinity and aridity (Si et al., 2014).

Water provision in plants relies on flow integrity through the entire water channel from roots to leaves and has significant effects on growth, function, structure, hydraulics, and ecology (Hernández et al., 2009). A decrease in water potential can be caused by both drought and salinity stress and can lead to water loss and even death of plant cells.

Water flow in plants involves the processes of water transport, utilization, and storage and affects water circulation in plants. Research on the variability in water transport efficiency provides further information on the coordination and cooperation among plant water processes and on the ecological strategy of plants to survive in detrimental environments (Pivovarov et al., 2014). Different tissues in plants exhibit a distinct water transport ability that is dynamic and variable in the life cycle of plants (Martin et al., 2010). Past studies have shown that hydraulic conductance, which represents the ability of plants to transport water, is related to plant drought resistance (Cochard et al., 2010; Pivovarov et al., 2016). Reducing water transport efficiency causes hydraulic limitation in woody plants. Various physiological processes, including photosynthetic production, can be constrained by hydraulic limitation caused by decreases in available water (Ambrose et al., 2010). Photosynthesis and other physiological processes may affect water use efficiency during the development of salinity stress due to a decrease in osmotic potential caused by the presence of salts in the soil solution and a reduction in water availability (Minh et al., 2016). Certain plants demonstrate improved water utilization in saline environments, whereas certain tree species display a decline in their water utilization efficiency (Li et al., 2022; Zhang et al., 2022). As a result, water utilization efficiency could be affected by water transport efficiency. Studies on the coordination between water transport efficiency and water use efficiency are necessary to understand the flexibility and adaptability of *P. euphratica* to salt-stress conditions; further, an increased understanding of the response of riparian plants to salinity gradients is crucial for ecosystem restoration.

Hydraulic limitations caused by water deficits can be compensated by utilizing water storage (Woodruff et al., 2004; Scholz et al., 2011). Enzymatic defense mechanisms, which activate antioxidant enzymes to safeguard against oxidative damage, are crucial in controlling harmful reactive oxygen species (ROS) levels, and they can affect water storage in plants (Karuppanapandian et al., 2011; AbdElgawad et al., 2016; Moukhtari et al., 2020). The formation and generation of ROS are induced in plant cells by high salinity; excess accumulation of ROS could lead to damage to membrane lipids, nucleic acids, and proteins (Gill and Tuteja, 2010; Sergio et al., 2012). Superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) are critical in enzymatic defense mechanisms and ROS elimination (Meriga, 2013; Hishida et al., 2014). Additionally, the formation of malondialdehyde (MDA) is used as an index of lipid

peroxidation, the concentration of which may reflect the levels of membrane lipid peroxidation induced by polyunsaturated fatty acids under stress conditions (Zhang et al., 2014).

In addition to enzymatic defense mechanisms, osmotic adjustment, a common response to water deficits or osmotic stress, can also have a beneficial effect on water storage and compensate hydraulic limitation in plants, lowering the osmotic potential to counteract loss of turgor by means of maintaining or increasing the quantity of intra-cellular compatible solutes (Woodruff et al., 2004; Scholz et al., 2011; Moukhtari et al., 2020). Adjustment of the cell osmotic potential is required to maintain water uptake capacity, and osmoprotectants are provided by compensatory changes in compatible solutes, including amino acids, sugars, and inorganic ions (Per et al., 2017; Meena et al., 2019). Proline and soluble sugars in plants are closely connected to osmotic adjustment and stress resistance (Zelm et al., 2020). Such substances rapidly accumulate to help plants maintain certain moisture and expand pressure in cells by osmoregulation. Accumulation of inorganic ions in the cytoplasm has an essential contribution to the intra-cellular osmotic balance, which may also protect cytosolic enzymes (Bezerra-Neto et al., 2022).

Previous studies on physiological and ecological responses to drought and salinity stress indicated that *P. euphratica* has a relatively efficient drought and salinity resistance and that it formed the characteristics of adaptability to counteract the presence of salt. However, the regulation involving water processes in the salt-induced environment is still not clear, and there are few reports on the coordination among water transfer processes, water use processes, and water retention processes in *P. euphratica*. Because of its ability to survive and form forests under stressful conditions, understanding the adaptation and coordination of water transport, water utilization, and water storage in *P. euphratica* will enhance our knowledge of plant adaptation to salt-stress adaptation and our ability to restore riparian ecosystems. Here, we established a study to address: 1) How does *P. euphratica* adjust water transfer processes under different salt stress? 2) What are the changes in water transport, water utilization, and water storage processes in *P. euphratica*? 3) Are the three changes synchronized? Can they coordinate and cooperate to maintain a balance of water processes?

2 Materials and methods

2.1 Study sites

The study was conducted at the Eco-Hydrology Experimental Research Station situated in the Alxa Desert, a northwestern region of China, specifically downstream of the Heihe River (42°01'N, 100°21'E) (Figure 1). In this region, the majority of precipitation, amounting to 75%, falls during June, July, and August, totaling an annual precipitation of 38 mm. However, evaporation is exceptionally high, reaching 3,390 mm per year, surpassing precipitation by over 90 times. Characterized by an average annual temperature of 8.2°C, this area is classified as one of the most arid regions in China, with peak temperatures typically occurring between June and August. Local groundwater serves as

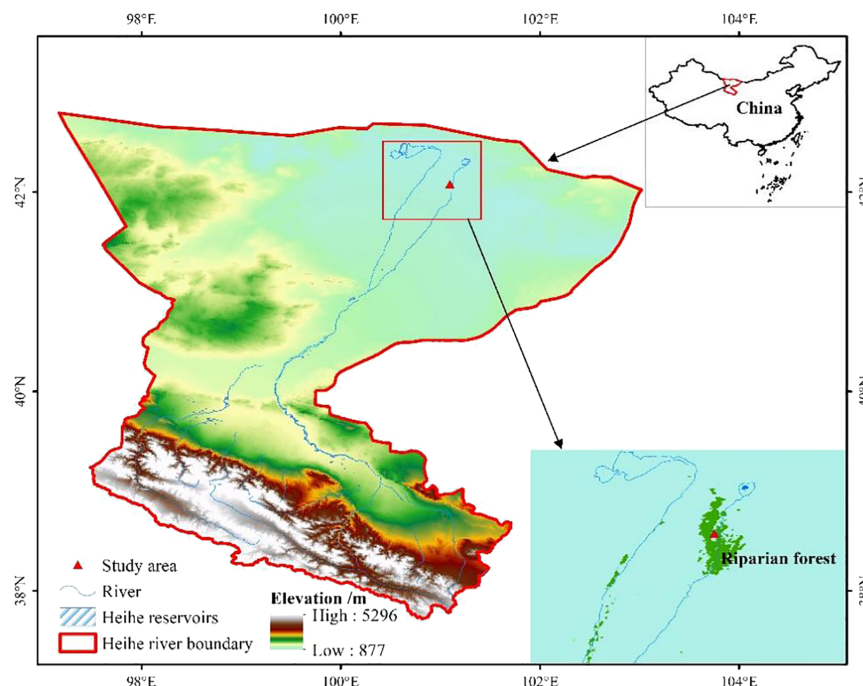


FIGURE 1
Remote sensing images of Heihe River Basin in the arid inland region of China.

the primary water source for plants in this area, primarily originating from the discharge of the upper and middle reaches of the Heihe River (Zhou et al., 2013). The soil in this region originates from fluvial sediments; soil salinity can reach 33% (Si et al., 2014).

2.2 Plant materials

For a duration of 2 years, *P. euphratica* saplings were nurtured at the Ejina Banner's local forest farm, before their transplantation to the designated study site. Subsequently, 100 of these saplings were transplanted into pots and placed outdoors in the natural environment during the early stages of April. Twenty well-growing, non-stressed, straight, and healthy samples (approximately 40 cm in height and 0.45 cm in diameter at breast height (DBH)) were chosen for salt treatments in July. These samples were grouped into five treatments with four replications per treatment. Treatments included different salt solutions at the following levels: control (CK; 0 mmol/L NaCl), 100 mmol/L NaCl, 200 mmol/L NaCl, 300 mmol/L NaCl, and 400 mmol/L NaCl. The solution volume was 3 L, and it was poured into pots all at once, followed by watering the rest of the time. A pilot study showed that the leaves were completely exfoliated after 35 days of 400 mmol/L NaCl concentration. Salt treatments lasted 28 days.

2.3 Measurement of leaf-specific hydraulic conductance

The original hydraulic conductance was determined using a high-pressure flow meter (HPFM-GEN3, Dynamax Inc., Houston,

TX, USA) using the method of water perfusion. The HPFM system included a mechanism that pumped distilled water into specific plant sections, allowing for the determination of homologous flow rates. By analyzing the correlation between flow rate and applied pressure, the original hydraulic conductance was derived. To measure the original hydraulic conductance in shoots, a pressure of approximately 300–350 kPa was applied until a stable water flow rate was achieved. Measurements of the original hydraulic conductance in roots were determined using imposed instantly ascending pressure from 0 kPa to 500 kPa; then, the data were obtained using linear regression. All measurements were conducted for approximately 10 minutes, and the initial values were subsequently adjusted to reflect those at 25°C. This correction was necessary to account for variations in water viscosity caused by differing temperatures during each measurement.

The original hydraulic conductance of roots and shoots was determined using the aforementioned method, with specific steps outlined below. Initially, the stalk was severed from the main root at a distance of 3–4 cm above the soil surface. Subsequently, the ends of the intact roots and shoots were connected to the testing instrument to measure their original hydraulic conductance. The whole shoot system underwent *in vitro* measurement, whereas the entire root system underwent *in situ* measurement. Subsequently, the leaves were removed to derive new values, revealing the original hydraulic conductance of the stem. Finally, the original hydraulic conductance of the leaves was determined using an analog based on Ohm's law, which utilized hydraulic pressure measurements (Alsina et al., 2011). Ultimately, the water transport efficiency of specific plant parts was quantified as leaf-specific hydraulic conductance values, which could reflect the capacity of the specific plant tissue to

supply water to the evaporation surfaces, expressed as hydraulic conductance per unit leaf area (k , $\text{kg}\cdot\text{s}^{-1}\cdot\text{MPa}^{-1}\cdot\text{m}^{-2}$) (Lawren et al., 2010). These values were derived by adjusting the corrected original hydraulic conductance based on the corresponding leaf area. The hydraulic resistance ratio, derived through hydraulic segmentation, serves as a metric to reflect the hydraulic contribution of specific plant parts. This ratio is calculated by comparing the hydraulic resistance (inverse of the original hydraulic conductance) of each plant part to the overall hydraulic resistance of the entire plant, expressed as a percentage.

2.4 Leaf area

To determine leaf area, the number of leaves per sapling in each treatment was placed on grid paper, and the edges of the leaves were traced. The total number of square grids was counted where the leaf area occupied more than 50% of each grid. Subsequently, the area of a single grid was multiplied by the count of these grids to calculate the total leaf area.

Leaves were washed and dried completely at 80°C, and their biomass was obtained by weighing them on an electronic balance. The SLW values for each sapling were calculated by dividing leaf area by biomass (Becker et al., 2000). These dried leaves were preserved for ion content measurements after leaf area determination.

Fresh leaves were preserved in liquid nitrogen for subsequent physiological and biochemical parameter measurements, and their leaf area was measured using the previously described method. To calculate the residual leaf area, the dry weight and specific leaf weight (SLW) values were utilized, assuming a consistent SLW across all saplings. The total leaf area of the entire plant was determined by summing the three separate leaf area measurements obtained previously.

2.5 Gas exchange parameters

Gas determinations were taken all at once following the salt treatments. The LI-6400 portable photosynthesis system (LI-COR, Lincoln, NE, USA) was used for determining transpiration (E , $\text{mmolH}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), net photosynthetic rate (P_n , $\mu\text{molCO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), and stomatal conductance (g_s , $\text{molH}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Water use efficiency (WUE , $\mu\text{molCO}_2\cdot\text{mmolH}_2\text{O}^{-1}$) was determined as the ratio of net photosynthetic rate to transpiration rate. Three or four fully expanded leaves from three to four branches on the top of each shoot were used for the measurement. Gas exchange parameters in *P. euphratica* were measured at noon using a Standard Chamber, which had clear-top chamber systems and could measure the ambient photosynthetically active radiation.

2.6 Physiological and biochemical parameters

Physiological and biochemical parameter measurements were performed using testing kits supplied by Comin Biotechnology in

China. Before weighing with an analytical balance, a 0.1-g sample was ground in liquid nitrogen. Subsequently, the sample was homogenized in a phosphate buffer with a pH of 7.8. After centrifuging the homogenate at 12,000 rpm at 4°C for 15 minutes, MDA, SOD, POD, and CAT analyses were conducted. The resulting supernatant was utilized for the determination of SOD, POD, and CAT activities, employing thiobarbituric acid chromometry, nitroblue tetrazolium, and guaiacol staining methods, respectively.

To determine MDA content, a 0.1-g sample was ground in liquid nitrogen, accurately weighed, and extracted with 3% sulfosalicylic acid in a 5-mL volume. This homogenate was centrifuged at 10,000 rpm for 10 minutes at 25°C after being placed in a centrifuge tube and extracted by vibrating in a hot water bath for 10 minutes at 95°C. Proline content was measured using acid ninhydrin colorimetry with the cooled homogenate. For this, 0.1–0.2-g samples were precisely weighed, fully ground with a small amount of distilled water, and filled to 10 mL with deionized water. After being incubated in a hot water bath for 30 minutes at 95°C, the supernatant was obtained by centrifuging at 3,000 rpm. Soluble sugar content in the supernatant was then determined using the anthrone colorimetric method.

Ion content was determined using an inductively coupled plasma–optical emission spectrometer (ICP-OES; Optima 8000, PerkinElmer, Waltham, MA, USA). Dried leaves were ground in the lab for further studies, and 0.25-g subsamples were nitrified in ceramic crucibles on an electric hot plate for 1 h at 200°C with 4 mL high-purity HNO_3 to achieve near dryness. The crucibles with dried samples were placed in a muffle furnace and ashed for 8 h at approximately 500°C. Finally, the residuum was fully dissolved using 4 mL HCl. The solution was filled to 10 mL with deionized water for measurements of Mg^{+2} , Ca^{+2} , K^{+} , and Na^{+} concentrations.

2.7 Data treatment and statistical analysis

To assess the impact of varying salinity treatments on hydraulic, gas exchange, and physiological and biochemical parameters, the analysis of variance (ANOVA) method was employed. The least significant difference (LSD) test, utilizing *post-hoc* means, was chosen for comparison. Statistical significance was determined using Pearson's product-moment correlation at a probability threshold of $p < 0.05$. Data were represented as mean values with standard deviation and were statistically analyzed using SPSS 19.0 software. Figures were graphically represented using Origin 8.0.

3 Results

3.1 Changes in hydraulic parameters

Leaf-specific hydraulic conductance of the root system increased gradually with increasing salinity concentration from CK to 300 mmol/L NaCl treatment and became significant at $1.57 \times 10^{-2} \text{ kg}\cdot\text{m}^{-2}\cdot\text{s}^{-1}\cdot\text{MPa}^{-1}$ in the 400 mmol/L NaCl salinity treatment. Whole shoot leaf-specific hydraulic conductance

increased gradually with increasing salt concentration from CK to 200 mmol/L NaCl and then decreased significantly in the 300 mmol/L NaCl treatment to $8.73 \times 10^{-4} \text{ kg}\cdot\text{m}^{-2}\cdot\text{s}^{-1}\cdot\text{MPa}^{-1}$ or approximately 16.9% lower than the values in CK. In addition, it was approximately 20.8% lower in 400 mmol/L NaCl than that in the CK treatment (Figure 2A). The trend in root water transport capacity showed that roots were more adaptable than shoots of *P. euphratica* under severe salt stress.

Leaf-specific hydraulic conductance increased significantly with increasing salt concentration from CK to 200 mmol/L NaCl treatment and was $2.59 \times 10^{-3} \text{ kg}\cdot\text{m}^{-2}\cdot\text{s}^{-1}\cdot\text{MPa}^{-1}$ in 200 mmol/L NaCl or 1.45 times the value in CK (without salinity), and then decreased significantly in 300 mmol/L NaCl. It was approximately 15.6% lower than that in the CK treatment in the salinity treatment of 400 mmol/L NaCl.

The trend in stems was the same as that in leaves. Both values in leaves and stems reached the highest value in 200 mmol/L NaCl treatment, and the values of the stem in other salt treatments were higher than those in CK. The final value of leaf-specific hydraulic conductance in the stem was $2.14 \times 10^{-3} \text{ kg}\cdot\text{m}^{-2}\cdot\text{s}^{-1}\cdot\text{MPa}^{-1}$ or 1.22 times the value in CK in the 400 mmol/L NaCl (Figure 2B) treatment. This indicated that leaves and stems of *P. euphratica* could effectively enhance the efficiency of water transport within the salt concentration of 200 mmol/L NaCl.

There was a gradual decline from 29.7% to 7.2% in the hydraulic resistance of roots relative to the plant. This suggested that the hydraulic contribution of the root system was significantly enhanced in salinity stress. The hydraulic resistance of stems initially accounted for 19.9% of that of plants. The hydraulic resistance of stems relative to the plant increased from 19.9% to 51.1% with an increase in salinity concentration. In contrast, the differences in hydraulic resistance of leaves were not statistically significant ($p > 0.05$), with values between 41.8% and 47.8%. This indicated that the hydraulic contribution of stems was significantly reduced, while that of the leaves was slowly enhanced in salinity stress. The hydraulic resistance of leaves was

higher than that of stems under all salinity treatments except for 400 mmol/L NaCl (Figure 3). This demonstrated that leaves had the greatest hydraulic limitation in overground parts and roots with lower hydraulic limitation than the plant, playing a vital role for *P. euphratica* in salt stress. Moreover, changes in the hydraulic resistance ratio of other plant tissues ensured the stability of the hydraulic resistance ratio of leaves, which sustained a stable water supply to the evaporation surface relative to the whole plant.

3.2 Changes in gas exchange parameters

The net photosynthetic rate (P_n) gradually increased from CK to 100 mmol/L NaCl treatment and was $23.95 \mu\text{molCO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; then, it decreased gradually with increasing salinity concentration until $16.71 \mu\text{molCO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in 400 mmol/L NaCl or approximately 23.7% lower than that in CK (Figure 4A). Stomatal conductance (g_s) in the CK treatment was $0.26 \text{ molH}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, and it gradually increased and then gradually decreased with increasing salinity concentration. The maximum value was $0.46 \text{ molH}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ in 200 mmol/L NaCl treatment, which was 1.8 times the value in CK. The values of g_s in other salinity treatments were greater than those in CK (Figure 4B). The water use efficiency (WUE) value in CK was $2.71 \mu\text{molCO}_2\cdot\text{mmolH}_2\text{O}^{-1}$, and the trend in water use efficiency was the same as that in stomatal conductance. The maximum value was $3.87 \mu\text{molCO}_2\cdot\text{mmolH}_2\text{O}^{-1}$ in 100 mmol/L NaCl treatment, which was 1.4 times the value in CK. The values of WUE in other salinity treatments were greater than those in CK (Figure 4C). The increase in CO_2 via open stomata increased carbon fixation in the blade, resulting in increased P_n ; meanwhile, the increase in transpiration rate was small, and plant WUE increased. This suggested that the degree of salinity concentration exerted different influences on gas exchange, and photosynthesis as well as water use efficiency and stomatal conductance could be enhanced under a certain degree of salt stress for *P. euphratica*.

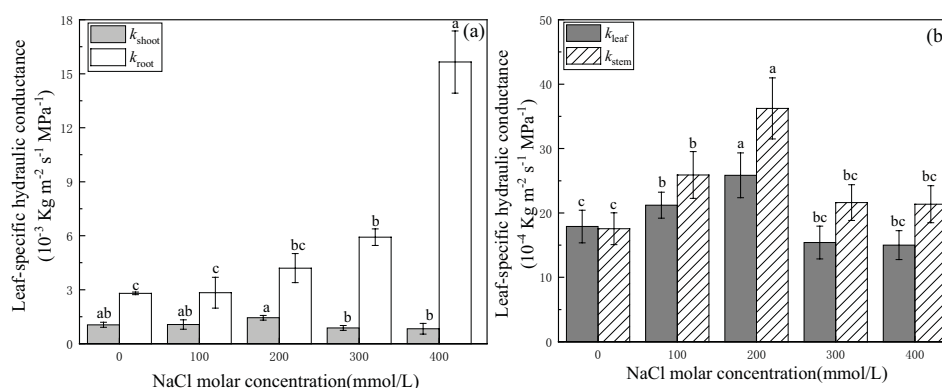


FIGURE 2

Changes in leaf-specific hydraulic conductance of the whole plant (A) and the aboveground parts (B) with different salinity concentrations. (A) k_{root} (open bars) indicates leaf-specific hydraulic conductance of whole roots, and k_{shoot} (light-shaded bars) indicates leaf-specific hydraulic conductance of whole shoots. (B) k_{leaf} (light-shaded bars) indicates leaf-specific hydraulic conductance of leaves, and k_{stem} (hatched bars) indicates leaf-specific hydraulic conductance of stems. Different lowercase letters denote significance levels based on ANOVA *post-hoc* means with least significant difference (LSD) analysis ($p < 0.05$). Data are means with standard error.

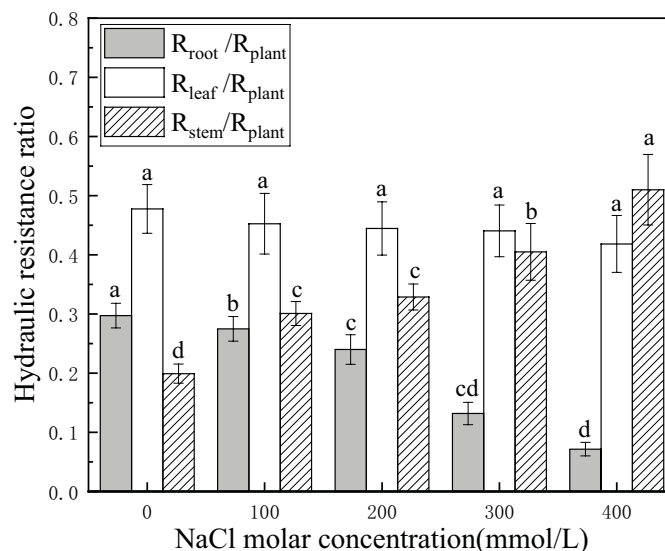


FIGURE 3

Changes in hydraulic resistance ratio with different salinity concentrations. $R_{\text{root}}/R_{\text{plant}}$ (light-shaded bars) indicates the hydraulic resistance ratio of whole roots to the whole plant, $R_{\text{stem}}/R_{\text{plant}}$ (hatched bars) indicates hydraulic resistance ratio of stems to the whole plant, and $R_{\text{leaf}}/R_{\text{plant}}$ (open bars) indicates the resistance ratio of leaves to the whole plant. Different lowercase letters denote significance levels based on ANOVA *post-hoc* means with least significant difference (LSD) analysis ($p < 0.05$). Data are means with standard error.

3.3 Changes in physiological and biochemical parameters

The SOD activity was 156.48 U/g in CK, and it increased to 221.07 U/g in leaves with an increase in salinity concentration, a value 1.4 times that in CK (Figure 5A). There also was a gradual increase from 354.37 U/g to 877.37 U/g in POD with increasing salinity concentration (Figure 5B). The CAT activity increased significantly at first and then gradually declined, with a maximum value of 127.81 nmol·min⁻¹·g⁻¹ in 100 mmol/L NaCl, which was 1.7 times the value in CK. The CAT activity in other salinity treatments was greater than that in CK (Figure 5C). This indicated that SOD, POD, and CAT could provide protection even under severe salt stress; meanwhile, SOD and POD could provide longer-lasting protection for *P. euphratica* with increasing salinity concentration.

MDA content was 37.64 nmol/g in CK, and it increased and then decreased slowly with increasing salinity concentration. MDA content decreased to 33.13 in 400 mmol/L NaCl, but the differences in MDA content between CK and 400 mmol/L NaCl treatment were not statistically significant ($p > 0.05$) (Figure 6). This demonstrated that MDA content could be maintained at a low level under severe salt concentrations, reflecting relatively minor damage to cell membranes induced by salt stress.

Proline content was 29.85 μg/g in CK, and it continued to increase with increasing salinity concentration. Proline content increased gradually from CK to the 300 mmol/L NaCl treatment, and then it significantly increased to 51.92 μg/g in 400 mmol/L NaCl (Figure 7A). The soluble sugar content was 18.85 mg/g in CK, and it increased greatly and then decreased gradually with increasing salinity concentration. The maximum value was 35.01

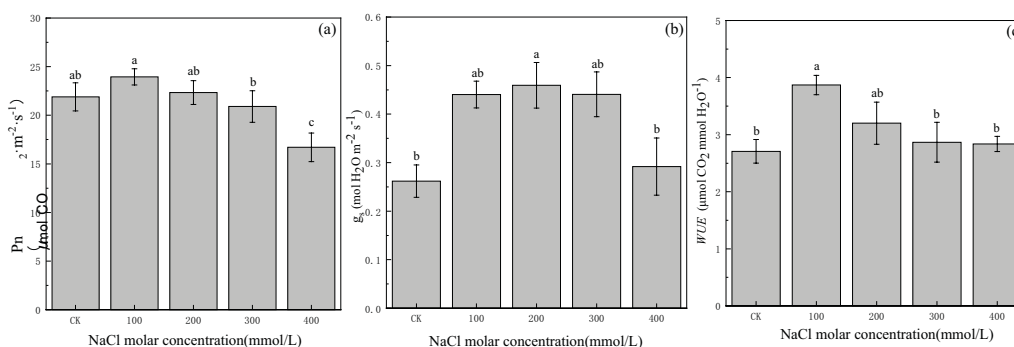


FIGURE 4

Changes in net photosynthetic rate (A), stomatal conductance (B), and water use efficiency (C) with different salinity concentrations. Lowercase letters over the bars denote significance levels based on ANOVA *post-hoc* means using least significant difference (LSD) analysis ($p < 0.05$).

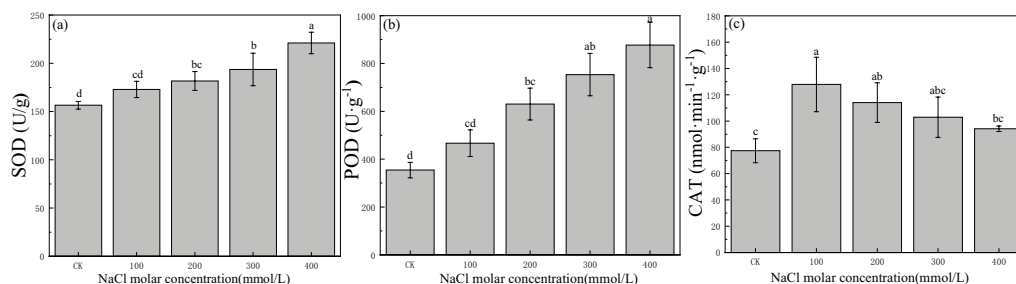


FIGURE 5

Changes in superoxide dismutase (SOD) (A), peroxidase (POD) (B), and catalase (CAT) (C) with different salinity concentrations. Lowercase letters denote significance levels based on ANOVA *post-hoc* means using least significant difference (LSD) analysis ($p < 0.05$). Data are means with standard error.

mg/g in the 200 mmol/L NaCl treatment, which was 1.9 times the value in CK. Concentrations of soluble sugars in other salinity treatments were greater than those in CK (Figure 7B). This indicated that proline and soluble sugars could accumulate in *P. euphratica* and were involved in osmotic regulation under certain salinity concentrations.

The concentration of Na^+ increased from 70.3 ppm to 198.1 ppm or 2.8 times the values in CK, with increasing salinity concentration. The concentration of K^+ increased with increasing salinity concentration from 175.58 ppm in CK to 205.15 ppm in 400 mmol/L NaCl or 1.17 times the value in CK. The concentration of Ca^{+2} increased from 169.88 ppm in CK to 217.58 ppm in 400 mmol/L NaCl or 1.3 times the value in CK. Concentrations of Ca^{+2} and K^+ increased in all salinity treatments. By contrast, Mg^{+2} content in CK was 98.51 ppm, increasing significantly to 116.38 ppm in 100 mmol/L NaCl, and then gradually declining to 77.11 ppm in 200 mmol/L NaCl, which was lower than that in CK (Figure 8). This demonstrated that Na^+ , K^+ , and Ca^{+2} could

continuously accumulate and were involved in osmotic regulation in *P. euphratica* with increasing salinity concentrations.

4 Discussion

4.1 Adaptability of plant water transport to salt stress

The leaf-specific hydraulic conductance of roots in *P. euphratica* improved under salinity stress. Meanwhile, the leaf-specific hydraulic conductance of specific tissues (i.e., whole shoots, leaves, and stems) improved under mild and moderate salt stress (less than 200 mmol/L NaCl), and these parts could maintain hydraulic conductance per leaf area under severe and without salt stress. The findings suggested that *P. euphratica* exhibited a distinct self-regulation ability under mild to moderate salt-stress conditions; however, its self-adaptive and regulatory capacity for water

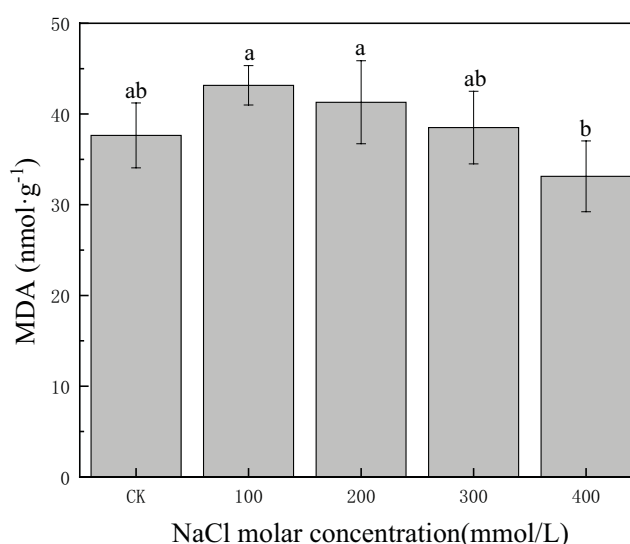


FIGURE 6

Changes in malondialdehyde (MDA) content with different salinity concentrations. Different lowercase letters denote significance levels based on ANOVA *post-hoc* means with least significant difference (LSD) analysis ($p < 0.05$). Data are means with standard error.

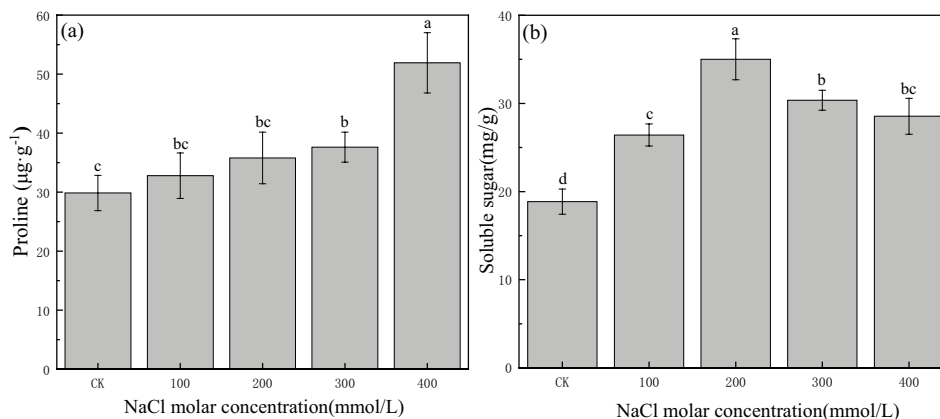


FIGURE 7

Changes in proline (A) and soluble sugars (B) with different salinity concentrations. Lowercase letters denote significance levels based on ANOVA post-hoc means using least significant difference (LSD) analysis ($p < 0.05$). Data are means with standard error.

transport diminished under severe salt stress (more than 300 mmol/L NaCl). This also showed that *P. euphratica* could maintain water transport efficiency, which ensured its survival in a salt-stress environment.

Roots are the main tissues in plants that absorb both water and nutrients from the soil. Roots experience water stress before other plant systems do, and the hydraulic characteristics of roots exhibited higher values than shoots of *P. euphratica* in salinity stress, demonstrating that the roots were more sensitive to salt stress than aboveground parts of *P. euphratica*. Therefore, roots of *P. euphratica* could significantly enhance water transport efficiency under salt stress. These results were similar to those in mangrove species, in which very high salt concentrations could help regulate hydraulic conductance in the pit membranes of vessels (Lopez-

Portillo et al., 2005). However, the water transport efficiency of roots in some tree species was reduced under salt-stress conditions (Rodríguez-Gamir et al., 2012; Calvo-Polanco et al., 2014). This was presumably owing to the specific hydraulic characteristics of tree species in arid regions. Previous studies suggested that the hydraulic resistance of roots in different tree species contributed between 20% and 90% to the whole plant under diverse conditions (Parent et al., 2009). This showed that the regulation of the root hydraulic contribution depended on both the living conditions and tree species. Hydraulic resistance of the root provided less than one-third of the internal hydraulic limitation in *P. euphratica* and gradually decreased with increasing salt stress. These results provided evidence that the root system was critical for water transport in salinity adaption for *P. euphratica*.

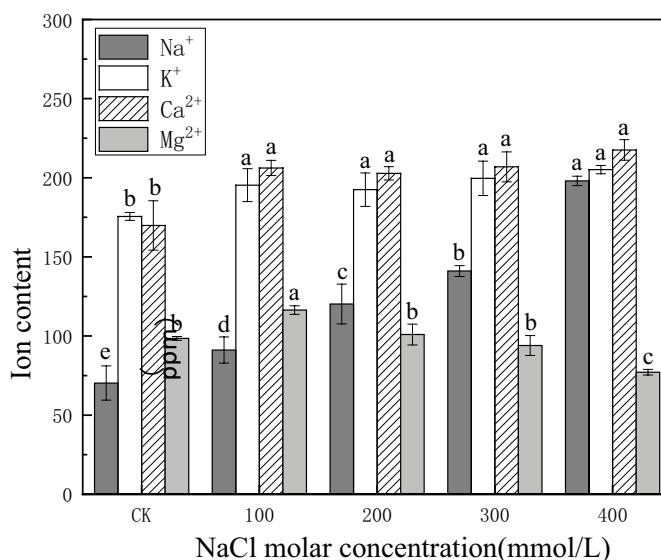


FIGURE 8

Changes in ion content with different salinity concentrations. Dark-shaded bars indicate Na⁺ concentrations, open bars indicate K⁺ concentrations, hatched bars indicate Ca²⁺ concentrations, and light-shaded bars indicate Mg²⁺ concentrations. Different lowercase letters denote significance levels based on ANOVA post-hoc means with least significant difference (LSD) analysis ($p < 0.05$). Data are means with standard error.

In addition, hydraulic limitation in stems progressively increased with salt stress, indicating that salinity stress may have a larger impact on changes in water transport efficiency in stems than in leaves (Li et al., 2019). It was likely that stems still had a water-transfer function under salt stress, while stems lost water transport and regulation function under extreme drought conditions due to the death of the aboveground parts. Furthermore, leaves contributed almost half of the plant's internal resistance, and that remained relatively stable in salt stress. This illustrated that *P. euphratica* leaves maintained a stable water supply relative to the whole plant. Under mild and moderate salt stress, increased water transport efficiency and enhanced water transfer process in all parts helped *P. euphratica* to improve its salinity-resistant capability. These results indicated that the water transfer process is elastic in relatively advantageous environments while a bold strategy in relatively unfavorable environments.

4.2 Adaptability of water utilization in plants to salt stress

Photosynthesis is a basic physiological process, the source of organic matter synthesis and biomass accumulation, which is also one of the main metabolic processes affected by salinity in plants (Zhang L. et al., 2014; Diao et al., 2014; Xu et al., 2015). Photosynthesis in *P. euphratica* was enhanced under relatively mild and moderate salinity stress but weakened under severe salinity stress. This showed that exposure to high salt concentrations diminished the water absorption capacity and hindered growth in certain plant species by compromising photosynthetic efficiency and disrupting metabolic processes (Deinlein et al., 2014; Duan et al., 2018; Batista et al., 2019). These results were similar to those in *Tetragymma hemsleyanum*, *Alhagi pseudalhagi*, and *Desmostachya bipinnata* (Asrar et al., 2017; Wungrampha et al., 2018; Guo et al., 2018). The acceleration of photosynthesis could offer more energy for transpiration and stomatal conduction with mild interference under lower salinity concentration; in contrast, the reduction in the rate of photosynthesis was due to diminished adaptability to the environment with severe interference under higher salinity concentration in *P. euphratica* (Yang et al., 2021).

Leaves are the main parts used in plant transpiration, and previous studies have shown a decrease in stomatal conductance and water use efficiency with stomatal closure, which further inhibits carbon fixation by reducing CO₂ availability in the leaves with an increase in salinity concentration (Duan et al., 2018; Liu et al., 2014; Lawson and Matthews, 2020). Both water use efficiency and stomatal conductance of *P. euphratica* were enhanced under lower salinity concentrations and weakened in severe salt stress. In this study, we found that under mild and moderate salt stress, the stomatal conductance of *P. euphratica* did not change significantly, which is attributed to the efficient water transport in stems and the sufficiency of water in leaves.

Stomatal conductance, the main regulator of water flow in plants in the short term, could be affected by increased water transport efficiency by magnifying the hydraulic signal (Liu et al., 2014; Pan et al., 2016). With the increase in salt concentration, the

stomatal conductance of *P. euphratica* leaves decreased, and stomatal closure limited water loss for maximum CO₂ assimilation through a short-term response; this led to a decrease in leaf transpiration rate and an increase in water utilization, thus improving the adaptability of plants to salt stress.

However, this adaptability is limited. With the extension of salt stress, plant water imbalance was aggravated, photosynthetic capacity continued to decline, and it finally inhibited the water use efficiency of *P. euphratica*. As a result, *P. euphratica* could enhance its water use efficiency coupled with increasing water transport efficiency when encountering a certain extent of salinity threat. The strengthened water use process coupled with the enhanced water transfer process of *P. euphratica* experiencing mild to moderate salt stress formed an increase in hydraulic capacity.

4.3 Adaptability of water storage in plants to salt stress

Salt stress induces excessive excitation energy by exposing chloroplasts, which could promote ROS generation and oxidative stress (Ray et al., 2012). Enhanced peroxidase enzymes enable plants to defend against oxidative stress and dissipate harmful molecules, indicating increased production of ROS (Demidchik, 2015; Rajput et al., 2015). POD and CAT are examples of enzymes that take part in catalyzing the conversion of H₂O₂ to H₂O and O₂, followed by the enzyme SOD converting ROS to H₂O₂, which promoted the scavenging of ROS (Liu et al., 2015). The activities of SOD and POD in *P. euphratica* were enhanced with salinity stress, while CAT activity was enhanced under low salt stress, which indicated that SOD and POD provided relatively long-lasting protection than CAT under salt stress.

The generation of ROS is highly harmful to plant cells, particularly to membrane integrity due to the acceleration of disruption membrane by the arachidonic acid decomposition and MDA generation with the extension of salt stress (Ray et al., 2012; Abdelgawad et al., 2016). Moreover, the less de-structured the membranes, the lower the MDA generation, which is an index that represents membrane functional integrity (Bezerra-Neto et al., 2022). Under salt-stress conditions, the MDA content in *P. euphratica* remained stable, preventing membrane damage. Prior studies on salt-tolerant species have demonstrated that low MDA levels could significantly contribute to plants' adaptability and tolerance to saline environments (Sergio et al., 2012). Higher activities of SOD, POD, and CAT, and low MDA content observed in salinity-treated plants indicated that *P. euphratica* had a higher ability to eliminate ROS and establish a mechanism of protection against oxidative damage as concluded in previous studies (Rajput et al., 2015). This showed that regulation of the antioxidant enzyme clearance system, including SOD, POD, CAT, and MDA, could help plant cells achieve effective water storage function under salinity stress.

Plants formed adaptations to soil salinity that alleviate the disadvantageous effects of ionic and osmotic stresses by producing osmotic compounds and regulating ion transfer, sustaining tissue metabolic activity and water storage in response

to slowly imposed salt-induced dehydration (Zelm et al., 2020). Production of cytoplasmic organic compounds such as amino acids and sugars eventually leads to the restoration of cellular homeostasis, detoxification, and therefore survival under stress (Parihar et al., 2015). Soluble sugars altered by salinity serve as signaling molecules and interact with hormones as part of the signaling network in plants under stress, which also may maintain cell turgor pressure and stabilize proteins, membranes, and enzyme activity (Per et al., 2017; Meena et al., 2019).

Soluble sugars and proline content in *P. euphratica* increased with salinity stress, which may be partly explained by the strengthening of enzyme activity under salt stress. Proline is an important component of aquaporins, the activity of which could affect the water transfer process by altering the physiology of branches during osmotic stress, and also plays a vital role in osmotic adjustment in plants under saline stress (Maurel et al., 2010; Romero et al., 2012). Proline content in *P. euphratica* increased with salinity stress, which may be partly explained by the strengthening of water transport efficiency of shoots under mild and moderate salt stress. This indicates that the accumulation of soluble sugars and proline in *P. euphratica* can increase osmoregulation capability, mitigate salt-induced damage, and ensure the growth and survival of *P. euphratica* subjected to salinity conditions.

In summary, our results suggested that the production of total soluble sugars and proline in leaves may be related to saline stress tolerance and osmotic adjustment, which concurred with the findings of prior studies (Moukhtari et al., 2020). Except for osmotic stress, ionic stress is triggered by superfluous salts, which leads to cell membrane stability and physiological activity in plants (Tavakkoli et al., 2011; Liang et al., 2018; Isayenkov and Maathuis, 2019). Homeostasis of the plant is crucial to guarantee osmotic adjustment, which relies on inorganic osmotic regulators to protect from toxicity in high salinity (Bezerra-Neto et al., 2022). In addition to Na^+ , the content of other main inorganic osmolytes K^+ and Ca^{+2} increased in *P. euphratica* with salinity stress. Meanwhile, Mg^{+2} content increased in response to low salt stress but decreased under conditions of high salt stress.

Our research suggested that the K^+ accumulation in the plant would probably be a strategy for salinity tolerance. Past research has also shown that plants with greater tolerance to salinity often exhibit slightly higher K levels (Pompelli et al., 2010; Silva et al., 2015; Borrelli et al., 2017). However, there could be such a risk that the exchange of Ca combined with the plasma membrane because of the high external salt concentrations is the principal factor in salinity stress (Ottow et al., 2005). The results showed that Ca accumulation in leaves increased slightly with salinity stress, and that was probably related to the accumulation of proline, which could improve ionic homeostasis (de Freitas et al., 2019; Rady et al., 2016). In addition, K and Mg are cofactors for various enzymes in photosynthesis (Tränkner et al., 2018; Bezerra-Neto et al., 2022), which may partly explain the enhanced photosynthesis under low salt conditions. In a salt environment, a momentum of expanding pressure in plant cells exists via osmoregulation of organic compounds and accumulation of inorganic osmolytes, in addition to an antioxidant enzyme scavenging system for maintaining a

certain moisture content. As a result, water storage in leaves decreases reliance on soil moisture content by alleviating water stress in leaves (Simonin et al., 2009; Ishii et al., 2014). Thus, the water retention process coordinated with the water transfer process and water use process, which played a vital part in the stress resistance of plants.

5 Conclusions

We showed coordination of water processes in *P. euphratica* under salt stress by analyzing gas exchange, hydraulic, and physiological and biochemical parameters in this riparian tree species. *P. euphratica* could improve its water transport efficiency in salinity stress, and roots contributed more to the water transfer process than the aboveground parts. In addition, *P. euphratica* could improve water use efficiency and increase water transport efficiency under mild and moderate salt stress but not under severe salt stress. Furthermore, *P. euphratica* could increase osmoregulation by accumulating organic compounds and inorganic osmolytes and strengthen the protection function of the antioxidant enzyme scavenging system in the water storage process to coordinate with increased water transport efficiency and water use efficiency. As a result, water transport, utilization, and storage processes worked together to promote plant survival in salinity.

Plants strive to increase water transport efficiency and water use efficiency and maintain water storage ability in mild and moderate salt stress. Plants can reduce stress-induced damage and achieve growth using defense and protection mechanisms in low unfavorable salt-stress environments. The effect of salt toxicity on physiological and metabolism processes involving water processes in plants depends on the salt content. The changes reflect adaption in the strategy involving water processes in riparian plants residing in diverse salt-stress environments.

Riparian plants can acclimatize to adverse conditions through performance improvement and adaptive functional characteristics. The alterations in water processes within riparian plants under varying salt-stress environments provide a scientific foundation for the restoration and preservation of riparian forests. Additional anatomical studies on *P. euphratica* grown in the wild combined with the local specific hydrological environment will enhance our comprehension of its internal adaptation mechanisms under saline conditions.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Author contributions

DL: Writing – original draft, Writing – review & editing. JS: Writing – original draft, Writing – review & editing. XR: Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Distribution pattern of soil nematode communities along an elevational gradient in arid and semi-arid mountains of Northwest China

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Soil nematodes are the most abundant soil metazoans, occupying multiple trophic levels in the soil food web and playing an important role in soil function. Research on the biogeographic distribution patterns of soil nematode communities and their drivers has received greater attention. However, the distribution characteristics of soil nematode communities along the elevational gradient in the arid and semi-arid regions of Northwest China remain unclear. In this study, four elevational gradients (1750–1900, 1900–2100, 2100–2350 and 2350–2560 m) were established on Luoshan Mountain, Ningxia, an arid and semi-arid region in Northwest China, and soil nematodes in the soil layers of 0–10, 10–20 and 20–40 cm were investigated using the improved Baermann funnel method. The results revealed a monotonically decreasing trend in the total number of soil nematodes along the elevational gradient and soil layer depth, decreasing by 63.32% to 79.94% and 73.59% to 86.90%, respectively, while the interactions were not obvious. A total of 1487 soil nematodes belonging to 27 families and 32 genera were identified across the elevational gradient, with *Helicotylenchus* as the dominant genus, accounting for 10.43% of the total number of nematodes, and bacterivore nematodes as the main trophic groups, accounting for 32.39% to 52.55% of the relative abundance at each elevation, which increased with increasing elevation. Soil nematode community diversity, richness and maturity indices were relatively low at high elevation and decreased by 44.62%, 48% and 54.74%, respectively, with increasing soil layer depth at high elevations. Compared to low elevations, high-elevation soils experienced greater disturbance, reduced structural complexity and nutrient enrichment of the soil food web, and a shift in soil organic matter decomposition from bacterial to fungal pathways as elevation increased. Finally, redundancy analysis showed that soil pH, bulk density, soil moisture, soil organic carbon, available nitrogen, available phosphorus and available potassium were the main soil factors affecting the composition of soil nematode communities, which well explained the differences in nematode communities at different elevations and soil depths.

This study can be used as basic information for further research on soil biota in this mountainous region, expanding our further understanding of the spatial ecology of soil nematodes in the arid and semi-arid mountain ecosystems.

KEYWORDS

soil nematodes, diversity, richness, maturity indices, soil factors

1 Introduction

Soil nematodes are a key biome in soil ecosystems and are numerous and diverse, accounting for four-fifths of all animals on land (Li G. X., et al., 2023; Kouser et al., 2021; van den Hoogen et al., 2019). As the most numerous soil metazoans, they exhibit high species diversity, dietary diversity, life history strategy diversity, and functional group diversity (Zhao et al., 2019; Pen-Mouratov et al., 2010). They can range from “colonizers” (i.e., r-strategist) to “persisters” (i.e., K-strategist) in nematode life-history strategies, encompassing all intermediate stages between these two extremes (i.e., “cp”) (Choudhary et al., 2023). Soil nematodes occupy various trophic levels (bacterivores, fungivores, omnivores-predators, and plant parasites (Ma et al., 2022; Yeates et al., 1993) and play multiple roles in the soil food web (nutrient cycling, organic matter decomposition, plant growth regulation and serving as bioindicators of soil health and environmental changes) (Bardgett and van der Putten, 2014; Bongers and Ferris, 1999). They also play crucial roles in improving soil physical structure, promoting nutrient cycling and organic carbon stabilization, and enhancing crop health, thus contributing significantly to soil functions (Bardgett and van der Putten, 2014; Fu et al., 2022; Tu et al., 2022). Soil nematodes also serve as bioindicators of soil health and environmental changes (Li G. X. et al., 2023), and the diversity and community structure can reflect subtle changes in the soil environment, making them important for ecosystem monitoring and management (Shen et al., 2023; Zhang et al., 2021; Inácio et al., 2023). Elevation has been reported to be a significant factor affecting the diversity and abundance of nematode communities because of differing climatic conditions (such as temperature and precipitation) and vegetation types at different elevations (Afzal et al., 2021). However, very few studies have been done on the distribution patterns and influencing factors of soil nematode communities along elevation gradients in mountain ecosystems of arid and semi-arid regions, limiting our understanding of soil biodiversity and ecological processes in these fragile ecosystems (van den Hoogen et al., 2019).

Recent studies on nematode communities across elevation gradients have yielded varied conclusions regarding their distribution patterns and influencing factors. For instance, Zhang et al. (2021) observed a monotonic decrease in nematode diversity along the elevation gradient in Oakley, Great Khingan, China. In contrast, Shen et al. (2023) found a non-monotonic decline in

nematode α -diversity, influenced by soil bulk density, moisture, dissolved organic carbon, temperature, pH, nitrate nitrogen, and total phosphorus. Choudhary et al. (2023) and Kashyap et al. (2022) reported a negative correlation between nematode diversity and abundance with elevation in the Himalayas, notably in the Pir-Panjal range (Afzal et al., 2021). In the Andes (southern Ecuador), nematode diversity was unaffected by elevation or soil depth, but community composition varied with elevation, influenced by litter C/N and fungal biomass (Traunspurger et al., 2017). Taylan et al., (2021) identified a ‘hump-shaped’ distribution of nematode species richness at mid-elevations on Mount Ararat, Turkey, while Kergunteuil et al. (2016) reported increased nematode diversity with elevation in the Alps. These conflicting results highlight the need for further investigation into nematode distribution patterns along elevation gradients. Furthermore, most existing studies are concentrated in tropical or temperate regions (Marian et al., 2018; Wu et al., 2022), with relatively few focusing on nematode communities in arid and semi-arid mountain regions. This is especially true for the northwestern arid and semi-arid mountains, where the response of soil nematode communities to elevation changes and the driving factors of these changes requires further investigation. Therefore, more research is needed in mountainous ecosystems to establish general patterns and the influencing factors of nematode community distribution across different elevation gradients (Dong et al., 2017).

Ningxia Luoshan, located in the arid and semi-arid region between the western Ordos Plateau and the northern Yellow River Plateau, serves as an important green ecological barrier and water conservation area in central Ningxia’s arid zone. It plays a critical role in regional biodiversity conservation, preventing soil erosion, and maintaining ecological security. Known as the “Emerald of the Desert” and the “Pearl of the Gobi,” it represents a typical fragile ecosystem of the northwestern arid and semi-arid mountainous region (Chen et al., 2023). At the same time, the vegetation shows distinct vertical distribution: at low elevations, it is primarily perennial herbaceous steppe; at mid-elevations, it consists mainly of evergreen coniferous and broadleaf shrubs; and at high elevations, it features mixed forests dominated by *Picea crassifolia*, *Pinus tabulaeformis* and *Populus davidiana*. This area provides a good experimental platform for our research. Therefore, in order to better understand soil biodiversity and ecological processes in the fragile ecosystems of northwestern arid and semi-arid mountains, this study investigates the distribution patterns

and influencing factors of soil nematode communities along elevation gradients in Luoshan, Ningxia.

The goals of this study are to provide new insights into the distribution patterns of soil nematodes along elevation gradients in the northwestern arid and semi-arid mountainous ecosystem and to offer scientific support for ecosystem management under global change. The specific objectives of the study are: (1) to determine the distribution patterns of soil nematode communities along the elevation gradient in the typical arid mountainous ecosystem; (2) to analyze whether elevation, soil depth, and the interaction of elevation and soil depth have an effect on soil nematode community diversity, richness, maturity, and total number of nematodes; (3) to assess the stability of the soil ecosystem along the elevation gradient using nematode faunal analysis; and (4) to identify the relationship between soil nematode communities and soil physicochemical properties and determine the main soil factors influencing nematode community distribution.

2 Materials and methods

2.1 Study site

The study area was located in the Luoshan National Nature Reserve (37°11'–37°25'N, 106°04'–106°24'E) of Ningxia Hui Autonomous Regions of China (Figure 1A). The reserve with a length of 36 km from north to south, a width of 18 km from east to west and an elevation of 1560–2624.5 m above sea level, and a total area of 33,710 hm² (Figure 1C). This area belongs to the arid and semi-arid zone in the western part of the Ordos Plateau and the northern part of the Yellow River Plateau. It has a mesothermal arid

continental climate, characterized by an annual average of 2,881.5h of sunshine, large annual and diurnal variations in temperature, and low and concentrated precipitation with an annual mean of 262.5 mm. The soil is mainly dominated by gray-brown soil and gray-calcium soil. The vertical distribution of vegetation is distinct (Figure 1B): at an elevation of 1750–1900 m, the area is mainly covered by perennial herbaceous steppe (Figure 1D); Between 1900–2100 m, the vegetation is mainly dominated by evergreen coniferous and broadleaf scrub such as *Ostryopsis davidiana* and *Cotoneaster multiflorus* (Figure 1E); At elevations ranging from 2100–2560 m, mixed coniferous and broadleaf forests prevail, dominated by *Picea crassifolia*, *Pinus tabulaeformis* and *Populus davidiana* (Figure 1F; Supplementary Table S1).

2.2 Soil sampling

In July 2022, we established four elevation gradients (E1: 1750–1900 m, E2: 1900–2100 m, E3: 2100–2350 m, E4: 2350–2560 m) in the Luoshan National Nature Reserve, Ningxia, where terrain factors such as slope shape, slope gradient, and slope aspect were consistent. At each elevation gradient, we randomly selected three replicate plots for soil sampling (1 m × 1 m for E1, 5 m × 5 m for E2, and 20 m × 20 m for E3 and E4). We randomly selected three replicate plots for each elevation gradient (E1 plots were 1 m × 1 m, E2 plots were 5 m × 5 m, and E3 and E4 plots were 20 m × 20 m) and collected soil samples from three random quadrats within each plot. After removing the litter and humus layers from each quadrat, we collected soil samples at depths of 0–10 cm, 10–20 cm, and 20–40 cm, taking five samples from each layer. In total, 540 soil samples were collected (4 elevation gradients × 3 replicate plots × 3 quadrats).

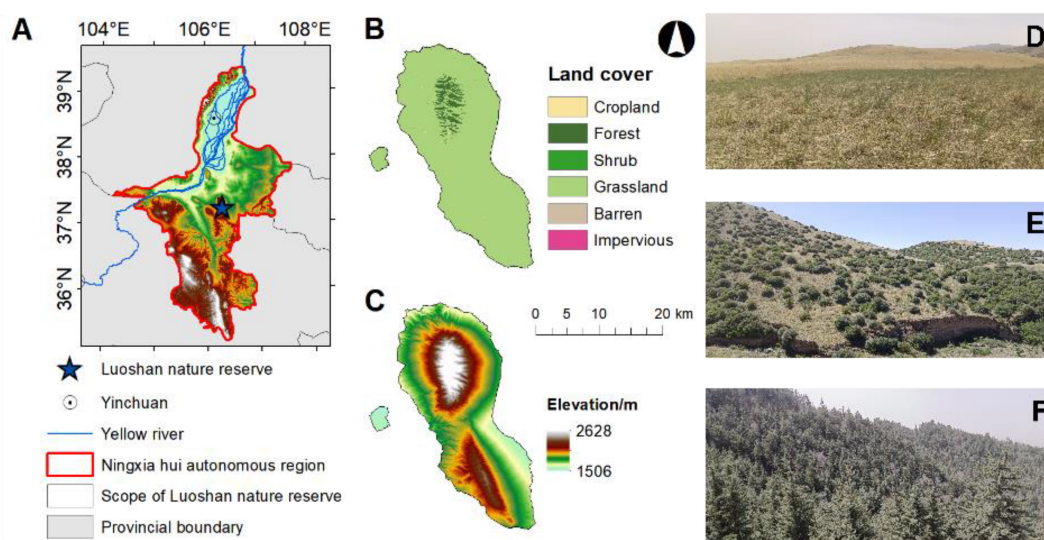


FIGURE 1 Location of Luoshan in Ningxia Hui Autonomous Region (A); Vertical distribution of vegetation in Luoshan, Ningxia (B); Elevation diagram of Luoshan, Ningxia (C); Schematic vegetation along the elevation gradient at Luoshan, Ningxia (D); In elevation 1750–1900 m, it is mainly Perennial herbaceous steppe (D); In 1900–2100 m, it is mainly evergreen coniferous and broad-leaved scrub dominated by *Ostryopsis davidiana* and *Cotoneaster multiflorus*, etc. (E); In the 2100–2560 m, the mixed coniferous and broad-leaved forests were mainly dominated by *Picea crassifolia*, *Pinus tabulaeformis* and *Populus davidiana* (F).

× 3 depths × 5 samples per depth), and 15 soil samples from each layer at each plot were mixed to form a composite sample, resulting in 36 composite samples (4 elevation gradients × 3 replicate plots × 3 composite samples). Gravel, roots, and animal residues were removed. The composite soil samples were divided into three portions. One portion was stored at 4°C for the determination of available nitrogen (AN), available potassium (AK), and available phosphorus (AP). Another portion was taken back to the laboratory, air-dried, ground, and passed through a 2 mm sieve for the determination of soil organic carbon (SOC), total nitrogen (TN), total phosphorus (TP), and total carbon (TC). The remaining portion was kept at 4°C for the measurement and analysis of soil nematodes.

2.3 Soil physicochemical properties

We used the cutting ring method to measure soil bulk density (BD) and the gravimetric method to determine soil moisture (SM). A pH meter (AS 600, Shanghai) was inserted into a soil-water suspension with a ratio of 1:5 to measure pH. SOC and TC were measured using the $K_2Cr_2O_7$ oxidation-external heating method. TN was determined using the H_2SO_4 digestion-Kjeldahl method (Kjeldahl, 1883; Choudhary et al., 2023). TP was measured using the alkaline NaOH fusion- molybdenum-antimony anti-spectrophotometry. AN was determined using the alkaline hydrolysis diffusion method. AK was extracted with CH_3COONH_4 solution and measured using the flame photometry method. AP was extracted with $NaHCO_3/NaF$ hydrochloric acid and measured using the molybdenum-antimony anti-colorimetry method (Li et al., 2007).

2.4 Soil nematode extraction and identification

In the laboratory, we separated soil nematodes using a modified Baermann funnel method (Zhang et al., 2023). The isolated soil nematodes were identified, classified, and counted using a stereo microscope or an inverted microscope (Nikon Ti2-U, 400× and 1000× magnification). The references used for identification included “Pictorial Keys to Soil Animals of China” (Yin, 2000), and the works of Ahmad and Jairajpuri (2010), as well as the Nemaplex database (<http://nemaplex.ucdavis.edu/>). Nematodes were classified to the genus level (Jairajpuri and Ahmad, 1992). For each sample, we randomly selected 100 nematodes for identification; if the sample contained fewer than 100 nematodes, all nematodes were identified (Huo et al., 2021). Soil moisture was measured using the drying method, and nematode density was converted to individuals per 100 g of dry soil. Based on feeding habits and morphological characteristics such as the head and oral cavity, nematodes were categorized into four trophic groups: bacterivores, fungivores, omnivores-predators, and plant parasites (Yeates et al., 1993).

Each nematode has a different life history c-p value. Nematodes with c-p values of cp1 to cp2 are r-strategists, characterized by short life cycles, tolerance to disturbances, and an ability to survive in harsh environments. In contrast, nematodes with c-p values of cp3

to cp5 are k-strategists, which have long life cycles, reduced reproductive rates, sensitivity to disturbances, and a tendency to thrive in stable, undisturbed systems (Bongers and Bongers, 1998; Franco et al., 2021).

2.5 Nematode community analysis

The classification of nematode dominance was based on the following criteria: taxa with individuals comprising more than 10% of the total number were considered dominant (+++); those comprising 1% to 10% were considered common (++); and those with individuals making up less than 1% were considered rare (+).

The analysis of soil nematode community structure used the nematode species diversity indices and the functional indices of nematode community structure. The diversity characteristics of soil nematode communities were commonly represented by indices like Shannon-Wiener diversity index (H'), Pielou's evenness index (J'), Simpson dominance index (λ) and Margalef richness index (SR). Indices like Maturity index (MI), Plant parasite index (PPI), Wasilewska index (WI), Nematode channel ratio (NCR), Enrichment index (EI) and Structure index (SI) were often used to represent the functional structure characteristics of soil nematode communities. The formulas were as follows:

1. Shannon-Wiener diversity index:

$$H' = -\sum p_i \times \ln(p_i) \text{ (Shannon and Weaver, 1949)}$$

2. Pielou's evenness index:

$$J' = \frac{H}{\ln(S)} \text{ (Pielou, 1966)}$$

3. Simpson dominance index:

$$\lambda = \sum (p_i)^2 \text{ (Simpson, 1949)}$$

4. Margalef richness index:

$$SR = \frac{S - 1}{\ln N} \text{ (Margalef, 1958)}$$

where $P_i = n_i/N$, n_i is the number of individuals in taxon i , N is the total number of individuals in all taxa of the community, and S is the number of taxa.

5. Maturity index:

$$MI = \sum c_i \times p_i \text{ (Bongers, 1990)}$$

where c_i is the c-p value for taxon i of soil nematodes and p_i is the ratio of individuals to the total number of taxon i of free-living nematodes. MI evaluates functional changes in soil ecosystems after disturbance and restoration. A low MI indicates that the soil is highly disturbed, and conversely, a high MI indicates that the soil is less disturbed, there is a high proportion of K-strategists, and the nematode community is in a relatively stable state (Li et al., 2021; Ren et al., 2020).

6. Plant parasite index:

$$PPI = \sum v_i \times f_i \text{ (Bongers, 1990)}$$

Where v_i is the c-p value of taxon i of plant parasites soil nematodes, and f_i is the ratio of individuals to the total number of individuals of taxon i of plant parasites. PPI is a maturity index that is specifically designed for the study of plant parasites. A high PPI indicates that plant parasites have more opportunities to feed on plants (Niu et al., 2020; Zhu et al., 2017).

7. Wasilewska index:

$$WI = (Ba + Fu)/Pp \text{ (Wasilewska, 1994; Yeates, 2003)}$$

where Ba, Fu and Pp are the number of bacterivores, fungivores and plant-parasites in the soil nematode community, respectively. WI was used to analyze the mineralization pathways in the soil food web.

8. Nematode channel ratio:

$$NCR = Ba/(Ba + Fu) \text{ (Yeates, 2003)}$$

NCR was used to characterize the importance of Ba and Fu in the decomposition channel. When the NCR is greater than 0.5, it indicates that the decomposition of soil organic matter is mainly dependent on the bacterial pathway, and on the contrary, the fungal pathway is dominant (Liu et al., 2022).

9. Enrichment index:

$$EI = 100 \times [e/(e + b)] \text{ (Ferris et al., 2001)}$$

10. Structure index:

$$SI = 100 \times [s/(s + b)] \text{ (Ferris et al., 2001)}$$

Where e , b and s denote the enriched, basal, and structural components of the food web, respectively. EI reflects the input of external nutrients and is used to assess the response of the food web to the available resources. SI denotes the connectivity, structural complexity, and length of the food chain of the soil food web. The larger the SI, the more complex the structure of the food web and the lesser resistance it has. EI and SI are considered simultaneously for assessing soil enrichment and food web development.

Nematode faunal analysis was performed based on EI and SI values of nematode communities at different elevations, and the results can provide a reference for soil food web status and soil environment (Chen et al., 2014).

2.6 Data analysis

A two-way ANOVA was used to examine the effects of elevation gradient, soil depth, and their interaction on soil physicochemical properties, soil nematode abundance, and ecological indices. A one-way ANOVA was used to test for differences in soil factors and nematode communities between different elevations and soil layers (LSD, $\alpha=0.05$). Pearson correlation analysis and redundancy analysis (RDA) were used to analyze the relationships between soil nematode communities and soil physicochemical properties. Data organization and statistical analysis were performed in Microsoft Excel 2016 and IBM SPSS Statistics version 26.0 (SPSS Inc., Chicago, IL, USA), redundancy analysis (RDA) was conducted using Canoco 5.0 software, and plotting was done in GraphPad

Prism 9 (GraphPad Software Inc., San Diego, CA, USA). All data were presented as mean $\pm$ standard error (SE).

3 Results

3.1 Soil physicochemical properties

Elevation and soil depth significantly affected soil physicochemical properties (Table 1). Elevation had a notable impact on BD, pH, SM, SOC, AK, TN, and AN across all soil layers. BD and pH both significantly decreased with increasing elevation, showing the highest values at E1, which were 0.97–1.03 g·cm⁻³ and 8.78–8.99, respectively. Conversely, SM, SOC, AK, TN, and AN exhibited a significant increasing trend with elevation. Notably, SOC and SM reached their highest values at E3 in the 10–20 and 20–40 cm soil layers, at 46.08 g·kg⁻¹ and 37.52%, respectively. AK, TN, and AN showed their highest values at E4, being 0.13–0.29 g·kg⁻¹, 2.37–4.35 g·kg⁻¹, and 0.09–0.16 g·kg⁻¹, respectively. AP, TC, and TP did not show significant changes with elevation in the 0–10, 20–40, and 10–20 cm layers. Soil properties significantly influenced by soil depth across the four elevations included pH, which increased significantly with depth and was highest in the 20–40 cm layer, with values ranging from 8.48 to 8.99. SOC and AK, on the other hand, significantly decreased with depth, showing the lowest values in the 20–40 cm layer, at 6.33–27.35 g·kg⁻¹ and 0.09–0.13 g·kg⁻¹, respectively. At the highest elevation (E4), SM significantly decreased with increasing soil depth, showing a 27.05% reduction. Furthermore, the interaction between elevation and soil depth significantly affected BD, SM, SOC, TN, and AN.

3.2 Composition and structure of soil nematode communities

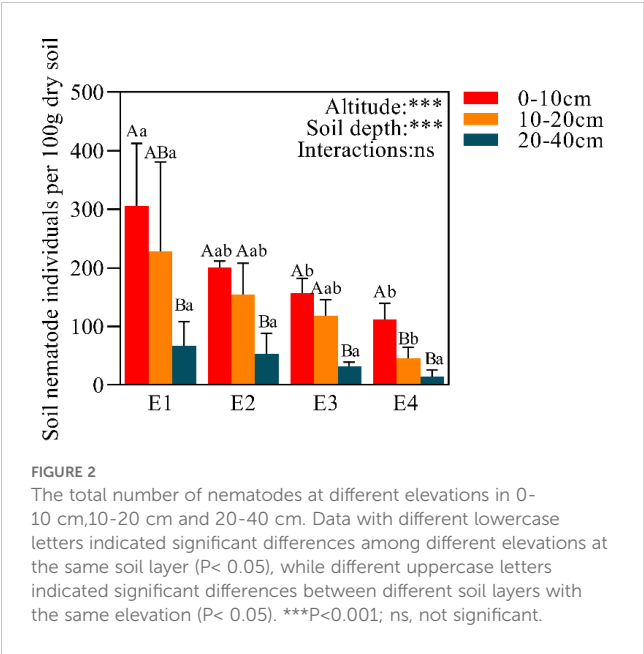
A total of 1487 soil nematodes were identified on all elevation gradients (Figure 2), belonging to 27 families and 32 genera (Table 2). Both elevation and soil depth had significant effects on the total number of nematodes, but the interaction was not significant. The number of nematodes exhibited a decreasing trend along the elevation gradient for all soil layers, with the order E1 > E2 > E3 > E4. This trend was especially pronounced in the 0–10 cm and 10–20 cm soil layers, with decreases of 63.32% and 79.94%, respectively. Within each elevation, nematode abundance showed a decreasing pattern across soil depths, following the order 0–10 cm > 10–20 cm > 20–40 cm, with the 20–40 cm layer being significantly lower than the 0–10 cm layer, showing decreases of 78.06%, 73.59%, 79.79%, and 86.90%, respectively.

Across the elevational gradient, the dominant taxon was *Helicotylenchus*, which accounted for 10.43% of the total number of nematodes; 17 genera such as *Mylonchulus* and *Dorylaimus* were common genera, which together accounted for 82.88% of the total number of nematodes; and 14 genera such as *Mesodorylaimus*

TABLE 1 Soil physical and chemical properties at different depths and elevations.

Depth (cm)	Elevation (m)	BD (g·cm ⁻³)	SM (%)	pH	TC (g·kg ⁻¹)	SOC (g·kg ⁻¹)	TN (g·kg ⁻¹)	TP (g·kg ⁻¹)	AN (g·kg ⁻¹)	AK (g·kg ⁻¹)	AP (g·kg ⁻¹)
0-10	E1	0.97± 0.06Aa	31.51± 2.26Ac	8.78± 0.06Ba	0.44± 0.01Ac	11.06± 0.29Ad	1.30± 0.06Ad	0.44± 0.01Ac	0.04± 0.00Ad	0.20± 0.02Ab	0.01± 0.00Aa
	E2	0.88± 0.04Aa	36.03± 0.89Ac	8.52± 0.04Cb	0.47± 0.01Ab	21.38± 0.97Ac	2.33± 0.06Ac	0.47± 0.01Ab	0.08± 0.00Ac	0.20± 0.02Ab	0.01± 0.00Aa
	E3	0.62± 0.01Ab	48.50± 2.53Ab	8.58± 0.02Bb	0.48± 0.01Ab	43.81± 3.32Ab	2.95± 0.05Ab	0.48± 0.01Ab	0.11± 0.00Ab	0.23± 0.00Aab	0.02± 0.00Aa
	E4	0.42± 0.02Bc	65.14± 3.95Aa	8.13± 0.09Bc	0.54± 0.01Aa	61.82± 2.44Aa	4.35± 0.01Aa	0.54± 0.01Aa	0.16± 0.00Aa	0.29± 0.00Aa	0.02± 0.00Aa
10-20	E1	0.97± 0.03Aa	29.70± 1.88Ac	8.94± 0.02Aa	0.43± 0.01Aa	7.54± 0.41Bc	0.96± 0.06Bc	0.43± 0.01Aa	0.03± 0.00Bc	0.14± 0.00Bab	0.01± 0.00Ab
	E2	0.90± 0.05Aa	33.19± 2.27Ac	8.67± 0.02Bb	0.44± 0.01Ba	19.35± 1.25ABb	2.31± 0.07Ab	0.44± 0.01Ba	0.08± 0.00Ab	0.11± 0.02Bb	0.01± 0.00Ab
	E3	0.67± 0.04Ab	45.17± 3.17Ab	8.52± 0.05Bc	0.47± 0.05Aa	46.08± 2.09Aa	3.07± 0.19Aa	0.47± 0.05Aa	0.11± 0.01Aa	0.12± 0.00Bb	0.02± 0.00Aa
	E4	0.52± 0.02Bc	63.71± 2.32Aa	8.33± 0.02ABd	0.49± 0.02Ba	42.98± 3.27Ba	3.12± 0.31Ba	0.49± 0.02Ba	0.12± 0.01Ba	0.17± 0.00Ba	0.01± 0.00Bb
20-40	E1	1.03± 0.03Aa	27.80± 1.00Ac	8.99± 0.05Aa	0.42± 0.01Aab	6.33± 0.85Bc	0.81± 0.04Bb	0.42± 0.01Aab	0.03± 0.00Bb	0.09± 0.01Cb	0.01± 0.00Aa
	E2	0.83± 0.02Ab	36.15± 0.97Ab	8.82± 0.06Aab	0.45± 0.01Bab	16.66± 0.66Bb	2.09± 0.04Aa	0.45± 0.01Bab	0.07± 0.01Aa	0.09± 0.00Bb	0.03± 0.01Aa
	E3	0.61± 0.06Ac	47.52± 4.25Aa	8.75± 0.05Ab	0.40± 0.02Ab	20.74± 3.24Bab	1.66± 0.24Ba	0.40± 0.02Ab	0.07± 0.01Ba	0.10± 0.00Cb	0.01± 0.00Aa
	E4	0.77± 0.04Ab	42.72± 2.42Bab	8.48± 0.06Ac	0.45± 0.01Ba	27.35± 2.25Ca	2.37± 0.29Ba	0.45± 0.01Ba	0.09± 0.01Ba	0.13± 0.01Ca	0.01± 0.00Ba
Mixed-effect ANOVA	Elevations	85.58***	70.14***	71.76***	7.47**	186.35***	105.60***	7.47**	136.73***	23.25***	0.85ns
	Soil depths	5.43*	7.22**	27.72***	10.86**	67.92***	40.55***	10.86**	37.97***	159.68***	0.53ns
	Interactions	6.65***	6.16**	1.67ns	1.42ns	16.69***	8.92**	1.42ns	6.93**	2.21ns	0.41ns

E, Elevation; E1, 1750-1900 m; E2, 1900-2100 m; E3, 2100-2350 m; E4, 2350-2560 m. BD, Bulk density; SM, Soil moisture; TC, Total carbon; SOC, Soil organic carbon; TN, Total nitrogen; TP, Total phosphorus; AN, Available nitrogen; AP, Available phosphorus; AK, Available potassium. Data with different lowercase letters indicated significant differences among different elevations at the same soil layer ($P < 0.05$), while different uppercase letters indicated significant differences between different soil layers with the same elevation ($P < 0.05$). * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, not significant.



and *Rhabditis* were rare genera, which together accounted for 6.69% of the total number of nematodes (Table 2). There were some differences in the dominant genera of soil nematode communities at different elevation gradients in each soil layer. In the 0–10 cm soil layer, there were no dominant genera in E1 and E4, mainly common genera, which accounted for 96.30% and 99.40% of the total number of soil nematodes, respectively; the dominant genera in E2 and E3 were *Ditylenchus*, *Cervidellus*, and *Helicotylenchus*, which accounted for 10.16%, 10.42% and 12.12%. In the 10–20 cm soil layer, the dominant genera in E1 were *Chiloplacus* and *Helicotylenchus*, which accounted for 10.25% and 11.13% of the total number of soil nematodes, respectively, while the dominant genera in E2 were *Mylonchulus* and *Helicotylenchus*, which accounted for 13.15% and 13.79% of the total number of soil nematodes, respectively; *Chiloplacus*, *Aphelenchoides*, *Ditylenchus*, and *Helicotylenchus* were the dominant taxa in E3, accounting for 11.35%, 10.21%, 13.05% and 11.91%, respectively; *Chiloplacus* and *Helicotylenchus* were the dominant taxa in E4, which accounted for 16.76% and 15.30%, respectively. In the 20–40 cm soil layer, *Mylonchulus* was the dominant genus in E1, accounting for 12.91% of the total number of soil nematodes; the dominant

TABLE 2 Soil nematode community composition and c-p values of trophic groups at different elevations and depths.

Genus	c-p value	Dominance											
		E1			E2			E3			E4		
		D1	D2	D3	D1	D2	D3	D1	D2	D3	D1	D2	D3
Bacterivores,Ba													
<i>Monhystera</i>	1	++	++	++	++	++	+++	++	++	++	++	++	++
<i>Rhabditis</i>	1	++							+		++		
<i>Plectus</i>	2	++	++	++	++	++	++	++	++		++		
<i>Wilsonema</i>	2	+			+						++		
<i>Chiloplacus</i>	2	++	+++	++	++	++	+++	++	+++	++	++	+++	+++
<i>Acrobeles</i>	2										++	++	
<i>Cervidellus</i>	2	++	++	++	++	++	+++	+++	++	+++	++	++	++
<i>Teratocephalus</i>	3	++	++	+	++	+	+	+			++		
<i>Rhabdolaimus</i>	3	+			+	+	++	++	+		+	+	
<i>Prismatolaimus</i>	3	++	++	++	++	++	+++	++	++	++	++	++	++
Fungivores,Fu													
<i>Filenchus</i>	2								+		++		
<i>Aphelenchoides</i>	2	++	++	++	++	++	+++	++	+++	++	++	++	
<i>Aphelenchus</i>	2								++		++		++
<i>Tylencholaimus</i>	4									+++			
<i>Leptonchus</i>	4	++			+	+	++	++	+				
Omnivores-predators,Om													
<i>Tripyla</i>	3	++	++	++	++	++	+++	++	++	++	++		
<i>Mylonchulus</i>	4	++	++	+++	++	+++	++	++	++	++	++		

(Continued)

TABLE 2 Continued

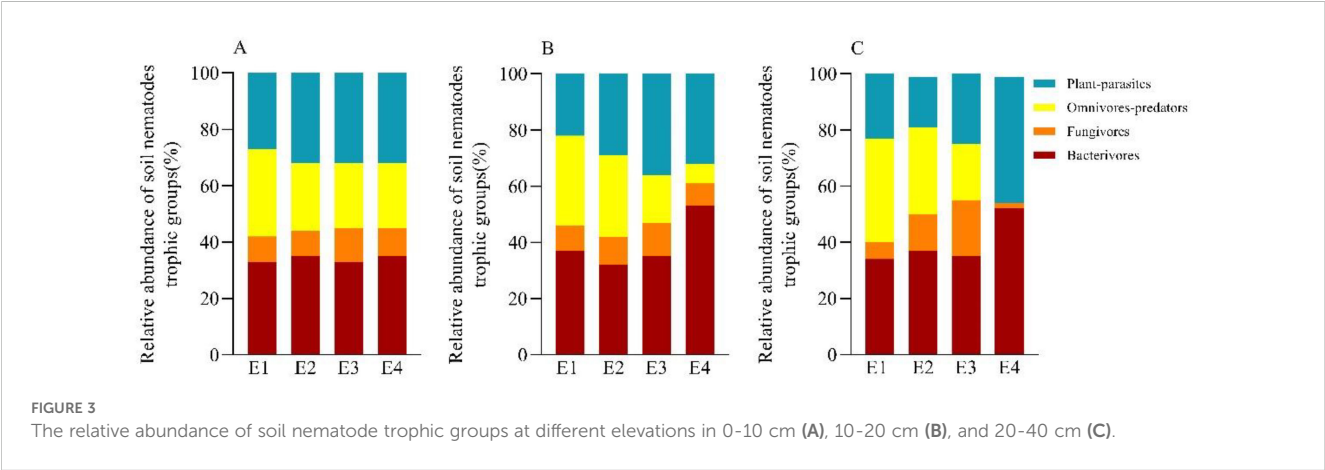
Genus	c-p value	Dominance											
		E1			E2			E3			E4		
		D1	D2	D3	D1	D2	D3	D1	D2	D3	D1	D2	D3
Omnivores-predators,Om													
<i>Dorylaimus</i>	4	++	++	++	++	++	++	++	++		++		
<i>Eudorylaimus</i>	4	++	++	++	++	++	++	++	++	++	++	++	
<i>Thornia</i>	4	++	++	++	++								
<i>Pungentus</i>	5	+									++		
<i>Mesodorylaimus</i>	5		+		+	+					++	+	
<i>Longidorus</i>	5	+									++	+	
Plant-parasites,Pp													
<i>Ditylenchus</i>	2	++	++	++	+++	++	++	++	+++	++	++	++	
<i>Cephalenchus</i>	2	++		++				++	++				
<i>Helicotylenchus</i>	3	++	+++	++	++	+++	+++	+++	+++	++	++	+++	+++
<i>Amplimerlinius</i>	3	++	+	++	+			++	++		++		++
<i>Tylenchorhynchus</i>	3	++	++	++	++	++	++	++	++	++	++		
<i>Pratylenchus</i>	3	++		+	++						++		++
<i>Criconema</i>	3										++	+	++
<i>Trichodorus</i>	4	++	+					+	+	++			
<i>Axonchium</i>	5	++	++	++	+				++	++	++	++	

+++, The group with more than 10% of the total number of individuals; ++, The group with individual number of 1%–10%; +, The group with less than 1% of the total number of individuals. D, soil depth; D1, 0–10 cm; D2, 10–20 cm, D3, 20–40 cm.

genera in E2 were *Monhystera*, *Chiloplacus*, *Cervidellus*, *Prismatolaimus*, *Aphelenchoides*, *Tripyla*, and *Helicotylenchus* with 18.24%, 26.42%, 30.82%, 10.06%, 26.42%, 13.84% and 10.06%, respectively; *Cervidellus* and *Tylencholaimus* were the dominant taxa in E3 with 12.63% and 10.55%, respectively; *Chiloplacus* and *Helicotylenchus* were the dominant taxa in E4 with 20.45% and 36.36%, respectively.

Among the different trophic taxa in each soil layer, bacterivore nematodes were the major trophic taxa with the highest total

abundance at all elevations, accounting for 32.39% to 52.55% of the relative abundance at each elevation; followed by plant-parasites and omnivores-predators, which accounted for 18.24% to 45.45% and 7.29% to 37.25% of the relative abundance at each elevation; and fungivore nematodes were the lowest, accounting for only 2.27% to 20.02% (Figures 3A–C). Overall, the relative abundance of bacterivore nematodes and plant parasites increased with elevation, showing an increasing trend; the relative abundance of omnivores-predators was the opposite of that of bacterivore



nematodes, decreasing with elevation; and the relative abundance of fungivore nematodes was in a “humpback pattern”, with a low-high-low pattern, with a maximum at E3.

3.3 Ecological indices and faunal analysis of soil nematode communities

Elevation and soil depth significantly affected H' , λ and SR, and their interaction also significantly influenced H' and SR (Figures 4A–D). Within each soil layer, the patterns of H and SR changes with elevation were consistent, while λ showed the opposite trend. In the 0–10 and 20–40 cm soil layers, H and SR decreased with increasing elevation, whereas λ increased with elevation; there was no clear pattern in the 10–20 cm soil layer. Generally, across all elevations, H and SR decreased with soil depth, while λ increased.

In each soil layer, NCR was less than 0.5 at higher elevations (E3, E4) and greater than 0.5 at lower elevations (E1, E2); MI decreased with increasing elevation, being highest at E1; PPI and PPI/MI generally increased with elevation; WI increased with elevation in the 0–10 cm soil layer, showed the opposite pattern in the 10–20 cm soil layer, and followed a unimodal pattern in the 20–40 cm soil layer (Figures 4E–I). Across all elevations, MI increased with soil depth at E1, E2 and E3, but decreased at E4; PPI showed the opposite trend to MI with soil depth; WI was

significantly higher in the 0–10 cm soil layer compared to the 10–20 and 20–40 cm layers (Figures 4E, F, H).

Nematode fauna analysis showed that in the 0–10 cm soil layer, the soil nematode communities at all four elevation gradients were located in quadrant C. In the 10–20 cm soil layer, the nematode communities at E1 and E3 were in quadrant C, while those at E2 and E4 were in quadrants B and D, respectively. In the 20–40 cm soil layer, the nematode communities at E1, E2, and E3 were in quadrant C, whereas the community at E4 was in quadrant D (Figures 5A–C).

3.4 Relationship between soil nematode communities and soil properties

The total explanatory rates of variance for the RDA1 and RDA2 axes were 80.00%, 81.99% and 78.25%, respectively (Figures 6A–C). In the 0–10 cm soil layer, SM and pH were the key factors influencing soil nematode variation, with contribution rates of 14.0% and 13.0%, respectively. In the 10–20 cm soil layer, pH, SM, AP and SOC were the key factors, with contribution rates of 29.6%, 13.2%, 12.1% and 10.3%, respectively. In the 20–40 cm soil layer, pH, AK, SOC, AN, SM and BD were the key factors, with contribution rates of 28.5%, 28.0%, 22.1%, 19.4%, 15.9% and 12.6%, respectively. In the 0–10 cm soil layer, the total number of nematodes and omnivores-predators were significantly positively correlated with pH and BD, and significantly

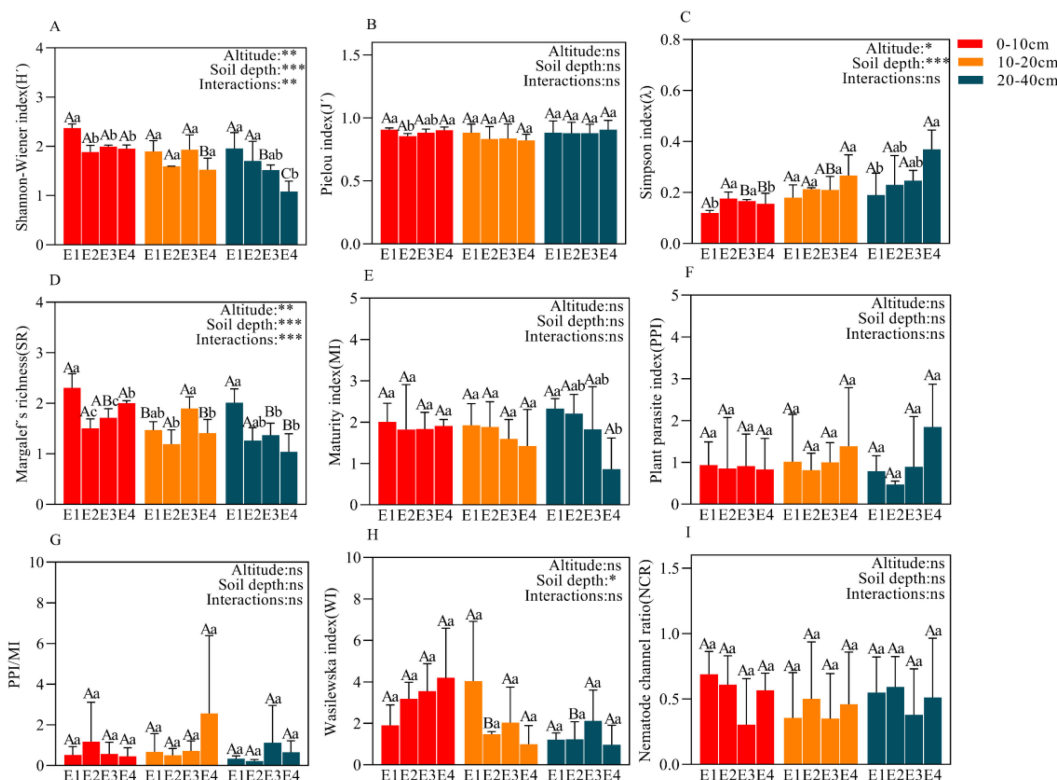


FIGURE 4

Ecological indices (H' , J' , λ , SR, MI, PPI, PPI/MI, WI, NCR) (A–I) of the soil nematode community at different elevations in 0–10 cm, 10–20 cm, and 20–40 cm. Data with different lowercase letters indicated significant differences among different elevations at the same soil layer ($P < 0.05$), while different uppercase letters indicated significant differences between different soil layers with the same elevation ($P < 0.05$). * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns, not significant.

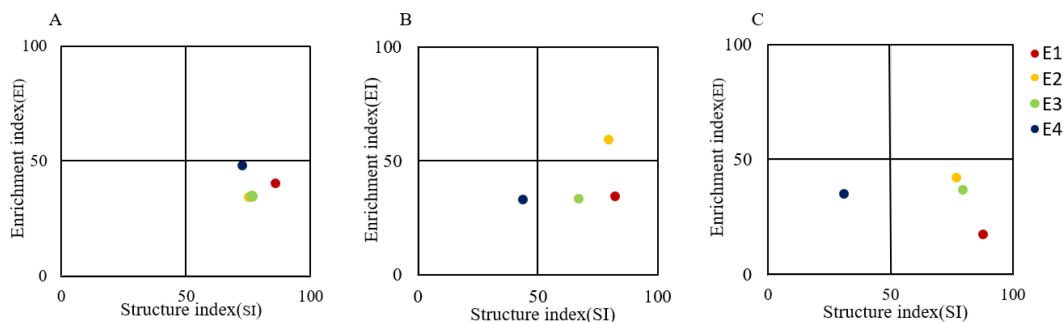


FIGURE 5
Nematode faunal analysis at different elevations in 0-10 cm (A) 10-20 cm (B) and 20-40 cm (C).

negatively correlated with SM (Figure 7A). In the 10-20 cm soil layer, the total number of nematodes was significantly positively correlated with pH, and significantly negatively correlated with SOC, AN, AK, AP and TC (Figure 7B). In the 20-40 cm soil layer, omnivores-predators were significantly positively correlated with pH and BD, and significantly negatively correlated with SOC, SM, AK, AP, AN and TC (Figure 7C).

4 Discussion

We observed a general decreasing trend in soil nematode numbers, diversity (H') and richness (SR) along the elevational gradient and soil depth in Luoshan, Ningxia. This result is consistent with other studies such as Oakley in the northern of the Greater Khingan Mountains, China (Shen et al., 2023) and the Pir-Panjel Mountains of the Himalayas (Kashyap et al., 2022; Afzal et al., 2021; Choudhary et al., 2023), but different from the results from the Mount Ararat in Turkey, the number of soil nematode species was found to reach its maximum at medium elevation, showing a “single peak pattern” (Taylan et al., 2021). This may be attributable to the changes in temperature, SM, and elevations. Firstly, nematodes are very sensitive to changes in temperature (Afzal et al., 2021; Albright et al., 2020). Litter decomposition and nutrient release are key ecological processes

linking the terrestrial and atmospheric carbon cycles, with a global average litter leaf carbon release of 0.69 yr^{-1} (Chen et al., 2024). As the elevational gradient increase and soil layer deepen, the temperature decreases, which reduces the rate of litter decomposition and microbial activity, leading to accumulation of soil organic matter and a decrease in nutrient levels, inhibiting nematode reproduction (Choudhary et al., 2023). Secondly, nematodes are very sensitive to changes in SM (Franco et al., 2021; Kardol et al., 2011). With higher elevation, increased precipitation will alter the coupling between aboveground and belowground, affecting nematode community diversity. In addition, the increase in soil water content may lead to hypoxia, reducing both nematode population and diversity (Afzal et al., 2021; Liu et al., 2019). Meanwhile, as the soil layer deepens and SM decreases, the activities of soil nematodes, especially free-living nematodes that are free in the water film, are limited, leading to a decline in nematode numbers and diversity at higher elevations (Tong et al., 2010). Thirdly, higher elevations present relatively hostile environments with relatively less resilient and sustainable ecosystems compared to lower elevations (Kashyap et al., 2022).

Interestingly, this study revealed that *Helicotylenchus*, with a p value of 3, was the dominant taxon across the elevational gradient. However, differences across the dominant genera of soil nematode communities were observed in different elevational gradients within each soil layer, with a relatively high number of dominant

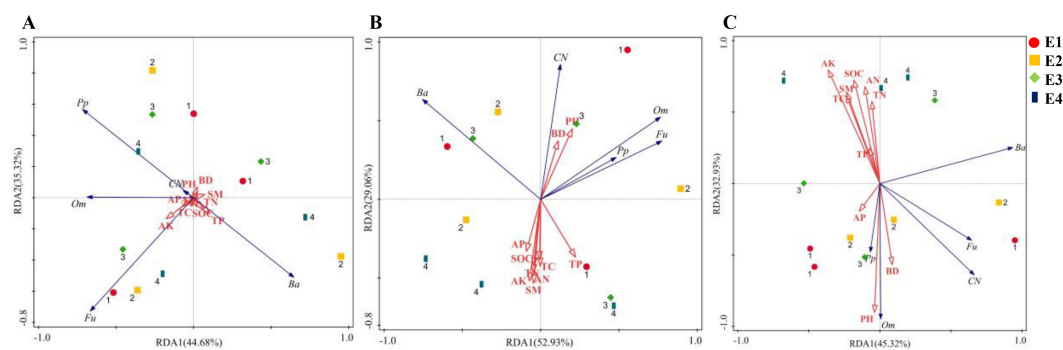


FIGURE 6
Redundancy analysis of soil nematode community with soil properties in 0-10 cm (A), 10-20 cm (B), and 20-40 cm (C). BD, Bulk density; SM, Soil moisture; TC, Total carbon; SOC, Soil organic carbon; TN, Total nitrogen; TP, Total phosphorus; AN, Available nitrogen; AP, Available phosphorus; AK, Available potassium. Ba, Bacterivores; Fu, Fungivores; Om, Omnivores-predators; Pp, Plant-parasites. CN represents the sum of the number of individuals in the nematode community.

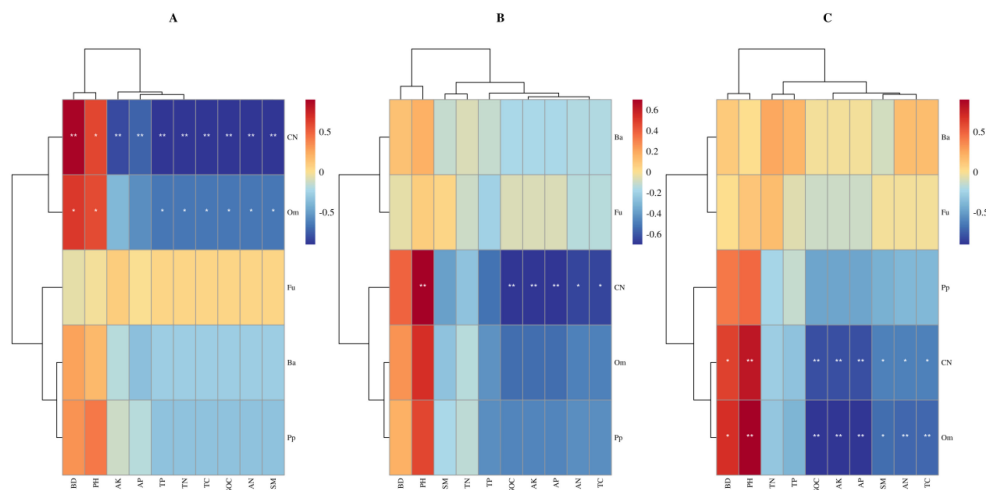


FIGURE 7

Correlation between different trophic groups of soil nematodes and soil properties in 0–10 cm (A), 10–20 cm (B) and 20–40 cm (C).

nematodes with a cp value of 2 at higher elevations (Yeates and Bongers, 1999). This indicates that nematodes in Luoshan, Ningxia, predominantly consist of k-strategists, which have low reproduction rates and high sensitivity to disturbance (Wagner et al., 2015; Bongers, 1990). Conversely, at higher elevations, r-strategists among nematodes were relatively dominated, characterized by opportunism, high reproductive ability, and resistance to disturbance, which further indicates that higher elevations present more harsh environments and more susceptible to environmental disturbances compared to lower elevations (Tong et al., 2016). Additionally, the above-ground vegetation and the below-ground microenvironment vary greatly with elevation, and different environmental conditions and resource heterogeneity shape the distributional differences of the soil nematode community (Bardgett and van der Putten, 2014; Choudhary et al., 2023).

We found that among the various trophic taxa in each soil layer, bacterivore nematodes were the dominant trophic taxa, and their relative abundance with plant-parasites, increased with elevation, which is consistent with the findings of Choudhary et al. (2023). A plausible explanation is that, at high elevations, the dominance of forests with well-developed and dense underground root systems supports the survival of plant-parasites. Furthermore, among the bacterivore nematodes, the majority had a CP value of 2, indicating strong adaptation to the harsh environments. In addition, the relative abundance of omnivores-predators exhibited an inverse pattern to that of bacterivore nematodes, decreasing with increasing elevation, which is in line with Kashyap et al. (2022). This may be because omnivores-predators occupy a high trophic level in the soil food web and can switch to different prey as needed (Afzal et al., 2021). The relative abundance of fungivore nematodes showed a low-high-low “humpback pattern”, peaking at E3. This suggests that the elevational distribution patterns of soil nematode trophic groups vary and warrant further investigated. The dominance of bacterivore nematodes among all trophic groups across the elevational gradient suggests that the relatively fast decomposition model of fungal energy pathways prevails in Luoshan, Ningxia.

In this study, several key nematode species diversity indices and functional indices of nematode community structure were used to analyze soil nematode community structure. It was shown that the diversity index (H'), richness index (SR) and maturity index (MI) tended to decrease with elevation, while PPI/MI and PPI generally tended to increase with elevation gradient. This is consistent with previous studies (e.g., Choudhary et al., 2023), but differs somewhat from others (e.g., Afzal et al., 2021). The decrease in MI and the increase in PPI/MI indicate that soil ecosystems are subjected to increased disturbance in high elevation regions, reducing soil food web stability and the proportion of k- strategists nematodes (Chen et al., 2014; Ciobanu and Popovici, 2017). The overall increasing trend of PPI with elevation gradient indicates that plant-parasites had more plants to feed on and increased in number, corroborating the observations that the relative abundance of plant-parasites increased with elevation. Our study also found that the value of NCR decreased from greater than 0.5 to less than 0.5 with elevation, indicating a shift in the decomposition pathway of soil organic matter from the bacterial channel to the fungal channel (Liu et al., 2022). This shift occurs because coniferous forests predominate at high elevations in the Luoshan Mountain of Ningxia, where an abundance of C/N-containing compounds in the coniferous litter favors the fungal decomposition pathway. Similar to the study of Huo et al. (2021) and Afzal et al. (2021), this further supports the argument that bacterivore nematodes increased with elevation, while fungivore nematodes decreased at high elevation. The lower temperature and harsh environment at high elevations make it difficult and slow for some coniferous forests to decompose their withered leaves, enhancing the fungal-based energy flow in the ecosystem (Choudhary et al., 2023). In addition, our nematode faunal analysis revealed higher SI and lower EI values in E1, E2 and E3, while E4 had lower SI and lower EI values. This pattern indicates that soil was subjected to increased disturbance at higher elevations, the degree of structuring of the soil food web and nutrient enrichment was weakened, and the stability of the soil ecosystem declined, further supporting the above conclusions (Ciobanu and Popovici, 2017).

Elevation directly leads to the distribution of vegetation types, which modifies abiotic and biotic factors that, in turn, change the soil environment and soil physicochemical properties, ultimately affecting soil nematode communities (Bardgett and van der Putten, 2014; Fu et al., 2022; Kashyap et al., 2022). Our findings indicated that pH, BD, SM, SOC, AN, AP and AK were the main soil factors affecting soil nematode community composition. Pearson correlation analysis further corroborated the relationship between nematode community characteristics and soil physicochemical properties (Figure 6), well explained the differences in nematode communities at different elevations and soil depths. These results align with the findings of Shen et al. (2023) and Choudhary et al. (2023). It has also shown that soil pH and BD had significant effects on nematode communities, especially on omnivores-predators and nematode populations. Changes in soil pH may affect nematode physiology and metabolism, and may also indirectly affect nematode communities by altering the soil microenvironment (Li Q. M. et al., 2023). BD affects pore interstitial space, SM, and SOC, which have an impact on root growth and inter-root nutrient supply, and consequently affecting nematode populations. This impact is likely due to the simultaneous effect of BD and other variables, rather than a response to BD alone (Shen et al., 2023). SM was negatively correlated with nematode communities, probably because increased SM creates an anaerobic environment in the soil-water film, leading to hypoxia and a decline in nematode populations (Franco et al., 2021; Afzal et al., 2021). We also found that fast-acting nutrients such as AN and AP had a significant effect on nematodes. N and P are the major limiting factors in northern Chinese soils, and their nutrient-limited nature indirectly affects soil nematodes through plant roots and soil microbial activity (Shen et al., 2023). N enrichment has been shown to suppress nematode abundance and diversity (Liang et al., 2009), and ammonium has been shown to be toxic to a wide range of organisms. However, soil nematode trophic taxa respond differently to NH_4^+ -N concentrations depending on feeding habits (Zhang et al., 2021).

5 Conclusion

Soil nematode distribution in Luoshan had a clear gradient effect. Our studied indicated that the number, diversity and richness of soil nematodes were significantly affected by elevation and soil depth, all exhibiting a decreasing trend with increasing elevation and soil depth. *Helicotylenchus* emerged as the dominant taxon, while bacterivore nematodes were the main trophic taxon, increasing with elevation. Key soil factors affecting soil nematode community composition included pH, BD, SM, SOC, AN, AP and AK. With increasing elevation, soil disturbance intensified, the degree of soil food web structuring and nutrient enrichment decreased, and the decomposition pathway shifted from bacterial to fungal. Our study provides strong results for the vertical distribution pattern of soil nematode communities in Luoshan, Ningxia, which can be used as the basic information for further study of soil biota in this mountainous area, and provides partial theoretical support for further exploration and study of the distribution pattern of soil nematode communities in the arid and semi-arid regions of Northwest China as well as globally.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding authors.

Author contributions

JC: Data curation, Formal analysis, Investigation, Software, Writing – original draft. YZ: Supervision, Writing – review & editing. CL: Resources, Writing – review & editing. LH: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Writing – review & editing.

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Supplementary material

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Effect of stand age on rhizosphere microbial community assembly of dominant shrubs during sandy desert vegetation restoration

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The rhizosphere microbial community helps govern biogeochemical cycling and facilitates complex plant-soil feedback. Understanding the evolutionary dynamics of microbial community structure and functional genes during vegetation succession is crucial for quantifying and understanding ecosystem processes and functions in restored sandy deserts. In this study, the rhizosphere microbial community structure of 11–66-year-old dominant shrubs in a desert revegetation area was examined using shotgun metagenomic sequencing. The interactions between the microbial community structure, functional gene abundances, soil properties, and plant characteristics of different stand ages were comprehensively investigated. The abundance of unique species first increased before subsequently decreasing with stand age, with shared species accounting for only 47.33%–59.42% of the total operational taxonomic units (OTUs). Copiotrophs such as Actinobacteria and Proteobacteria were found to dominate the rhizosphere soil microbial community, with their relative abundance accounting for 75.28%–81.41% of the total OTUs. There was a gradual shift in dominant microbial functional genes being involved in cellular processes towards those involved in environmental information processing and metabolism as stand age increased. Additionally, temporal partitioning was observed in both the microbial co-occurrence network complexity and topological parameters within the rhizosphere soil. Redundancy analysis revealed that dissolved organic carbon was the primary determinant influencing shifts in microbial community structure. Understanding the evolution of microbial community structure and function contributes to identifying potential mechanisms associating the soil microbiome with

dominant sand-fixing shrubs as well as understanding the rhizosphere microbiome assembly process. These results shed light on the role of the rhizosphere microbiome in biogeochemical cycling and other ecosystem functions following revegetation of temperate sandy deserts.

KEYWORDS

microbial community, metagenome, microbial functional genes, plant-soil interaction, desert ecosystem restoration

1 Introduction

Although they have low productivity, dryland systems prominently influence global biogeochemical cycles and climate change, as they constitute 41% of the terrestrial land area (Safriel and Adeel, 2005). However, approximately 10%–20% of the world's drylands are subject to desertification, soil degradation, and vegetation decline from anthropogenic disturbances and climate change (Safriel and Adeel, 2005). Vegetation restoration is an important practice for the containment and reversal of desertification, as well as an effective approach for rehabilitating degraded land (Zonn et al., 2017). Since the 1950s, China has made enormous efforts in ecological restoration and reconstruction, effectively combating deserts and reconstructing desert ecosystems through the installation of sand barriers and the planting of xerophytic shrubs (Korkanç, 2014; Gellie et al., 2017; Hu et al., 2021). This practice significantly impacts ecosystem health and global biochemical cycles due to its significant influences on ground cover (Hu et al., 2021; Scotton and Andreatta, 2021), soil hydrothermal conditions (Zhang et al., 2013; Li et al., 2022a), soil properties (Korkanç, 2014; Hu et al., 2021), and microbial community structure (Gellie et al., 2017; Huang et al., 2022).

Soil microorganisms play a pivotal role in fundamental ecosystem functions, serving as crucial players and mediators in soil biogeochemical cycles such as C sequestration and N retention (Baldrian et al., 2012; Sun and Badgley, 2019). Microbial communities are regulated by varying external factors such as available resources, plant inputs, plant age, environmental stresses, and biological interactions (Zumsteg et al., 2012; Knelman et al., 2014; Salles et al., 2017; Karliński et al., 2020; Qiao et al., 2024). Soil microbial communities undergo shifts along ecosystems age after restoration, mirroring changes in ecological conditions and exerting influence on the restoration of ecosystem functions (Sun et al., 2017; Sun and Badgley, 2019). However, many studies have focused only on describing alterations in microbial taxonomy (Zhao et al., 2018). Investigating changes in functional gene abundance involved in various ecological processes in soil microbial communities as restoration progresses provides a direct understanding of how revegetation affects ecosystem function (Sun and Badgley, 2019). Several studies have confirmed substantial shifts in the abundance of C- and N-cycle functional genes as

restoration progresses (Brankatschk et al., 2011; Zeng et al., 2016; Salles et al., 2017; Sun and Badgley, 2019). The abundance of key genes involved in the microbial N cycle such as *nifH*, *nirS*, and *nirK* reached their maximum values at the middle stage of the restoration chronosequence (35 years) (Salles et al., 2017). Additionally, the abundance of *nirS* and ammonia oxidation genes decreased in some studies (Brankatschk et al., 2011), while others observed an increase in abundance with stand age (Zeng et al., 2016). Microbial functional genes related to the N and CH₄ cycles varied linearly with restoration chronosequence in one study (spanning 6–31 years) (Sun and Badgley, 2019). Considering that the rhizosphere soil is the most intense site of plant-microbe-soil interactions, it is still unclear how the abundance of functional genes in rhizosphere soil microbial communities evolve or what the primary driving factors during the recovery of desert ecosystems are (Pausch and Kuzyakov, 2018).

Rhizosphere microbial community structure, specific functional genes, and ecological functions are closely related to stand age (Liu et al., 2018a; Song et al., 2022). As stand age increases, plants regulate the availability of soil nutrient resources through root exudates, which affects the formation of rhizosphere microbial community and functional gene abundance (Song et al., 2022). The microbial community diversity and the abundance of N and S cycling functional genes increased with stand age of *Eucalyptus* (Qu et al., 2020). Soil bacterial communities also showed a positive response with increasing stand age of *Robinia pseudoacacia* (Liu et al., 2018). Bacterial diversity, community structure, and potential metabolic functions in the rhizosphere also changed with the growth of *Spartina alterniflora* and *Kandelia obovate* (Song et al., 2022). However, in the special environment of desert ecosystems, the specific alterations in plant rhizosphere microbial community structure and functional gene groups with shrub age, along with their driving factors, remain unclear. This information is important in better guiding and managing desert revegetation systems.

The rhizosphere is a narrow area within 1–3 mm from the plant root surface and is influenced by plant growth and metabolic activity (Wang et al., 2016; Pausch and Kuzyakov, 2018). It represents a hot zone of heightened microbial activity and a major location for intricate interactions among plants, soil, and microorganisms. Rhizosphere microorganisms play indispensable roles in ecological

and metabolic processes, serving as vital constituents of the rhizosphere (Zhang et al., 2021; Zhang et al., 2022). Changes in rhizosphere microbial communities not only directly reflect variations in vegetation and soil properties but also have significant implications for the formation and succession of microbial communities in bulk soil (Korniłłowicz-Kowalska et al., 2022; Zhou et al., 2022). Investigating rhizosphere microbial communities and their functional genes can provide a more direct understanding of how revegetation of desert ecosystems affects microbial processes associated with ecosystem function (Sun and Badgley, 2019; Yu et al., 2024), playing a critical role in revealing the impacts of long-term vegetation restoration on microbial communities.

This study leveraged metagenomics to monitor the temporal changes in microbial community structure and function along a chronosequence of restoration stand age in a desert revegetation area, aiming to investigate how the age of dominant shrubs affects soil microbial community assembly and functional gene group abundance as well as reveal the effects of dominant shrub stand age on rhizosphere soil microbial network complexity and stability. It was hypothesized that soil microbial community composition would evolve from oligotrophic to copiotrophic groups as the soil environment becomes more complex with increasing stand age, creating an increased need for cooperative, rather than competitive, relationships. Additionally, increasing stand age was expected to increase microbial network complexity and stability, enhancing microbial processes associated with ecosystem function. The results of this study will help to improve our understanding of the evolution of soil microbial communities and functions during the restoration of shrub-dominated desert ecosystems, as well as deepen our understanding of plant-microbe-soil interactions.

2 Materials and methods

2.1 Study area

The study area was situated within the revegetation zone at Shapotou, which lies on the southeastern fringe of the Tengger Desert in China (37°32' N, 105°02' E). The climate is characterized by aridity, low rainfall, and windy conditions. The annual average temperature is 10°C; the mean annual precipitation is 186.2 mm, and the mean annual evapotranspiration is 2800 mm. The soil is classified as wind-borne sand (Yang et al., 2020). The natural landscape is blowing dunes with vegetation coverage < 1%. The depth of the groundwater table is about 80 m from the surface, which is unavailable even to deep-rooted plants; rainfall serves as the sole resource for plant growth and development.

In the 1950s, a combination of checkerboard and shrub plantation was practiced to inhibit the erosion of mobile sand and keep the Lanzhou-Baotou railway from being buried. After the checkerboard of straw sand barriers was erected, xerophytic shrubs (mainly *Caragana korshinskii* Kom., *Artemisia ordosica* Krasch. and *Hedysarum scoparium* Fisch.) were planted at the checkerboard barriers with 16 individuals per 100 m². Subsequently, this pattern was replicated along the north-south direction in 1964, 1973, 1987, 1999, and 2011. Presently, a protection system of rainfed artificial

sand-fixing vegetation that is 16 km long and 0.7–1.0 km wide has been created. Following the establishment of the protection system, the composition of the vegetation community shifted from a shrub-dominated to a combined shrub and herbaceous pattern (Li et al., 2016). Soil properties, soil carbon sequestration (Yang et al., 2014; Li et al., 2022b), and microbial community structure (Liu et al., 2018b) were also significantly improved.

2.2 Soil sampling preparation

The soil samples for this study were collected in July 2022 from four revegetation sites constructed in 1956, 1964, 1987, and 2011, and were 66, 58, 35, and 11 years old, respectively. The soil type, elevation, slope, and aspect were similar at each sampling site. Three sampling plots (10 × 10 m) more than 50 m apart from each other were established at each revegetation area. Five *C. korshinskii* were investigated randomly across each plot, recording plant height, crown size, and basal diameter. The rhizosphere soil of corresponding plants was collected; the topsoil (0–20 cm) was removed as it did not have roots, then transects were established around the plant. Fine roots (< 1 mm) and attached rhizosphere soil were selected from the transects with sterile forceps, and loose soil was removed. The soil that remained adhered to the roots was considered rhizosphere soil. The fine roots with adhering soil were kept cold in the field and preserved in an ice box and then transported to the laboratory. Subsequently, the rhizosphere soil and fine roots were carefully separated on a sterile operating table. A total of 15 subsamples were collected, and a mixed sample was obtained by thoroughly mixing an equal number of the subsamples. Three replicate samples were collected at each site using the same method. Each composite sample was divided into two parts: one part was stored at –80°C and another was air-dried at room temperature for subsequent analyses.

2.3 Determination of soil physicochemical properties

The levels of total C (TC) and dissolved organic C (DOC) in rhizosphere soil were assayed using a TOC analyzer (Vario II, Elementar, Germany). Total nitrogen (TN) contents were determined using an element analyzer (Vario MACRO cube, Elementar INC., Germany). Soil pH was detected with a pH meter (CRISON 20, Barcelona, Spain) in a 1:5 soil–water mixture.

2.4 Shotgun metagenome sequencing and sequence processing

DNA was extracted from rhizosphere soil samples using the CTAB method (Yi et al., 2018). The DNA degradation degree, potential contamination, and concentration were measured using Agilent 2100 (Agilent Technologies Co. Ltd., USA) to screen qualified samples for sequencing. Sequencing libraries were generated using an NEBNext UltraTM DNA Library Prep Kit

for Illumina (NEB, USA) and index codes were added to attribute sequences to each sample. Clustering of index-coded samples was performed on a cBot Cluster Generation System (Clark et al., 2011). After cluster generation, library preparations were sequenced on an Illumina Novaseq 6000 platform and 2×150 bp paired-end reads were generated. Raw sequencing data were filtered with Trimmomatic to obtain high-quality clean reads (Bolger et al., 2014). The clean reads after quality control and de-host were matched against a database (Uniref90) using Humann2 software; the resulting genes were searched against the NCBI and KEGG databases using Kraken 2 (v2.0.7-beta) for taxonomic and functional annotations (Segata et al., 2011; Lu et al., 2017; Franzosa et al., 2018).

2.5 Statistical analyses

Changes in the plant traits, soil properties, and relative abundances of phylogenetic groups and functional genes (KEGG level2) between samples were analyzed using single-variable methods with R. LEfSe analysis identified significantly different taxa at each stand age, and the impact of these species was further evaluated and downscaled using linear discriminant analysis (LDA) (Kitani and Murakami, 2020; Gojevic et al., 2022). The Bray-Curtis distances between sample pairs were estimated from species composition and visualized by non-metric multidimensional scaling (NMDS) using the 'metaMDS' function in the "vegan" package for R. The dissimilarity of communities between rhizosphere soil samples was assessed by generating a Venn diagram of shared and unique OTUs at 97% similarity. Soil microbial dominant phyla were visualized as heatmaps using the R package 'pheatmap', and the relationship between the abundance of major microbial taxa and stand age was evaluated by linear regression analysis.

Co-occurrence networks were constructed based on Spearman's rank correlation coefficients of OTU abundances. First, OTUs whose average relative abundance was less than 0.1% and whose occurrence frequency was less than 1/10 of the total sample size were removed. Then, a pairwise similarity matrix (based on Spearman's coefficients) and p values were computed for OTU abundances using the "WGCNA" package in R. Network diagrams

were visualized in Gephi. In addition, regression analysis was conducted on the network complexity attribute, the network topological indices including n (total number of nodes), L (total number of links), modularity (the degree to which a network is compartmentalized into different modules), average degree, and positive and negative correlation links. Redundancy analysis (RDA) was performed to link microbial community structures to plant characteristics and soil properties using the "vegan" package in R. Variation partition analysis (VPA) was conducted to evaluate the impact of plant characteristics and soil properties on soil microbial community structure using Canoco 5.0.

To estimate the impact of stand age on soil properties, plant characteristics, microbial community structure, functional gene abundance, and microbial community co-occurrence network complexity, a partial least squares path model (PLS-PM) was built and tested. Soil properties were defined as a proxy including TN, TC, C:N, DOC, and pH. Plant characteristics were defined as a proxy including height, crown size, and basal diameter. Network complexity was defined as a proxy including n , L , modularity, average degree, and positive and negative correlation links. The microbial community structure was represented by the first and second principal components of the NMDS based on the OTU level. The functional gene abundance was represented by the first and second principal components of the principal components analysis based on significant differences in the OTU levels among different stand ages. A complete PLS-PM model was first built based on existing theories and concepts that included all the available variables mentioned above. Following this, variables with low contributions were deleted. The goodness of fit of the PLS-PM model was assessed. The PLS-PM model was built using SmartPLS 3.0 (Ramayah et al., 2018).

3 Results

3.1 Characteristics of plants and soil

The plant height and crown size initially increased significantly along the chronosequence of restoration, reaching maximum values at 58 y at 199.33 cm and 6.22 m², respectively; after this, it decreased with increasing stand age ($p < 0.05$; Table 1). The basal diameter

TABLE 1 Characteristics of plant, and rhizosphere soil properties along a chronosequence of revegetation.

Properties		11y	35y	58y	66y
Plant	Height (cm)	145.00 $\pm$ 9.00b	167.00 $\pm$ 7.55ab	199.33 $\pm$ 23.80a	125.33 $\pm$ 20.50c
	Crown size (m ²)	0.92 $\pm$ 0.23c	3.08 $\pm$ 0.51b	6.22 $\pm$ 0.62a	3.96 $\pm$ 0.63b
	Basal diameter (cm)	2.49 $\pm$ 0.34d	6.54 $\pm$ 0.66c	9.69 $\pm$ 0.65b	13.10 $\pm$ 0.56a
Rhizosphere soil	TC (%)	0.39 $\pm$ 0.03b	0.44 $\pm$ 0.01b	0.44 $\pm$ 0.02b	0.66 $\pm$ 0.04a
	DOC (mg/kg)	264.68 $\pm$ 2.88a	172.90 $\pm$ 1.92d	193.20 $\pm$ 4.55c	223.68 $\pm$ 11.51b
	TN (g/kg)	0.23 $\pm$ 0.05b	0.26 $\pm$ 0.02b	0.28 $\pm$ 0.04b	0.55 $\pm$ 0.07a
	pH	8.06 $\pm$ 0.04a	8.11 $\pm$ 0.02a	7.92 $\pm$ 0.02b	7.76 $\pm$ 0.05c
	C: N ratio	17.34 $\pm$ 2.07a	17.21 $\pm$ 0.64a	15.68 $\pm$ 0.85ab	12.07 $\pm$ 1.05b

Values are mean $\pm$ SE. The different lowercase letters indicate significant differences at $p < 0.05$ level between the different stand age. TC, soil total carbon; DOC, dissolved organic carbon; TN, total nitrogen.

and the levels of TC and TN increased significantly along the chronosequence, whereas pH and C:N ratio decreased significantly ($p < 0.05$; Table 1). With the increase of stand age, the content of DOC first decreased and reached a minimum value at 35 y at 172.90 mg kg⁻¹, before then increasing. At 66 y, the basal diameter increased by 426.10% compared to that at 11 y, and the contents of TC and TN increased by 69.23% and 139.13%, respectively. In contrast, the pH and C:N ratio had decreased by 3.72% and 30.39%, respectively (Table 1).

3.2 Microbial community composition of the rhizosphere soil

The microbial community composition in the rhizosphere soil of *C. korshinskii* showed significant differences between stand ages ($p < 0.05$; Figure 1). A total of 613 unique OTUs were obtained for the 58 y site, whereas unique OTUs for other sites ranged between 272–317 (Figure 1A). The rate of similar OTUs between different groups was 47.33%–59.42% (Figure 1A), indicating that the number of microbial communities affected by stand age was large.

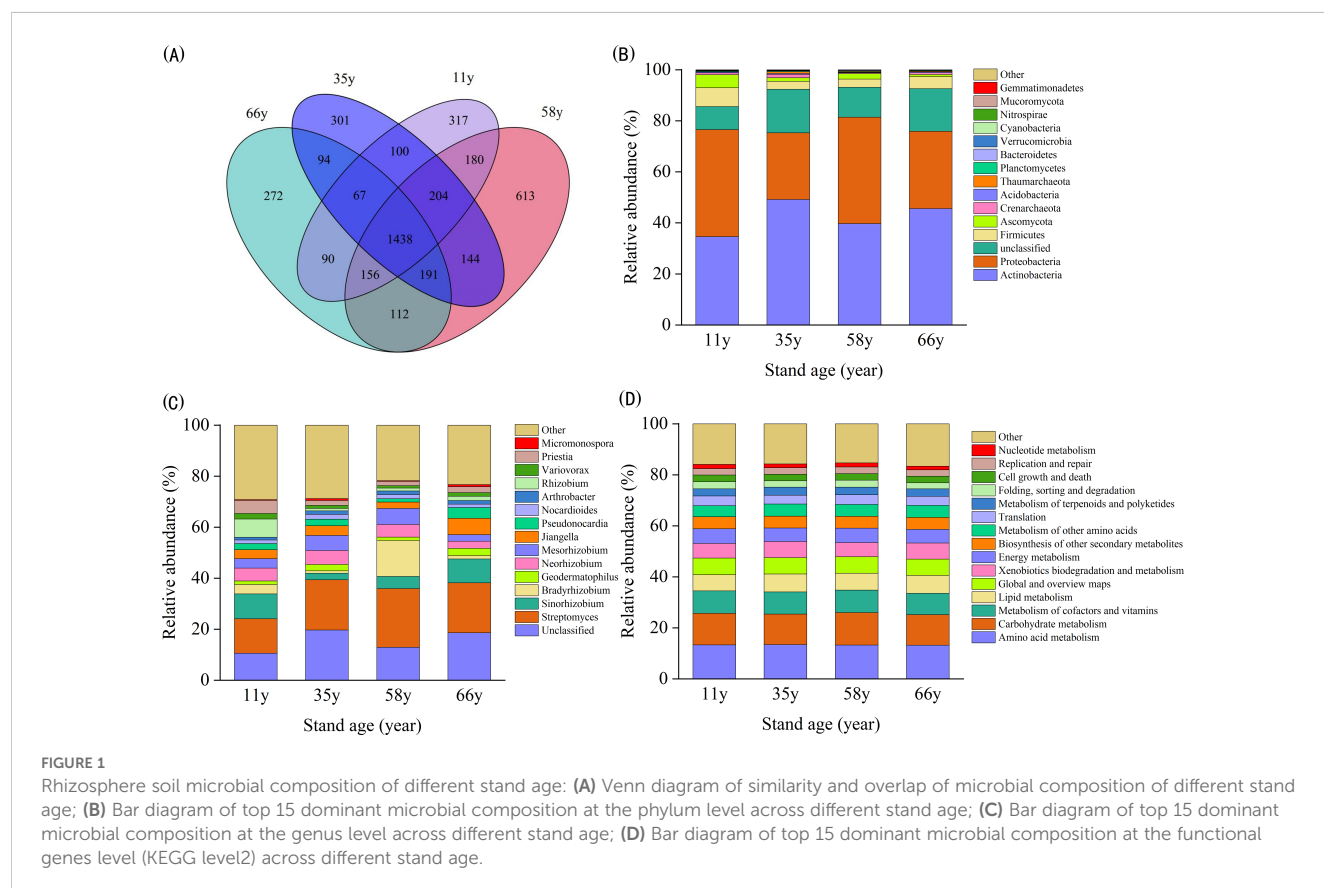
Analysis of microbial community structures at the phylum, genus, and functional gene levels showed that the top 15 dominant species did not differ from 11- to 66-year-old samples, but did change in relative abundance (Figures 1B–D). At the phylum level, the main community members included Actinobacteria (34.59%–49.17%), Proteobacteria (26.11%–41.95%), Unclassified (9.04%–

17.08%), Firmicutes (3.11%–7.37%), Ascomycota (0.82%–5.14%), Crenarchaeota (0.40%–1.31%), Acidobacteria (0.18%–0.37%), Thaumarchaeota (0.18%–0.75%), Planctomycetes (0.25%–0.29%), Bacteroidetes (0.11%–0.22%), and Verrucomicrobia (34.59%–49.17%). Proteobacteria, Firmicutes, and Ascomycota were more abundant in earlier samples, while Acidobacteria and Unclassified were more abundant in later samples (Figure 1B).

At the genus level, the main community members included *Unclassified* (10.57%–19.68%), *Streptomyces* (13.55%–22.99%), *Sinorhizobium* (2.54%–9.72%), *Bradyrhizobium* (0.96%–14.08%), *Geodermatophilus* (1.35%–2.84%), *Neorhizobium* (2.83%–5.52%), *Mesorhizobium* (2.53%–6.29%), *Jiangella* (2.52%–6.45%), *Pseudonocardia* (1.27%–4.21%), *Nocardioides* (1.34%–1.86%), *Arthrobacter* (1.06%–1.43%), *Rhizobium* (0.96%–7.14%), *Variovorax* (0.95%–2.23%), *Priestia* (1.65%–5.08%), and *Micromonospora* (0.32%–0.82%) (Figure 1C).

At the functional gene level, the percentage of relative abundance of the top 15 functional genes ranged between 83.37%–84.67%. The dominant gene groups in the community included amino acid metabolism (13.23%–13.46%), carbohydrate metabolism (11.96%–12.75%), metabolism of cofactors and vitamins (8.36%–8.81%), and lipid metabolism (6.35%–7.03%) (Figure 1D).

The LEfSe analysis indicated that there were significant differences in the relative abundance of eight phyla, 21 classes, and 21 functional gene groups between the four sites (LDA > 2) (Figure 2). More phyla and classes were enriched in the 11 and 66 y samples of rhizosphere soil



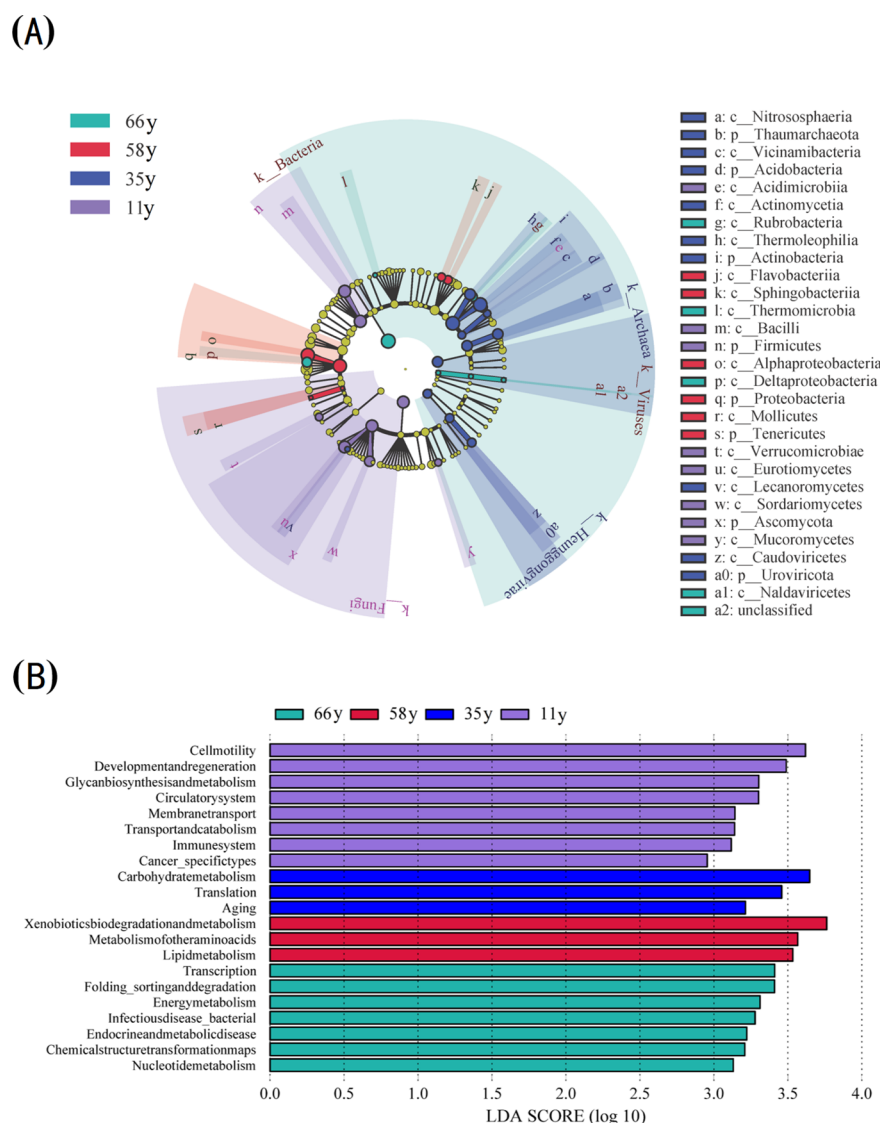


FIGURE 2

Analysis of biological markers with significant differences between different stand ages: **(A)** LefSe cladogram of soil microbial among different stand ages; **(B)** Horizontal bar plot of the LDA scores calculated for features differentially abundant among stand ages. Alpha value for the factorial Kruskal-Wallis test among classes and for the pairwise Wilcoxon test between subclasses uses the default one. Threshold on the logarithmic LDA score for discriminative features is 2.0.

(Figure 2A). At the class level, the main microorganisms enriched in 66 y soil included Thermomicrobia, Rubrobacteria, Deltaproteobacteria, and Naldaviricetes; those in 58 y soil included Flavobacteriia, Sphingobacteriia, Mollicutes, and Alphaproteobacteria; those in 35 y soil included Caudoviricetes, Vicinamibacteria, Actinomycetia, Lecanoromycetes, Thermoleophila, and Nitrososphaeria; and those in 11 y soil included Verrucomicrobiae, Eurotiomycetes, Sordariomycetes, Bacilli, Acidimicrobiia, and Mucoromycetes.

At the functional gene level, the functional groups and numbers of microorganisms changed significantly along with stand age (Figure 2B). The numbers of functional groups with significant differences first decreased before increasing along with stand age. The functional genes with significant differences included glycan biosynthesis and metabolism, immune system, circulatory system, cell motility, membrane transport, cancer_specifictypes, transport

and catabolism, and development and regeneration in 11 y samples, whereas transcription, folding_sorting and degradation, energy metabolism, chemical structure transformation maps, endocrine and metabolic disease, infectiousdisease_bacterial, and nucleotide metabolism were enriched in 66 y samples.

3.3 α -diversity of microbial communities in the rhizosphere soil

The α -diversity of rhizosphere soil microbial communities significantly differed with stand age (Supplementary Table S2). The richness estimate indices (Chao1, Shannon, Simpson's) showed a turning point at 58 y. The Chao1 index gradually increased with stand age and reached the highest level at 58 y,

before then decreasing with stand age. Shannon and Simpson's indices decreased with the stand age and reached their minimum levels at 58 y, before then increasing.

3.4 β -diversity of microbial communities in the rhizosphere soil

The soil microbial community composition significantly differed between stand ages ($p = 0.001$). The patterns of β -diversity based upon species composition changed along with stand age from 11 to 66 y (Figure 3A). There were significant differences in rhizosphere soil microbial communities between stand ages at the phylum, genus, and functional gene levels (Figures 3B, C). There were significant differences in the relative abundances of microorganisms between stand ages in eight phyla (Actinobacteria, Proteobacteria, Unclassified, Firmicutes, Ascomycota, Crenarchaeota, Acidobacteria, and Thaumarchaeota; Figure 3B), 11 genera (Unclassified, Streptomyces, Sinorhizobium, Geodermatophilus, Mesorhizobium, Jiangella, Pseudonocardia, Rhizobium, Variovorax, Priestia, and Micromonospora; Figure 3C), and 16 dominant functional gene groups (Figure 3D). Actinobacteria, Thaumarchaeota, Streptomyces, and the folding, sorting and degradation genes group increased significantly in abundance with stand age, whereas Proteobacteria, Firmicutes, Ascomycota, Rhizobium, Variovorax, Priestia, and cell motility genes decreased.

3.5 Changes related to taxa and functional genes

Multiple taxa with relative abundances $> 0.1\%$ varied across the chronosequence of stand ages at the phylum level (Figure 4A). Ascomycota and Firmicutes were more abundant at 11 y, whereas Acidobacteria were more abundant at 66 y. Linear regression analysis showed that the relative abundances of Ascomycota and Firmicutes significantly decreased with sample age from 5.14% and 7.37% at 11 y, respectively, to 0.82% and 4.70% at 66 y ($p < 0.01$, $R^2 = 0.54, 0.83$); in contrast, the relative abundances of Thaumarchaeota and Actinobacteria significantly increased from 0.18% and 34.59% at 11 y to 0.28% and 45.63% at 66 y ($p < 0.05$, $R^2 = 0.47, 0.40$) (Figure 4A).

There were also multiple taxa with relative abundances $> 1\%$ across the chronosequence of stand age that varied at the genus level (Figure 4B). *Rhizobium* and *Priestia* were more abundant at 11 y, whereas *Pseudonocardia* and *Jiangella* were more abundant at 66 y. The linear regression indicated that *Rhizobium*, *Priestia*, and *Variovorax* significantly decreased with age from 7.14%, 5.08%, and 2.23% at 11 y, respectively, to 1.63%, 2.33%, and 1.43% at 66 y ($p < 0.05$, $R^2 = 0.47, 0.45, 0.29$); in contrast, the relative abundance of *Streptomyces* significantly increased from 13.55% at 11 y to 19.59% at 66 y ($p < 0.05$, $R^2 = 0.36$) (Figure 4B).

The dominant functional genes with relative abundances $> 1\%$ were clustered based on the KEGG database at level 2. Among all

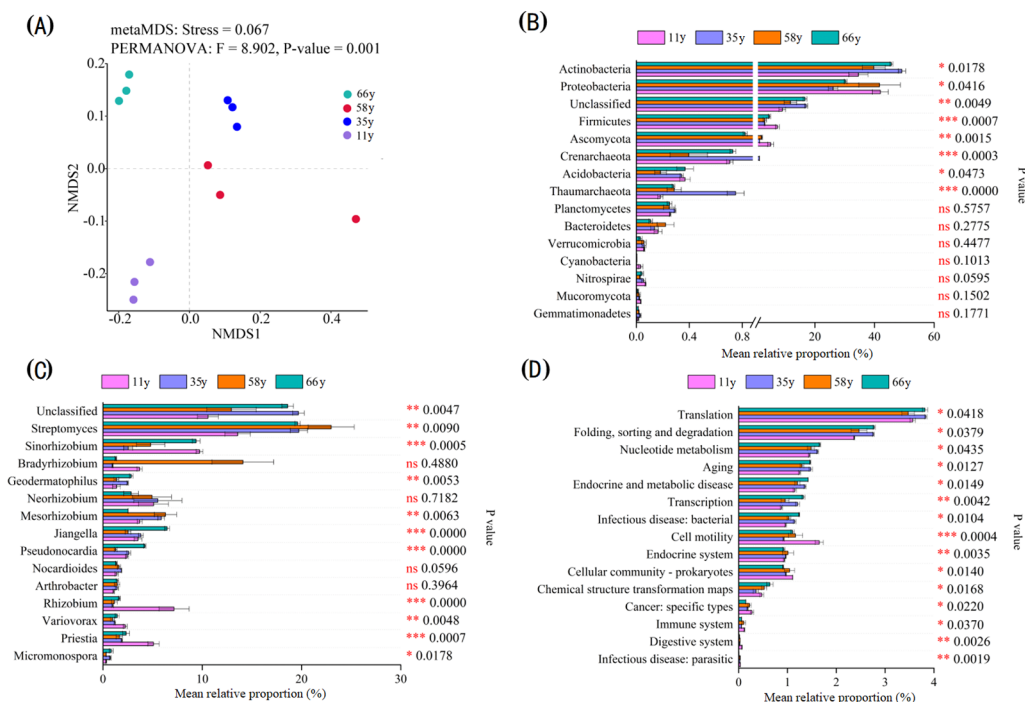


FIGURE 3

Microbial community beta diversity analysis and significance test for differences among stand ages: (A) The microbial community shift was visualized with NMDS based on species composition; (B) Significance test for differences among stand ages at major phylum (top 15 of relative abundance); (C) Significance test for differences among stand ages at major genus (top 15 of relative abundance); (D) Significance test for differences among stand ages at major functional gene (top 15 of relative abundance). The rightmost is the P value, * $0.01 < p \leq 0.05$, ** $0.001 < p \leq 0.01$, *** $p \leq 0.001$.

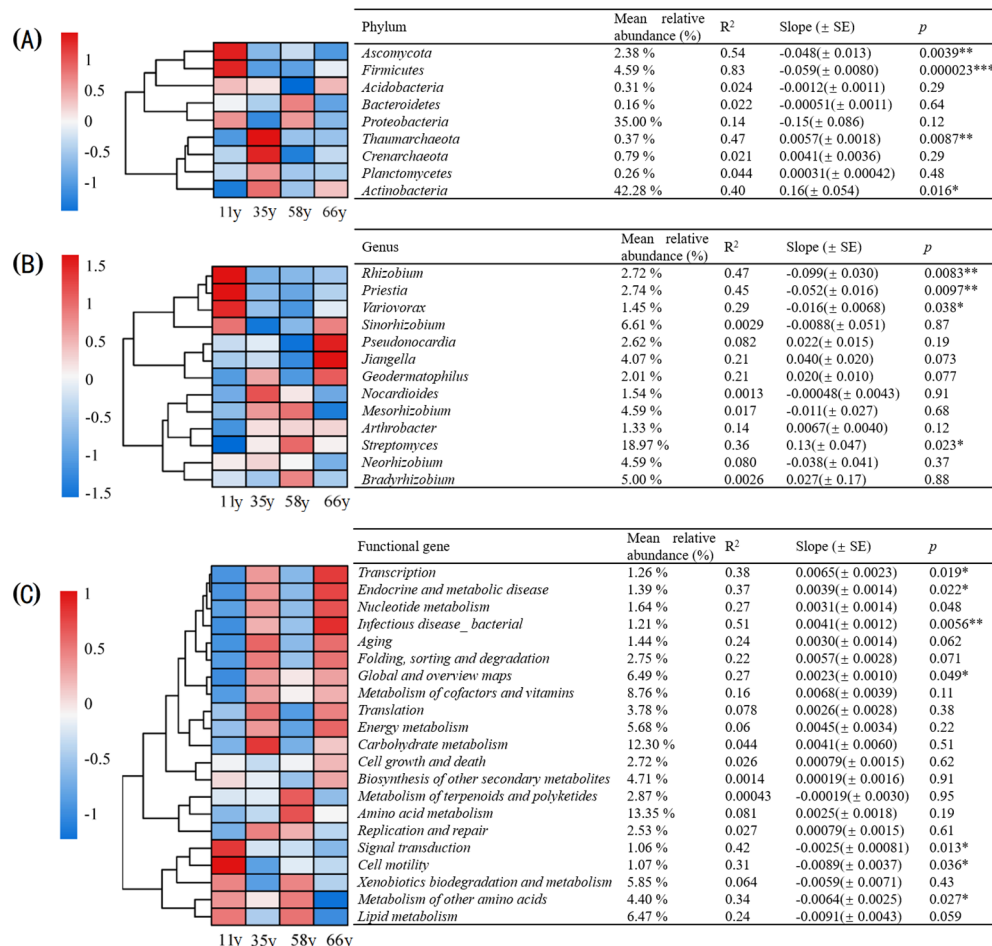


FIGURE 4

The variations of phyla, genus and functional genes over stand ages. The heatmap shows the age variations. The key shows the z-scores of the relative abundances. The relative abundance, variance explained (R^2), regression slope and P value of the linear regression with stand age were shown in the table (* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$): (A) The variations of major phyla over stand ages (relative abundance > 0.1%); (B) The variations of major genus over stand ages (relative abundance > 1%); (C) The variations of major functional genes over stand ages (relative abundance > 1%).

categories, signal transduction and cell motility were more abundant at 11 y, whereas genes related transcription, energy metabolism, nucleotide metabolism, and endocrine and metabolic disease were dominant in later stages (Figure 4C). The relative abundance of transcription, endocrine and metabolic disease, infectious disease_bacterial, and global and overview maps increased significantly with stand age ($p < 0.05$), whereas the relative abundance of signal transduction, cell motility, and metabolism of other amino acids decreased significantly ($p < 0.05$) (Figure 4C).

3.6 Microbial community co-occurrence network complexity in the rhizosphere soil

Stand age significantly altered rhizosphere soil microbial community complexity and stability (Figure 5). For microbial co-occurrence network complexity, the nodes, links, modularity, average degree, and positive and negative correlations all

suggested “temporal partitioning” (Figures 5A–G). Co-occurrence network complexity increased with age during the first 35 years, reaching its highest at 35 y before experiencing a sudden decrease at approximately 58 y, then slowly increasing in the later stages (Figures 5B–D). The average degree and positive links sharply increased and reached their maximum at 48 y, before then decreasing with stand age (Figures 5E, F). The negative links in the microbial network first sharply increased with stand age and reached their highest level at approximately 21 y, decreasing to a lower level at approximately 55 y, and then increasing from 55 to 68 y (Figure 5G).

3.7 Influence of environmental variables on microbial community structures

The changes in microbial community structures were critically linked to the variations in plant traits and soil properties (Figure 6A). The first and second axes explained 23.51% and

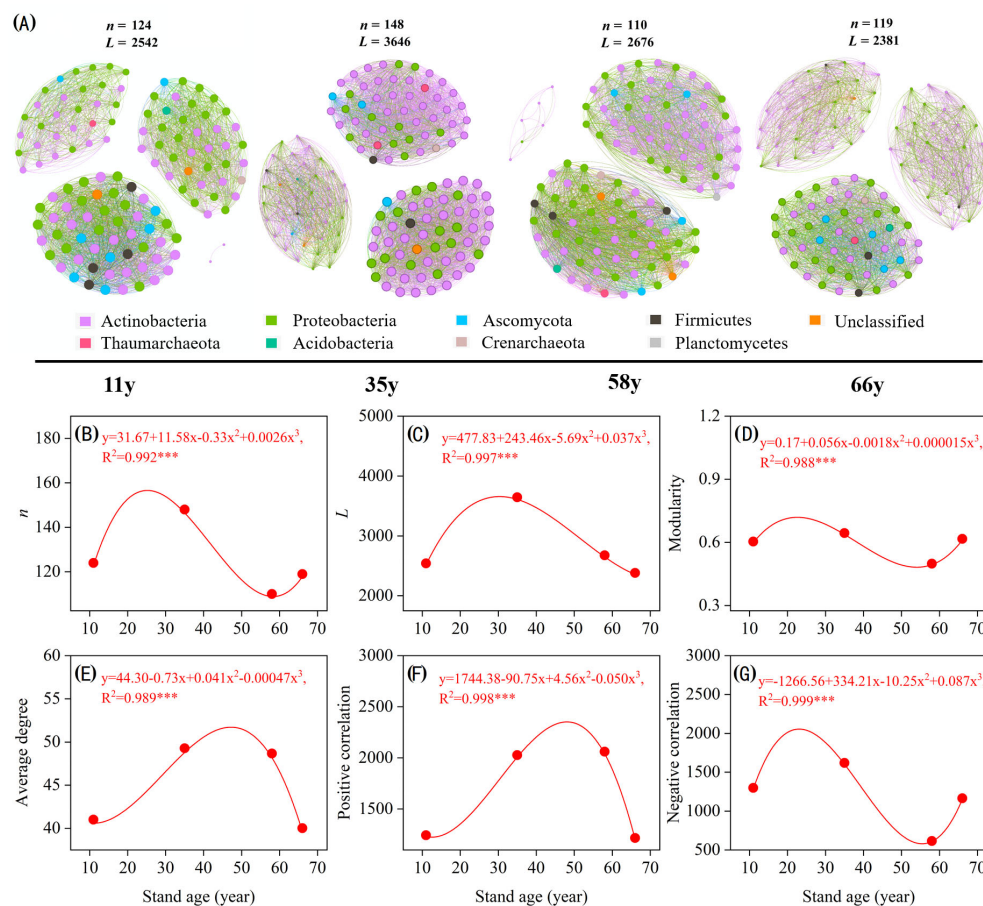


FIGURE 5

Rhizosphere microbial co-occurrence networks of with *Caragana korshinskii* different stand ages (A). Connections indicate significant correlations (Screening conditions: Spearman's $\rho > 0.8$, $p < 0.001$), the nodes are colored by phylum and represent an operational taxonomic unit (97% sequence identification threshold, OTU), the size of each node is proportional to the number of connections (degrees), and the thickness of each connection between two nodes (edge) is proportional to the values of Spearman's correlation coefficient. Temporal changes in microbial community networks topology, including n (B), L (C), modularity (D), average degree (E), positivity correlation (F), and negativity correlation (G). The fitting formula and adjusted R^2 and p values from polynomial fitting are shown. * $0.01 < p \leq 0.05$; ** $0.001 < p \leq 0.01$; *** $p \leq 0.001$.

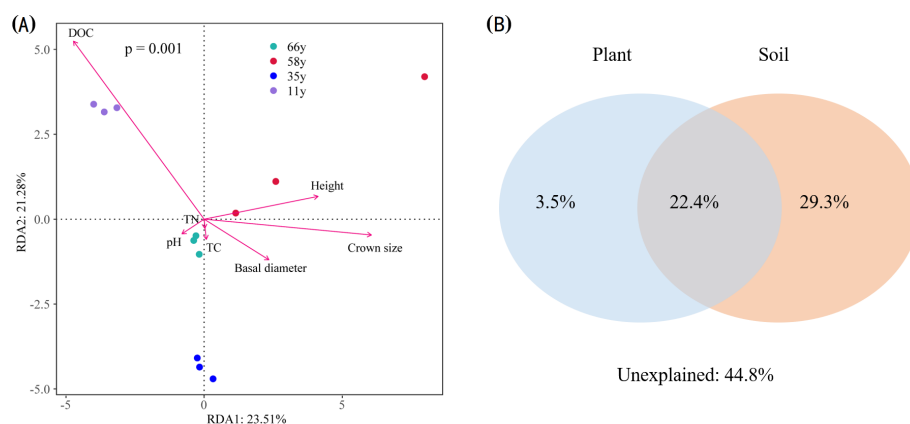


FIGURE 6

Redundancy analysis (RDA) (A) and variation partition analysis (VPA) (B) for the relationship between plant characteristics and soil properties and soil microbial communities across different stand ages.

21.28% of the variation in microbial community structure, respectively. The DOC content correlated most strongly with axis 1, with a correlation coefficient of 0.92. Permutation analyses showed that the DOC and crown size were the key factors that explained the variation in microbial community structures ($p < 0.01$) (Figure 6A). VPA results showed that the selected environmental variables explained 55.2% of the microbial community composition variation (Figure 6B). Soil properties independently explained the largest fraction of the variation (29.3%), plant variables independently explained 3.5% of the variation, and the interaction of soil and plants explained 22.4% of the variation (Figure 6B).

Stand age directly drove changes in soil properties and plant characteristics, affecting changes in the microbial community structure, the relative abundance of functional genes, and the microbial community network complexity (Figure 7). Both microbial community structure and functional genes had significant positive effects on network complexity ($p < 0.001$). Plant characteristics had a significant negative impact on microbial community structure ($\beta = -0.53$, $p < 0.01$) and soil properties ($\beta = -0.91$, $p < 0.001$), whereas soil properties positively impacted microbial community structure ($\beta = 0.90$, $p < 0.001$). In addition, the positive effect of soil properties ($\beta = 0.656$, $p < 0.01$) was greater than the negative effect of plant characteristics ($\beta = -0.28$, $p < 0.05$) on functional gene abundance. There was a positive direct effect of stand age on plant characteristics ($\beta = 0.95$, $p < 0.001$), but the positive direct effect of stand age on soil properties was not significant ($\beta = 0.01$, $p > 0.05$) (Figure 7). The final model explained 73.9% of the variation in soil properties, 90.8% of the variation in plant characteristics, 77.2% of the variation in the microbial community

structure, 67.2% of the variation in the relative abundance of functional genes, and 73.5% of the variation in the microbial community network complexity (Figure 7).

4 Discussion

Revegetation is one of the effective methods for rehabilitating degraded ecosystems, which has been widely adopted worldwide. In the desert ecosystem assessed in this study, there were significant changes in soil properties, nutrient effectiveness, hydrologic processes, plant diversity, and the structure and functional groups of soil microbial communities after revegetation. The quality and function of the environment gradually improved through the impact and regulation of plant-microbe-soil interactions. This study revealed the effects and mechanisms of dominant xerophytic shrub age on soil microbial community structure, functional groups, and network stability in temperate desert revegetation areas. It also sheds light on the ecological impacts of revegetation through soil microbial processes and provides new insights into our understanding of the relationship between deep-rooted plants and the environment.

4.1 Effects of stand age on rhizosphere microbial taxa

The microbial community composition of rhizosphere soil changed significantly with stand age at the phylum and genus level (Figures 1–3), which is consistent with previous studies (Sun and Badgley, 2019; Song et al., 2022). The strongest changes

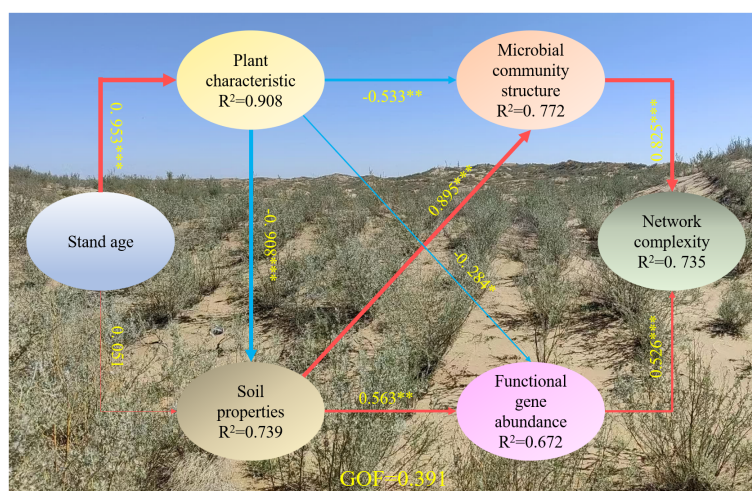


FIGURE 7

The direct and indirect effects of environmental factors on soil microbial community structure, functional gene and network complexity using partial least squares path models (PLS-PM). The width of the arrows is proportional to the strength of the causal relationship, and numbers are the correlation coefficients. Red solid lines indicate positive relationships and blue solid lines indicate negative relationships. R^2 values represent the explained variance of each factor. The solid represent significant (***) $p < 0.001$, ** $p < 0.01$, * $p < 0.05$). The soil properties included DOC and pH; the plant characteristics included basal diameter and height; the microbial community structure included the first and second principal components of the NMDS based on the OTU level; the functional gene abundance included the first and second principal components of the PCA based on significant differences in the OTU levels among different stand ages; the network complexity included modularity and positivity correlation links.

observed were the decrease in Ascomycota and Firmicutes and the increase in Actinobacteria, indicating a shift from oligotrophic to copiotrophic groups (Orwin et al., 2018; Yang et al., 2021; Liao et al., 2023). These shifts were closely related to soil property and plant traits. VPA analysis showed that the soil properties and plant characteristics selected in this study explained 55.2% of the variation in microbial community structure and that the effect of soil properties was much stronger than that of plants (Figure 5B). This implies that changes in plant traits induced by plant age indirectly impact soil microorganisms through variations in soil properties.

Actinobacteria and Proteobacteria were the dominant communities in rhizosphere soil. Actinobacteria play an important role in degrading organic matter such as polysaccharides, cellulose, starch, chitin, organic acids, proteins, and fats, as well as promoting plant growth (Hazarika and Thakur, 2020). Proteobacteria is one of the largest bacterial phyla, with significant metabolic multifunctionality, and plays a key role in C, N, S, and P cycling as well as that of metallic elements such as Fe and Mn (Wang et al., 2024). The abundance of Actinobacteria increased in a wave-like manner with stand age, while that of Proteobacteria showed an opposite trend (Figure 1). This can be attributed to changes in the soil environment, where improved soil nutrient conditions (such as increased SOC and TN) and the accumulation of plant secretions provided sufficient nutrients and a suitable environment for Actinobacteria (Dai et al., 2018).

Typically, the ratio of Proteobacteria/Acidobacteria represents the organic C quality of labile organic C pools, and its changes with stand age were consistent with the changes in DOC, correlating with most previous studies (Thomson et al., 2013). However, this is inconsistent with Sun et al. (2020) who found that the Proteobacteria/Acetobacteria ratio decreases with increasing TOC, which they attributed to the fact that the lower soil pH is more suitable for the growth of Acidobacteria. Proteobacteria and Bacteroidetes can metabolize complex organic molecules (Penn et al., 2014; Shao et al., 2021), and their reduced abundance with stand age implies a change in soil organic matter quality. The results suggest that soil C retention was better with increasing stand age; this was also a reasonable explanation for the gradual increase in TC content.

Rhizosphere soil microbial α - and β -diversity varied significantly with stand age (Figure 3A; Supplementary Table S2). The soil microbial Chao1 index first increased and then decreased with stand age, which was related to changes in plant traits and soil properties. The β -diversity increased with increasing stand age, implying that the heterogeneity of soil microbial communities was increased. This is due to the adaptation of the soil microbial community to the rhizosphere environment, especially the recovery of less resilient members. The variation in the abundance of dominant microorganisms as well as the lower number of unique OTUs at 66 y suggested that the cooperation among soil microorganisms increased with stand age and that they became more efficient in utilizing resources (Ren et al., 2016). The variation in rhizosphere soil microbial β -diversity could also be attributed to the consequence of habitat heterogeneity (Sun et al., 2020), similar to the findings of Sun et al. (2020) and verified by our

RDA results (Figure 5A). As stand age increased, soil nutrient and organic matter content also increased significantly; these changes alleviate resource limitations for microbial growth, impacting the composition and diversity of the microbial community. Microbial network complexity initially increased and then decreased with stand age, matching the trend of plant traits (Figure 5; Table 1). Before trees reach maturity, the root secretions are dominated by lipids, sugars, and carbohydrates, which provide sufficient substrates for tree and microbial growth and promote the development of microbial networks; after the tree enters the mature stage, the secretions shift to defense-related substances, limiting the substrates available to microorganisms (Dayrell et al., 2018; Chen et al., 2023). Consequently, the microbial relationship network gradually becomes simpler and more stable.

Resource availability and microbial interactions are important environmental factors regulating changes in the soil microbiota during revegetation (Hoogmoed et al., 2016; Ren et al., 2016; Zhao et al., 2018). Our study showed that the spatial variation of soil microorganisms in the rhizosphere was associated with soil properties and plant characteristics (Figure 5). Soil pH was the key factor affecting the spatial and temporal distribution of bacteria, and a lower pH was more conducive to the colonization of acidic bacterial groups. The extractable C represents the available soil C pool, which is released by microorganisms in the form of respiration or incorporated into a more stable soil C pool through mineralization. The DOC gradually increased with stand age, providing more available substrates for microorganisms. The accumulation of rhizosphere soil C and N also resulted in a reduction in the C:N ratio (Table 1), suggesting that more labile substances were available for microbial processing and could increase plant productivity (Paul, 2007). Additionally, the changes in plant characteristics are also a major driver of microbial succession, since microbial community structure is related to variations in plant litter deposition and root exudates during revegetation (Zumsteg et al., 2012; Salles et al., 2017). A study on the Loess Plateau also obtained similar results; as the plant age increased, the bacterial community showed a positive response (Liu et al., 2018). As plant age increases, crown shading gradually increases, causing changes in microbial community structures (Song et al., 2022). The changes in plant characteristics affect soil properties and nutrients by modifying litter and root exudates; these alterations in soil nutrient resources lead to shifts in the microbial community composition, such as a gradual transition from oligotrophic to copiotrophic microbial groups. Ultimately, this influences the complexity and stability of the microbial community network (Figure 7).

4.2 Effects of stand age on rhizosphere microbial functional gene groups

Microorganisms are major players and key influencers of all biochemical processes (Gougoulas et al., 2014; Classen et al., 2015), and functional gene abundance reflects the microbial processes associated with ecosystem function (Sun and Badgley, 2019). In this study, the rhizosphere soil microbial functional groups changed

significantly with stand age, being dominated by cellular processes (cell motility, development, and regeneration) in the early stages and by environmental information processing (transcription, chemical structure transformation maps) and metabolism (energy metabolism, endocrine and metabolic disease, nucleotide metabolism) functional groups in the later stages (Figure 2). This suggests faster biochemical cycling and higher resource effectiveness in rhizosphere soil, indicating that the interactions between plants and microbes were more intense in the later stages of restoration (66 y). Additionally, transcription, endocrine and metabolic diseases, infectious disease_bacterial, and global and overview maps groups increased linearly with shrub age (Figure 4); these changes were also driven directly or indirectly by changes in soil properties and plant characteristics caused by stand age (Figure 7). Previous studies have found that the younger trees secrete more metabolites related to nutrient acquisition, such as primary metabolites like carbohydrates and sugar. In contrast, older trees secrete more defensive metabolites in response to environmental changes (Dayrell et al., 2018; Chen et al., 2023). These changes in metabolite types reflect and result from alterations in microbial metabolic functions, which explains the results observed in this study.

Environmental factors that change with stand age also affect microbial function. A previous study found that *Rhizobiales* and *Cytophagales* were significantly positively correlated with the decomposition of plant residues because the degradation of plant residues (such as cellulose) is largely dependent on increased N availability achieved through N₂ fixation (Tao et al., 2019). In the present study, these functional groups differed significantly among the different stand ages (Figure 3C), indicating that the ability to decompose organic matter changed with stand age and was associated with an increase of TN in rhizosphere soil. Song et al. (2022) found that the rhizosphere environment and biomass had a significant effect on the potential for N fixation with changing plant age. This was also confirmed in our study, where N-fixing rhizobia differed significantly in rhizosphere soils of different stand ages (Figures 3, 4). Soil pH was also an important predictor of the abundance and diversity of C-degrading genes. Additionally, soil pH is considered an integrator factor for soil function; the gradual decrease in the abundance of Bacteroidetes in line with soil pH suggested that soil recalcitrant carbon will gradually accumulate, as this phylum is considered to specialize in the degradation of complex organic compounds (Fernandez-Gomez et al., 2013). This also implies that the ecological functions of the soil environment (such as carbon sequestration and enhanced nitrogen cycling potential) were progressively enhanced as the stand age increased.

4.3 Effects of stand age on the survival strategies of the rhizosphere microbial community

Soil nutrient resources shape the abundance of microbial communities and functional genes, and are also important factors in affecting the trophic phenotypes of soil microorganisms (Liao et al., 2023). Typical copiotrophic bacteria include Actinobacteria, Proteobacteria, and Bacteroidetes, whereas typical oligotrophic

bacteria include Acidobacteria and Chloroflexi (Zechmeister-Boltenstern et al., 2015; Zhang et al., 2016). Here, the rhizosphere soil microbial community was dominated by copiotrophic bacteria (Actinobacteria, Proteobacteria, Bacteroidetes), although they varied in abundance between stand ages. This is consistent with previous research where microorganisms shifted from oligotrophic to copiotrophic groups with increasing restoration age (Zechmeister-Boltenstern et al., 2015; Sun and Badgley, 2019; Liao et al., 2023). This change is mainly related to variations in soil nutrient resources and properties, causing the competitive relationships within the soil microbial community to intensify and their utilization of nutrient resources to improve with increasing stand age.

Microbial functional genes are commonly considered microbial characteristics at the community level because even microorganisms of the same phylum also have different ecological functions due to physiological and developmental diversity (Chen et al., 2021a, b). The evolution of microbial functional genes in the process of vegetation restoration reflects a shift in microbial ecological strategies (Zechmeister-Boltenstern et al., 2015; Manoharan et al., 2017; Zheng et al., 2018). Generally, oligotrophic microorganisms are characterized by poor growth, greater affinity for substrates, preferential degradation of resistant C, and high metabolic rates (Starke et al., 2021); in contrast, microbial copiotrophs have vigorous growth, poor affinity for substrates, preferentially utilize labile C, and have high metabolic rates (Tan et al., 2019; Kelly et al., 2021). In this study, the predominance of copiotrophic groups in rhizosphere soil implies that soil microorganisms spent more energy on reproduction than on growth, metabolism, and improving competitiveness, which would favor the accumulation of resistant C pools (Tan et al., 2019; Kelly et al., 2021). This further suggests that changes in shrub age lead to alterations in plant characteristics and soil properties, driving changes in microbial community structure and functional genes. Consequently, this results in changes in the complexity of microbial networks. These findings indicate that ecological functions are gradually improved with increasing stand age under microbial regulation.

This study was conducted during the growing season, a period when plant life activities are at their peak and the dynamics of rhizosphere soil nutrients and microbial activities are most active (Huo et al., 2017). The microbial community structure and soil characteristics during this season best reflect the differences between forests of different ages. However, previous studies have reported that trees absorb nutrients from the soil even during the long winter dormancy period (Ueda et al., 2015; Zavišić and Polle, 2018), and can also release a certain amount of root exudates at the beginning of the dormancy season (Nakayama and Tatenno, 2018). It is estimated that young trees release about 7.5% of their total below-ground C allocation as rhizosphere C flux during dormancy (Fahey et al., 2013). Additionally, soil microbial communities remain active at sub-zero temperatures and are capable of decomposing and mineralizing organic matter (Hishi et al., 2014; Isobe et al., 2018). During dormancy, plants could stimulate microbial growth and extracellular enzyme production to effectively absorb nutrients from the rhizosphere. The nutrients absorbed in winter are used for spring growth (Ueda et al., 2011; Nakayama and Tatenno, 2022). Future study needs to assess winter rhizosphere processes to better

understand forest soil nutrient cycling and plant growth. The results observed in this study may differ significantly from those in winter, potentially affecting our comprehensive understanding of plant-microbe interactions and plant growth strategies.

5 Conclusions

This study represents the first integration of soil microbial metagenomic information and driving factors to provide novel insights into alterations in both microbial community structure and functional genetics within the rhizosphere soil of dominant shrubs following vegetation restoration in desert ecosystems. Along four time series from 11 to 66 years after planting, significant changes were seen in the rhizosphere soil microbial community structure and functional genes that were closely related to plant characteristics and soil physicochemical properties. The restored desert ecosystem is more conducive to the accumulation of resistant organic matter in the soil due to the dominance of copiotrophic microorganisms such as Actinobacteria and Proteobacteria, which preferentially use labile substrates. In addition, the interactions between microorganisms become more robust in terms of cooperation and competition as stand age increases. This was attributed to a gradual shift of microbial functional genes from cellular processes to environmental information processing and metabolic processes. Additionally, changes in microbial community structure were primarily regulated by DOC, confirming the predominance of copiotrophic groups in the rhizosphere soil microbial community. Overall, this study establishes a foundation for comprehending the structure and functional genes of soil microbial communities, and their linkages with environmental changes in the rhizosphere of dominant shrubs during succession of sand-fixing vegetation. The results provide a novel perspective for understanding microbial processes in soil biogeochemical cycles in desert revegetation areas.

Data availability statement

The data presented in the study are deposited in the NCBI Sequence Read Archive (SRA) database, accession number PRJNA1178012, <https://www.ncbi.nlm.nih.gov/bioproject/PRJNA1178012>.

Author contributions

YL: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Supervision, Visualization, Writing –

original draft, Writing – review & editing. BW: Conceptualization, Data curation, Formal analysis, Investigation, Software, Visualization, Writing – original draft. YW: Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft. WH: Formal analysis, Investigation, Visualization, Writing – original draft. XW: Conceptualization, Funding acquisition, Visualization, Writing – original draft. XZ: Data curation, Formal analysis, Investigation, Visualization, Writing – original draft. XT: Formal analysis, Supervision, Writing – review & editing. LL: Supervision, Writing – review & editing. HY: Conceptualization, Funding acquisition, Project administration, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fpls.2024.1473503/full#supplementary-material>

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Increasing plant diversity enhances soil organic carbon storage in typical wetlands of northern China

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Soil organic carbon plays an important role in climate change mitigation, and can be strongly affected by plant diversity. Although a positive effect of plant diversity on soil organic carbon storage has been confirmed in grasslands and forests, it remains unclear whether this effect exists in wetlands. In this study, we investigated plant diversity, soil properties and soil organic carbon across five typical wetlands of northern China, to test the effect of plant diversity on soil organic carbon and clarified the regulators. Increasing plant diversity significantly increased belowground biomass of wetland plant communities, and both soil organic carbon content and storage were significantly positively related to wetland plant diversity. The positive effect of plant diversity was influenced by belowground biomass of wetland plant communities, soil microbial biomass carbon, and soil properties, especially soil water content and bulk density. The structural equation model showed that soil organic carbon storage was dominantly affected by microbial biomass carbon, plant diversity and biomass, with standardized total effects of 0.66 and 0.47, respectively, and there was a significant positive relationship between soil organic carbon and microbial biomass carbon. These results suggest that increasing plant diversity can potentially promote the ability of wetlands to store organic carbon in soils. The findings highlight the importance of plant diversity on soil organic carbon in wetland ecosystems, and have implications for managing wetlands to increase carbon sinks and to mitigate global climate change.

KEYWORDS

microbial biomass carbon, plant species diversity, soil organic carbon, semi-arid region, wetland ecosystems

1 Introduction

Wetland ecosystems stored more than 30% of terrestrial soil organic carbon (SOC) despite occupying less than 6% of land area (Poulter et al., 2021). As one of the highest carbon sinks and carbon-dense ecosystems, wetland ecosystems can significantly affect global carbon cycling (Zhang et al., 2023). Plant diversity plays an important role in community structuring and ecosystem functioning such as carbon sequestration (Hector et al., 1999; Xue et al., 2022; Huang et al., 2023; Liu et al., 2024). Increasing plant diversity has been shown to enhance soil organic carbon storage (SOCS) in forests (Chen et al., 2023), grasslands (Steinbeiss et al., 2008; Cong et al., 2014; Chen et al., 2018), and agricultural ecosystems (Chen et al., 2020). However, the relationship between plant diversity and SOCS in natural wetland ecosystems remains unknown. Understanding such a relationship can potentially help manage wetland ecosystems to promote carbon sequestration and thus to mitigate global climate change.

Plant diversity can influence SOCS through plant biomass and plant-derived carbon inputs (Gould et al., 2016; Li et al., 2022; Xi et al., 2023), because high plant diversity may promote the complementarity among species and the selection of some highly productive plant species (Loreau and Hector, 2001; Allan et al., 2011; Adomako et al., 2019; Wang X. et al., 2022). Previous studies have confirmed that increasing plant diversity promotes plant biomass (Chen et al., 2018; Bai et al., 2021; Wang et al., 2023), although there are still inconsistent conclusions (Gherardi and Sala, 2015; Zou et al., 2024). Plant diversity can affect SOCS by influencing soil labile organic carbon and soil properties in forest ecosystems (Ratcliffe et al., 2017; Adair et al., 2018). Additionally, increasing plant diversity has been found to promote dissolved organic carbon (DOC) and microbial biomass carbon (MBC) (Thakur et al., 2015; Mellado-Vazquez et al., 2016; Lange et al., 2021), thereby increasing SOCS in grassland ecosystems (Prommer et al., 2020). For wetland ecosystems, plant diversity can also impact SOC accumulation through changing plant detritus inputs (Gould et al., 2016; Li et al., 2022; Xi et al., 2023). A previous study demonstrated that root biomass was significantly correlated with plant richness in freshwater wetlands (Schultz et al., 2011). Thus, it is likely that there is also a positive effect between plant diversity and SOCS in wetland ecosystems. The effect of plant diversity on SOCS can vary with environmental conditions such as climate (Spohn et al., 2023). In semi-arid grasslands, for instance, mean annual temperature (MAT) and precipitation (MAP) significantly regulate the effect of plant diversity on SOCS (Tian et al., 2016). Furthermore, in wetland ecosystems, there were significant correlations between plant diversity and soil properties, which maybe complexly drive SOC sequestration (Ma et al., 2021; Zhao et al., 2021). Increasing plant diversity may enhance SOCS through increasing the availability of labile carbon from plants to microbes (Lange et al., 2015; Mellado-Vazquez et al., 2016; Chen et al., 2018; Prommer et al., 2020). Previous studies have demonstrated that increased plant litter inputs provide more substrate for soil microorganisms, enhancing SOCS through increased microbial residue accumulation (Eisenhauer et al., 2010; Liang et al., 2011; Lange et al., 2015). Additionally, high plant richness

and biomass have been shown to increase microbial enzyme activity in wetlands, which maybe affect SOCS, similar to those observed in other terrestrial ecosystems (Kim et al., 2022). Moreover, SOCS is also significantly affected by soil properties, i.e., the soil water content and pore size distribution (Fukumasu et al., 2022). As these biotic and abiotic factors are closely linked with SOCS, increasing plant diversity would theoretically enhance SOCS in wetland ecosystems. However, few studies have tested the potential mechanisms underlying the relationship between plant diversity and SOCS in wetlands.

Here, we conducted a field experiment in five typical wetlands (Daihai, Chagannor, Dalinor, Horqin and Wulagai) in a semi-arid region of northern China. We tested the effects of increasing plant diversity on SOCS and biomass, and clarified the key determinant regulating SOCS. Given that SOCS is influenced not only by plant carbon input but also by soil properties and mineralization processes, we hypothesized that: (1) increasing plant diversity would increase plant community biomass, and thereby enhance SOC and its fractions (DOC and MBC) in wetlands; (2) SOCS is jointly regulated by plant diversity and biomass, soil properties such as soil water content and MBC.

2 Materials and methods

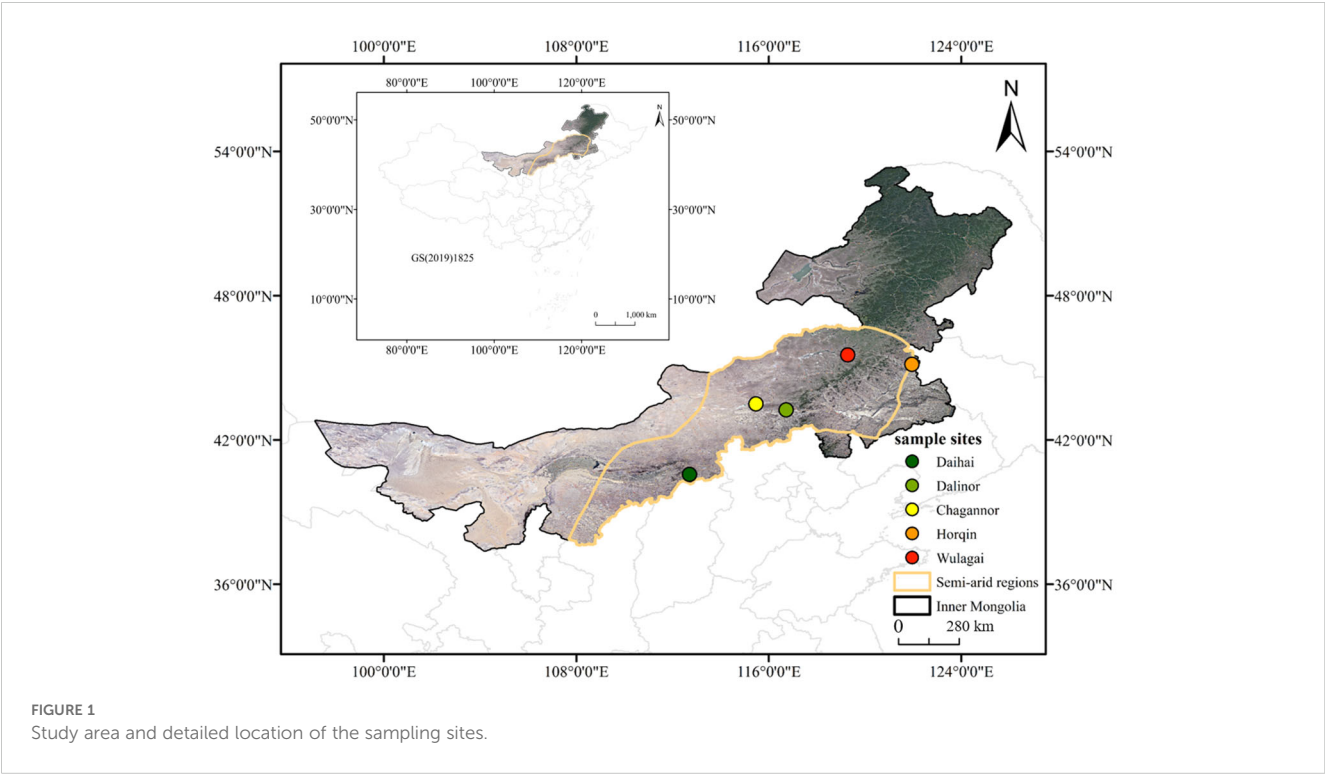
2.1 Site description

We selected five typical wetlands (Daihai, Chagannor, Dalinor, Horqin and Wulagai) with minimal anthropogenic interference in Inner Mongolia, semi-arid region in northern China (40°13'–45°54' N, 115°27'–121°57' E; 179 m–1242 m a.s.l.; Figure 1). This region has a typical continental monsoon climate, with MAP of approximately 350–500 mm and MAT of around 3–7 °C (Yao et al., 2023). The growing season spans from May to September, with about 70% of the yearly rainfall occurring during June to August (Wu et al., 2010; Fang et al., 2018). The dominant plant species are *Equisetum hyemale*, *Leymus chinensis*, *Potentilla anserina* and *Phragmites australis* (Table 1).

2.2 Field surveys and experimental analyses

In each wetland, we set up 12 plots of 2 m × 2 m with different plant species richness, totaling 60 plots for all five wetlands. In each plot, we recorded the name of each plant species, measured its height, and counted its individuals (Table 1). We then harvested aboveground and belowground parts in a randomly selected 20 cm × 20 cm quadrat in each plot.

In each plot, we collected soil samples from 0–10 cm, 10–20 cm and 20–30 cm soil depth using the five-point sampling method for physicochemical analysis. We also collected three soil cores (100 cm³) at each depth in each plot to measure soil water content and bulk density. Plant and soil samples were placed in self-sealing bags and transported to the laboratory. Plant samples were oven-dried at 65°C for 48 h, and weighed to obtain aboveground biomass and belowground biomass. One half of each soil sample was stored at -18 °C for subsequent measurements of DOC and MBC. The other



half of the soil sample was air-dried at room temperature and then sieved through a 2-mm sieve. We measured pH and electrical conductivity (EC) using a pH meter (PHB-3, China) and a conductivity meter (FE30, USA) with a soil:water ratio of 1:5 (w:w), respectively (Zhao et al., 2020). DOC, MBC and SOC were measured by TOC-analyzer (N/C 3100, Germany). Specifically, DOC was extracted with a mass ratio of 1:5 (soil/purified water) and subsequently analyzed by TOC-analyzer (N/C 3100, Germany). MBC was determined by the chloroform fumigation method with TOC-analyzer (N/C 3100, Germany) (Vance et al., 1987). SOC was measured using a high-temperature combustion method with the solid module of TOC-analyzer (N/C 3100, Germany) after inorganic carbon was removed (Bisutti et al., 2004; Liang et al., 2021).

2.3 Calculations

Diversity indices (species richness, Shannon-Wiener index, and Simpson's dominance index) were used to characterize plant species diversity (Fang et al., 2009).

Shannon-Wiener index (H) measures the degree of diversity in plant communities (Shannon and Weaver, 1949) and was calculated as:

$$H = -\sum_{i=1}^s P_i \ln(P_i)$$

(1)

where S represents the total number of plant species in a given plot, P_i represents the relative abundance of plant species i within that plot.

TABLE 1 Mean annual precipitation (MAP), mean annual temperature (MAT) and plant communities at sampling sites.

Site	MAP (mm)	MAT (°C)	Longitude (°N)	Latitude (°W)	Plant species
Daihai	450.56	6.71	121.95	45.14	<i>Phragmites australis</i> , <i>Cyperus pygmaeus</i> , <i>Schoenoplectus tabernaemontani</i> , <i>Schoenoplectus triquetus</i> , <i>Suaeda salsa</i> , <i>Alisma plantago-aquatica</i> , <i>Knorringia sibirica</i> , <i>Aster tataricus</i> , <i>Inula japonica</i> , <i>Typha orientalis</i>
Chgannor	410.49	2.95	115.46	43.49	<i>Phragmites australis</i> , <i>Agropyron cristatum</i> , <i>Potentilla anserina</i> , <i>Artemisia</i> , <i>Ranunculus japonicus</i> , <i>Leymus chinensis</i> , <i>Scirpus triquetus</i> , <i>Saussurea amara</i>
Dalinor	432.11	3.76	116.72	43.25	<i>Suaeda salsa</i> , <i>Phragmites australis</i> , <i>Potentilla anserina</i> , <i>Parnassia palustris</i> , <i>Inula japonica</i> , <i>Cyperus rotundus</i> , <i>Melilotus officinalis</i> , <i>Calamagrostis epigeios</i>
Horqin	466.67	6.44	112.63	40.57	<i>Phragmites australis</i> , <i>Equisetum hyemale</i> , <i>Leymus chinensis</i> , <i>Artemisia</i> , <i>Lespedeza bicolor</i> , <i>Echinochloa crusgalli</i> , <i>Poaceae</i> , <i>Setaria viridis</i> , <i>Gramineae</i> , <i>Allium senescens</i> , <i>Parthenocissus Planch</i>
Wulagai	532.45	1.67	119.49	45.90	<i>Phragmites australis</i> , <i>Polygonum hydropiper</i> , <i>Vicia sepium</i> , <i>Cicuta virosa</i> , <i>Lactuca indica</i> , <i>Equisetum hyemale</i> , <i>Potentilla anserina</i> , <i>stertataricus</i> , <i>Sanguisorba officinalis</i> , <i>Swertia bimaculate</i> , <i>Poaceae</i> <i>Gramineae</i>

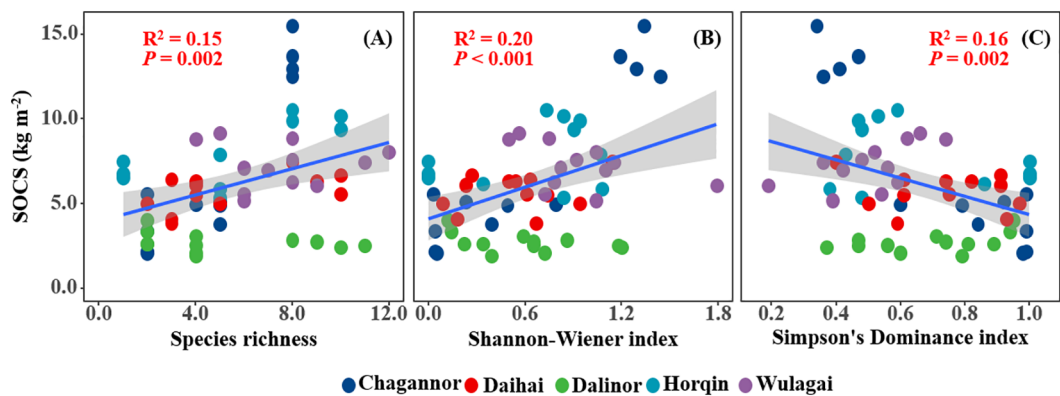


FIGURE 2 Relationships between plant diversity (Richness index, Shannon-Wiener index, Margalef index and Simpson's dominance index) and soil organic carbon storage (SOCS). R^2 and P -values of linear regressions are presented, and the shaded areas represent the 95% confidence intervals ($P < 0.05$). SOCS, soil organic carbon storage.

Simpson's dominance index (D) reflects evenness in distribution among species (Simpson, 1949) and was calculated as:

$$D = 1 - \sum_{i=1}^s (ni/N)^2 \tag{2}$$

The variable ni represents the number of individuals belonging to plant species i , while N is the total number of individuals across all plant species within a given plot.

Soil organic carbon storage (SOCS, $\text{kg}\cdot\text{m}^{-2}$) in a given soil layer (Satdichanh et al., 2023) was calculated as:

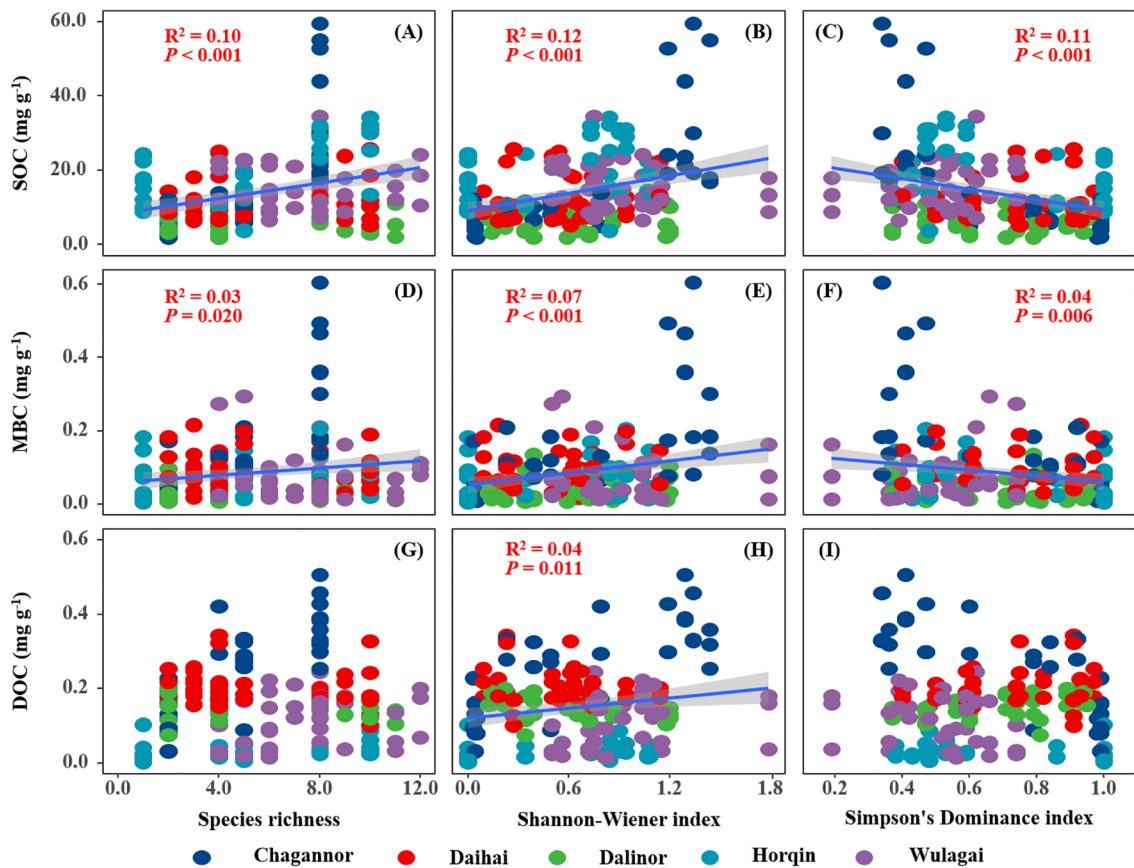


FIGURE 3 Relationships between plant diversity (Richness index, Shannon-Wiener index, Margalef index and Simpson's dominance index) and soil carbon (SOC, MBC and DOC). R^2 and P -values of linear regressions are presented, and the shaded areas represent the 95% confidence intervals ($P < 0.05$). SOC, soil organic carbon; MBC, microbial biomass carbon; DOC, dissolved organic carbon.

$$\text{SOCs} = \text{SOC}_i \times \text{BD}_i \times H \times (1 - \text{CF}/100) \times 0.01 \quad (3)$$

where SOC_i is SOC contents of the soil layer i ($\text{mg}\cdot\text{g}^{-1}$), BD_i is the soil bulk density of soil layer i ($\text{g}\cdot\text{cm}^{-3}$), H is the layer thickness (cm), CF is the percentage of coarse fragments > 2 mm, and 0.01 is a unit conversion coefficient.

2.4 Statistical analyses

Regression analyses was used to explore the relationships between plant diversity (species richness, H and D), plant biomass (total biomass, aboveground biomass, and belowground biomass) and soil carbon (DOC, MBC, SOC and SOCS). Random forest model (RF) was used to explore the relative effects of each variable on SOC. We used the “rfPermute” package to determine the significance of variables (Jiao et al., 2018). The importance of factors was estimated by calculating the percentage increases in the MSE (mean squared error) of variables. For instance, higher values of MSE% indicate more significant variables (Breiman, 2001). Based on the expected relationship between SOC and potential drivers as well as the results of the RF analysis, we developed a structural

equation model (SEM) to analyze the direct and indirect SOC determinants by using the “lavaan” package. Path diagrams are commonly used in SEM analysis to illustrate directional relationships between different variables. We used the maximum likelihood method to estimate path coefficients, and fit indices were utilized to evaluate model fit ($\chi^2/\text{df} < 3$, GFI > 0.9 and RMSEA < 0.08). All statistical analyses were conducted using R 4.2.1 (<https://www.r-project.org/>).

3 Results

3.1 Effects of plant diversity on soil organic carbon

SOCS of the wetland had a significant positive relationship with species richness and Shannon-Wiener index, but a negative relationship with Simpson's dominance index (Figures 2A-C). Similarly, there was a significantly positive correlation between plant diversity (species richness and Shannon-Wiener index) and SOC (Figures 3A, B), MBC (Figures 3D, E). Simpson's dominance index is significantly negatively related to SOC and MBC

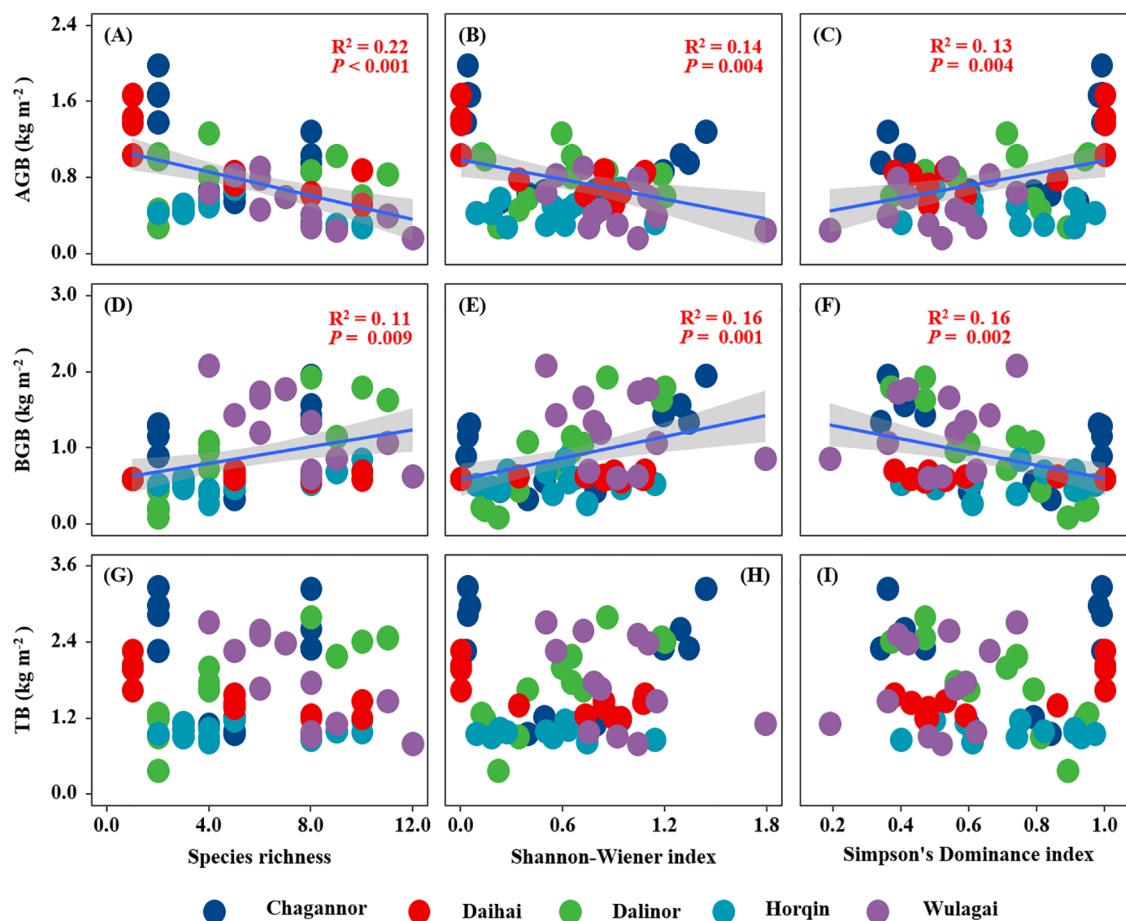


FIGURE 4

Relationships between plant diversity (Richness index, Shannon-Wiener index, Margalef index and Simpson's dominance index) and plant community biomass (AGB, BGB and TB). R^2 , and P -values of linear regressions are presented, and the shaded areas represent the 95% confidence intervals ($P < 0.05$). AGB, aboveground biomass; BGB, belowground biomass; TB, total biomass.

(Figures 3C, F). DOC had no significant relationship with species richness and Simpson's dominance index, but a positive relationship with Shannon-Wiener index (Figures 3G-I).

3.2 Effects of plant diversity on community biomass

Belowground biomass of the wetland plant communities had a significant positive relationship with species richness and Shannon-Wiener index, but a negative relationship with Simpson's dominance index (Figures 4D-F). Conversely, aboveground biomass of the wetland plant communities was significantly negatively related to species richness and Shannon-Wiener index and positively related to Simpson's dominance index (Figures 4A-C). There was no significant relationship between plant diversity and total biomass of the wetland communities (Figures 4G-I).

3.3 Dominant determinants of SOC

The results of RF analysis showed that MBC was the most important determinant influencing SOC, followed by soil bulk density and soil water content (Figure 5A). DOC, plant diversity

and climate had similar contributions in regulating SOC across the study region. SOC was significantly and positively related to MBC ($R^2 = 0.46$, $P < 0.001$), soil water content ($R^2 = 0.25$, $P < 0.001$), significantly and negatively related to bulk density ($R^2 = 0.29$, $P < 0.001$, Figure 5B).

The SEM analysis results showed that SOCS was dominantly and directly affected by MBC, soil, and plant, with standardized direct effects of 0.66, 0.25, and 0.17, respectively (Figure 6). Furthermore, plant and DOC indirectly affected SOCS, with standardized indirect effects of 0.30 and 0.47 (Figure 6). Moreover, soil water content and bulk density significantly and indirectly affected SOCS through a positive path of MBC (path coefficient = 0.47). Thus, increasing soil MBC resulted in enhanced SOCS with belowground biomass and soil properties changed (Figure 6).

4 Discussion

Plant diversity enhanced SOCS in typical wetlands of northern China, consistent with previous studies in forest (Chen et al., 2023), grassland (Steinbeiss et al., 2008; Cong et al., 2014), and agricultural ecosystems (Chen et al., 2018; Spohn et al., 2023). Previous studies indicated that plant diversity could indirectly affect SOCS by

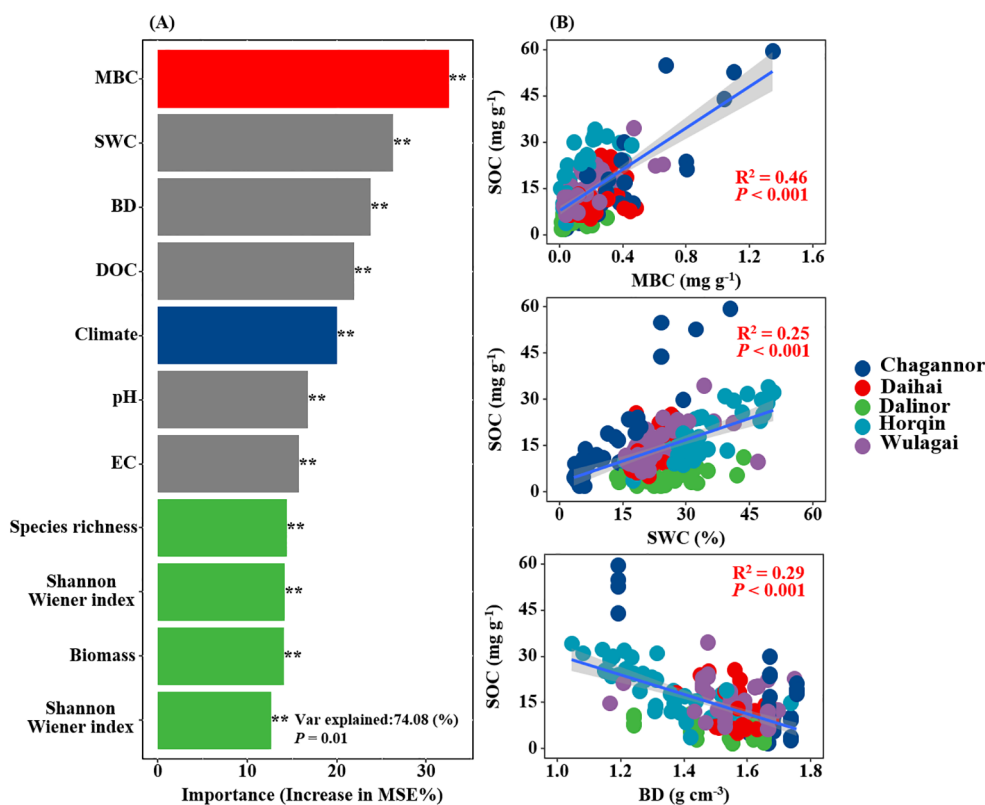


FIGURE 5

Relative importance of Climate, plant (species richness, Shannon-Wiener index, Simpson's Dominance, and Biomass), soil (BD, SWC, EC, pH and DOC), as well as microorganisms (MBC) on SOC was measured by the percentage increase of the mean squared error (MSE%) using random forest (RF) models (A). Relationships between SOC and MBC, BD and SWC (B). MBC, microbial biomass carbon; BD, soil bulk density; SWC, soil water content; DOC, dissolved organic carbon; EC, electrical conductivity; SOC, soil organic carbon. R^2 and P -values of linear regressions are presented, and the shaded areas represent the 95% confidence intervals ($P < 0.05$).

regulating soil labile carbon process (Chen et al., 2018; Lange et al., 2021). In our study, plant diversity significantly increased belowground biomass. This was consistent with previous studies which showed that diversity effect enhanced belowground productivity (Chen et al., 2018; Myllemngap and Barik, 2019; Li et al., 2022; Zhou et al., 2022). Generally, different plant species exhibit diverse growth strategies and root structures, which promote the accumulation of belowground biomass through species complementarity (Loreau and Hector, 2001; Allan et al., 2011). However, we found that plant diversity significantly decreased aboveground biomass and had no significant effect on total biomass. Previous studies showed that plant diversity could promote aboveground biomass and total biomass in forests and grasslands (Myllemngap and Barik, 2019; Token et al., 2022; Wang et al., 2023), which was not consistent with our results in wetlands. In natural wetlands, monodominant community with less plant species, such as *Phragmites australis*, tend to have high aboveground biomass, supported by the relationship between plant biomass and Simpson's dominance index. Due to the opposite effects of plant diversity on aboveground and belowground biomass, there is no significant effect of plant diversity on total biomass in this study.

Our results showed that plant diversity increased soil carbon storage by increasing belowground biomass, DOC and MBC. Previous studies showed that plant biomass and MBC were significantly correlated with plant residues carbon and microbial necromass carbon, which were key sources crucial of SOC (Xu et al., 2023; Zheng et al., 2024). High plant diversity may increase the input of plant residues carbon by affecting the quantity and quality of plant litter, and promote the cumulation of microbial necromass carbon by regulating the structure and function of soil microbial community and MBC (Lange et al., 2015; Shen et al., 2022; Wang C. et al., 2022). In our study, both RF and SEM analyses demonstrated that MBC was the most significant determinant, and there was a significantly positive relationship between SOC and MBC (Figure 5B). This may be due to the fact that increased plant diversity with high belowground biomass and DOC transportation enhanced microbial activity (Dietrich et al., 2017), thereby promoting microbial-derived carbon contribution to SOCS through microbial turnover processes (Thakur et al., 2015; Prommer et al., 2020; Jia et al., 2021), consistent with a previous research (Lange et al., 2021). The positive effect of plant diversity on SOCS was also regulated by soil properties (Zhang et al., 2011; Yang et al., 2020). In our study, the relationship between plant diversity

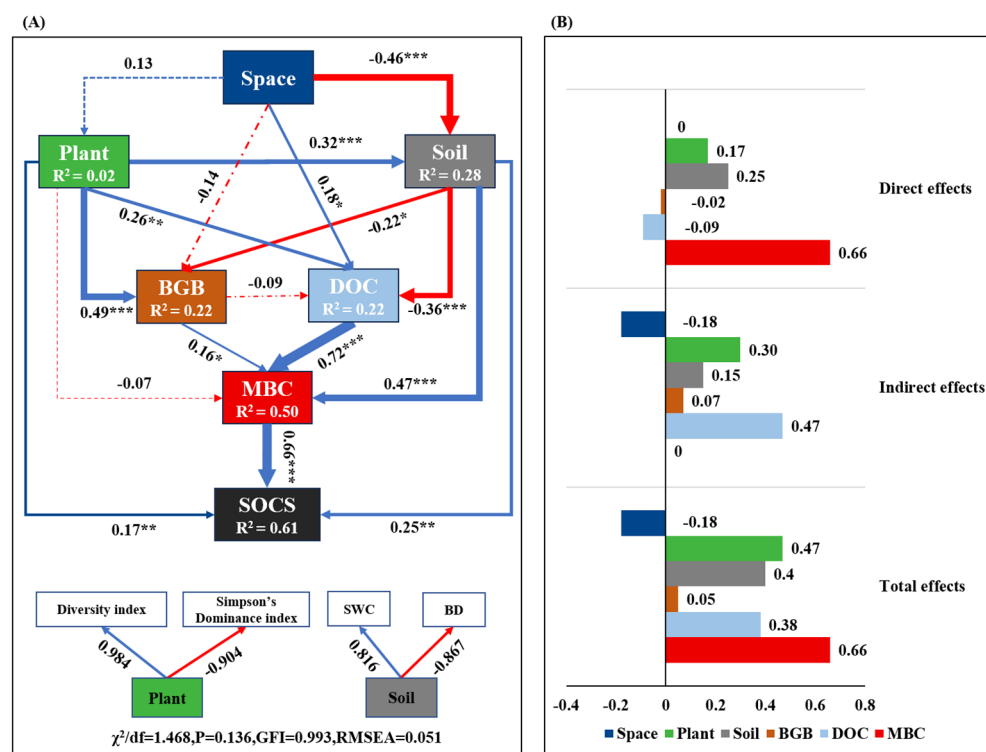


FIGURE 6

Structural equation modeling (SEM) for the effects of the variables on SOCS (A), direct, indirect, and total standardized effects of each variable on SOCS from SEM (B). The Plant and Soil were indicated by the first axis of principal component analysis (PCA). Space includes Sites and Climate. Plant includes Diversity index (species richness and Shannon-Wiener index) and Simpson's Dominance index. Soil in this model includes SWC and BD. Numbers adjacent to arrows are standardized path coefficients (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$), with dotted lines indicates non-significant pathways and solid lines indicates significant effects. The blue arrow indicates positive pathway, and the red arrow indicates negative pathway. The width of arrows is proportional to the strength of path coefficients, and indicative of effect size of the relationship. R^2 denotes the proportion of variance explained. The goodness-of-fit (GFI) and root mean square error of approximation (RMSEA) are shown beside the model. BGB, belowground biomass; DOC, dissolved organic carbon; MBC, microbial biomass carbon; SOCS, soil organic carbon storage; SWC, soil water content; BD, soil bulk density.

and SOCS might be related to the alternation of soil water content and bulk density. There was a significantly positive relationship between soil water content and SOC, and a negative relationship between bulk density and SOC, which was consistent with previous researches (Leimer et al., 2014; Fischer et al., 2015, 2019). Appropriate soil water content is beneficial for high plant diversity, enhancing plant residues carbon input, and also conducive to microbial decomposition; however, excessive soil water content can increase the anaerobic conditions in the soil, tend to form a single plant community, reduces the decomposition by aerobic microorganisms, thereby promoting carbon storage (Martinez Richart et al., 2019; Wang S. et al., 2022; Yan et al., 2020). Plant diversity may regulate soil water status by changing soil structure via plant roots, thus affecting SOC dynamics through microbial decomposition (Kammer et al., 2013; Wang et al., 2014; Ma et al., 2020; Lange et al., 2021). Therefore, how to promote SOC storage based on soil water regulation and plant diversity protection, and clarify the microbial mechanisms in wetland ecosystems still need further research. Given the nature of field surveys and sampling, it is possible that we may have overlooked the dynamic changes of plant diversity. In the future, long-term monitoring of plant diversity, coupled with systematic soil sampling, will be essential to reveal the complex mechanisms.

5 Conclusions

Plant diversity significantly enhanced SOC content and storage in typical wetlands of northern China by increasing belowground biomass and MBC, together with soil properties, especially soil moisture and bulk density. This study strengthens our knowledge about the positive effect of plant diversity on soil organic carbon storage in wetlands, and underscores the importance of considering plant diversity as a key component in the toolbox of wetland management and climate change mitigation strategies. Continued further research and long-term monitoring are necessary to understand the regulatory mechanism and management strategies of dynamic plant diversity and SOC storage under changing climatic conditions.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

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Conflict of interest

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Supplementary material

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Effects of fertilization on litter decomposition dynamics and nutrient release in orchard systems

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Plant litter decomposition is a significant ecosystem function that regulates nutrient cycling, soil fertility, and biomass production. It is heavily regulated by nutrient intake. The effects of exogenous nutrients on litter decomposition are not yet fully understood. To determine how *Eriobotrya japonica* litter decomposition responds to adding nutrients, we used the decomposition litter bag method in the laboratory for 180 days. There were five different nutrient treatment levels were used: control (no addition), low nitrogen addition (LN; 100 kg N·ha⁻¹·year⁻¹), high nitrogen addition (HN; 200 kg N·ha⁻¹·year⁻¹), phosphorus addition (P; 50 kg P·ha⁻¹·year⁻¹), and micronutrient addition (M; 50 kg M·ha⁻¹·year⁻¹). According to a repeated-measures analysis of variance, adding N reduced the remaining mass ($p < 0.01$) by 4.1% compared to the CK group. In contrast, adding M increased the remaining mass ($p < 0.01$) by 6.8% compared to the CK group. Adding P had no significant effect on the remaining mass. Although the amount of residual carbon (C) was unaffected, adding N increased the level of residual N in the litter. Litter C content, K content, N concentration, and C/N ratio were linearly correlated to the remaining litter ($p < 0.01$). Although adding nutrients decreased soil enzyme activity later in the decomposition process, no significant correlation was detected between enzyme activity and the remaining mass. N fertilization treatments decreased the soil microbial diversity index. The addition of nitrogen and micronutrients reduced the abundance of Acidobacteria, while HN addition increased the abundance of Actinobacteria. The addition of micronutrients increased the abundance of Proteobacteria. These results imply that N-induced alterations in the element content of the litter regulated the effects of nutrient inputs on litter decomposition. This study can be a reference for the fertilization-induced decomposition of agricultural waste litter.

KEYWORDS

litter decomposition, nutrient additions, element release, nitrogen, phosphorus

Introduction

In addition to maintaining ecosystem production and fertilizer application, litter decomposition supplies vital nutrients for plant development and consumption by soil microbes (Aerts et al., 2006; Huangfu and Wei, 2018; Canessa et al., 2021). According to previous studies, the environmental factors (temperature and moisture), initial litter element quality (N content, C content, C/N ratio, and lignin/N ratio), enzyme activities, and the decomposer community of soil microorganisms and fauna all have a significant impact on litter decomposition rate (Diepen et al., 2016; Lucas et al., 2016; Zhou et al., 2017). Nutrient availability is considered a key indicator of the initial stages of litter decomposition (Hobbie, 2005; Van et al., 2013).

The decomposition of litter is suppressed (Zhou et al., 2017; Tao et al., 2019) or accelerated (Downs et al., 1996; Ren et al., 2018) by the addition of N. N fertilizer frequently affects how quickly litter decomposes by altering the soil conditions in which litter decomposes (Gill et al., 2021). N, for example, may alter the activity of soil organisms by enriching fungi and bacteria, increasing the density of soil fauna (Carrera and Bertiller, 2013), or changing their enzyme activity (Song et al., 2018). While phosphorus (P), calcium (Ca), magnesium (Mg), manganese (Mn), and iron have been less frequently evaluated in research on litter decomposition, they are nonetheless closely associated with decomposition rates. For example, P was necessary to supply nutrients to the decomposers in the early stages of decomposition (Van et al., 2016). Due to the effect of Mn on the synthesis and activity of lignin-degrading enzymes, Mn addition had a favorable impact on litter decomposition (Keiluweit et al., 2015). Trum et al. (2015) discovered that Mn enhancement improved the dissolution of dissolved organic C components during degradation by increasing lignin decomposition. Therefore, Mn addition may influence litter decomposition by increasing the fragile substrates available to decomposers (Wu et al., 2022). In summary, the addition of trace elements changes litter decomposition by affecting the decomposers (Berg et al., 2007). It has an ambiguous impact on litter decomposition by increasing microbial diversity and altering the soil microbial community (fungi:bacteria ratio) (Gill et al., 2021).

Nutrient inputs to soil can regulate microbial communities through their influence on the soil resources by providing energy and nutrients or through predation by protists (Asiloglu et al., 2021). It is thought that in nutrient-limited environments, microbial development and activity are constrained by the low availability of C and nutrients. Therefore, the input of nutrients will promote microbial activity (Renella et al., 2006). For example, exogenous N inputs can inhibit phagotrophic protists and thus promote the growth of specific bacterial groups in subtropical ecosystems (Zhao et al., 2020). However, excessive input of nitrogen leads to soil acidification, reducing the specific abundance of ammonia-oxidizing bacteria or overall microbial diversity (Zhong et al., 2016). When P was added, the bacterial diversity and the abundance of *nirK* and *nirS* genes were increased (Wang et al., 2018). However, the influence of fertilization on microbial activity has been inconclusive, with studies reporting

increases (Jing et al., 2024; Fu et al., 2023), decreases (Kumar et al., 2018; Morrison et al., 2018), and even no effect (Hobbie and Vitousek, 2000) on microbial abundance with fertilization. Overall, studies have shown that fertilizer inputs can increase the abundance of protists that consume microbes (Delgado-Baquerizo et al., 2017; Guo et al., 2021), but can have negative effects when added excessively.

The effects of nutrient addition on soil enzyme activity and microbial community are well established. In the presence of easily accessible nutrients, microbes reduce the distribution of resources for enzyme synthesis and release (Kumar et al., 2018). The addition of one nutrient can affect not only the activities of the enzymes participating in that specific nutrient cycle but also the activities of other enzymes involved in the cycling of other nutrients. For instance, xylanase activity (engaged in the degradation of hemicellulose) diminished in the presence of mineral nitrogen (Chen et al., 2014). Nutrient addition has an impact on enzyme activity, while soil enzymes are responsible for the biological composition of organic matter (Allison and Vitousek, 2004). Various correlations exist between soil enzyme activity and litter mass reduction (Song et al., 2018). Therefore, additional research on enzyme activity and microbial alterations during decomposition is required to comprehend how litter decomposes in the face of environmental change.

Furthermore, because it is the primary source of agricultural waste, litter management has always been a priority in orchard management. Although N, P, and micronutrients are ubiquitous fertilizers, how they affect litter decomposition is still unknown. As a result, while investigating litter decomposition responses, it is becoming increasingly important to investigate the effects of external fertilizer inputs. We collected fresh leaf litter of *Eriobotrya japonica* from plantations in southern China. We investigated the interaction between the soil microbial community and enzyme activities for 180 days of decomposition in a stable temperature and humidity environment and the influence of exogenous nutrient additions on litter decomposition rates with the decomposition bag method. We hypothesized that adding exogenous nutrients would increase soil enzyme activity and microbial diversity, increasing litter decomposition.

Methods

Materials and samples

Litter samples were collected from plantations in Jiangsu Province, southern China (31°2'42"N, 120°19'7"E). This site has a subtropical monsoon marine environment with 1,100 mm of annual mean rainfall and 15.7°C of annual mean air temperature. *E. japonica*, *Citrus reticulata*, and *Pyrus* spp. are the main tree species in this area. In October 2021, fresh *E. japonica* litter samples (intact and unpurified) were collected. [Supplementary Table S1](#) displays the initial values of the elements found in *E. japonica* litter. The litter was air-dried before being packed into nylon mesh bags (10 cm × 8 cm, with 0.1-cm apertures). Soil samples were collected

from an artificial forest at the Chinese Academy of Environmental Sciences, Beijing. The basic chemical properties of the soils are listed in [Supplementary Table S2](#).

Plot design and fertilization

The experiment was run in a greenhouse (25°C–30°C) to reduce the influence of climatic variations on litter decomposition. There were five treatment groups set up: control (CK; no addition), low N addition (LN; 100 kg N·ha⁻¹·year⁻¹), high N addition (HN; 200 kg N·ha⁻¹·year⁻¹), P addition (P; 50 kg P·ha⁻¹·year⁻¹), and micronutrient addition (M; 50 kg M·ha⁻¹·year⁻¹). The raw materials applied were nitrogen fertilizer (467 kg N·kg⁻¹), phosphorus fertilizer (70 kg P·kg⁻¹), and agricultural fertilizers (40 kg micronutrients·kg⁻¹) rich in calcium, magnesium, iron, and manganese. Five 60 × 50 cm plots were created in the greenhouse at the beginning of November 2021. With 18 duplicate bags, each containing 2 g of litter, evenly distributed over the soil surface, each plot corresponded to a treatment. The soil of each plot was evenly sprayed with 1,000 mL of pure water after the fertilizer had been dissolved in it. The CK treatment was sprayed with 1 L of water without fertilizer. Water was replenished regularly by weighing methods to control the soil moisture content to 60% of the field's water capacity throughout the experiment.

Litter sampling and analysis

Three bags from each plot were sampled after 9, 18, 36, 64, 117, and 180 days had passed since decomposition began. Prior to being oven-dried to a constant weight at 60°C and weighed, the remaining litter in the nylon bags was meticulously cleaned of soil and other residues. A percentage of the initial litter mass was used to calculate the remaining litter (%). The dry litter's total C and N contents were calculated ([Zhang et al., 2015](#)) using an elemental analyzer (2400 IICHNS/O, PerkinElmer, Waltham, MA, USA). Total P content was determined colorimetrically after acidified ammonium persulfate digestion ([Chen et al., 2013](#)).

Soil sampling and analysis

The soil from the plots was promptly collected at the end of the experiment. Any remaining plant, root, or gravel components were manually removed from the soil samples. One part of the sample was used to determine enzyme activity, and the other part was used to analyze microbial diversity and composition. Four soil enzyme activities were measured for this study: 1,4-β-glucosidase (BG) for cellulose decomposition, phenol oxidase as a typical ligninolytic oxidoreductase, 1,4-β-N-acetylglucosaminidase (NAG) for chitin decomposition, and acid phosphatase (ACP) for the hydrolysis of ester-bonded phosphate and protein. Nitrobenzene-β-D-glucopyranoside, pyrogallol, *p*-nitrophenyl-β-D-glucopyranoside, and phenyl-disodium phosphate were the substrates used to determine the enzyme activity ([Saiya-Cork et al., 2002](#)). To assess the component

of the soil microbial population, phospholipid fatty acid analyses were performed. Soil genomic DNA was taken out following the manufacturer's instructions using a FastDNA[®] Spin kit for soil. Purified PCR products were quantified by Qubit[®] 3.0 (Life Invitrogen, USA, Alaska), and all 24 amplicons whose barcodes were different were mixed equally. The pooled DNA product was used to construct the Illumina paired-end library following Illumina's genomic DNA library preparation procedure. Then, the amplicon library was paired-end sequenced (2 × 250) on an Illumina MiSeq platform (Shanghai BIOZERON Co., Ltd., Shanghai, China) according to the standard protocols. Operational taxonomic units (OTUs) were clustered with a 97% similarity cutoff using UPARSE, and chimeric sequences were identified and removed using UCHIME. A rarefaction analysis based on Mothur v.1.21.1 was conducted to reveal the diversity indices, including the Chao, ACE, and Shannon diversity indices ([Frostegård et al., 1993](#)).

Data analysis

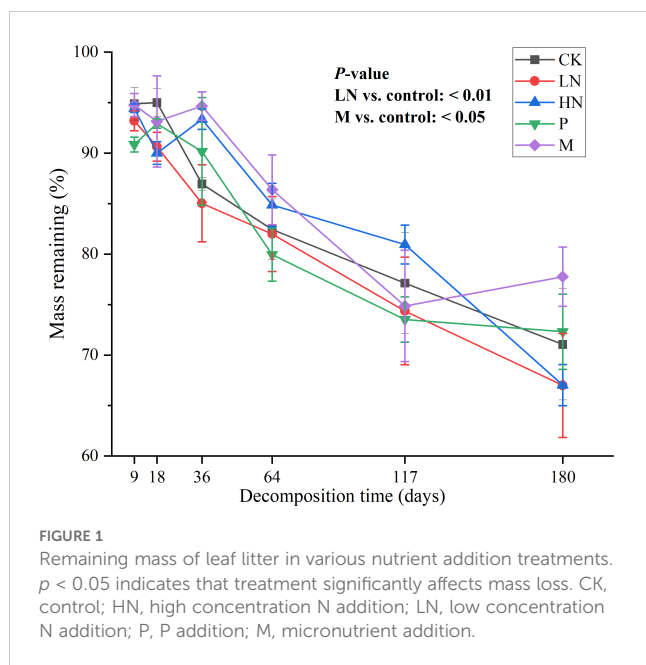
The Kolmogorov–Smirnov and Levene's tests served to determine the normality and homogeneity of variance of the data. The between-group difference in soil enzyme activity and the microbial diversity index at a specific time was confirmed using Dunnett's *t*-test for multiple comparisons. A multi-factor analysis of variance was performed to determine the effect of nutrient addition on the remaining mass and nutrients in the litter. The relationships between remaining mass (%), remaining nutrients, soil enzyme activity, and microbial diversity indices were analyzed using linear regression. SPSS, Inc., 13.0 was used for the given statistics (Chicago, IL, USA).

Results

Effects of nutrient addition on litter decomposition and element content

The two treatment groups with N addition had lower remaining mass than the CK group after 180 days of decomposition. However, during the period of 36–117 days, the remaining mass of the high N addition group was higher than that of the CK group. The M and high N addition groups significantly inhibited and promoted mass loss, respectively ($p < 0.05$) ([Figure 1](#)).

[Figure 2](#) shows the patterns of element release during litter decomposition. *E. japonica* litter had initial C, N, and K contents of 46%, 1.6%, and 1.4%, respectively. After 180 days of decomposition, the C content was lower than the initial value. However, there was no significant difference in the trend of C release between the fertilization group and the CK group. The trend of the N content fluctuates and eventually indicates net N accumulation. In all N-addition treatments, the average percentage of N concentrations still in the litter was 146%. During the first 18 days, the remaining groups briefly released N. Following that, they increased to approximately 100% and remained constant. The content of K decreased continuously during decomposition, and the lowest K content was 11.73% in CK group. The other groups had K levels between 25% to 42%. The N addition treatments caused a significant increase in N concentration ($p < 0.05$).



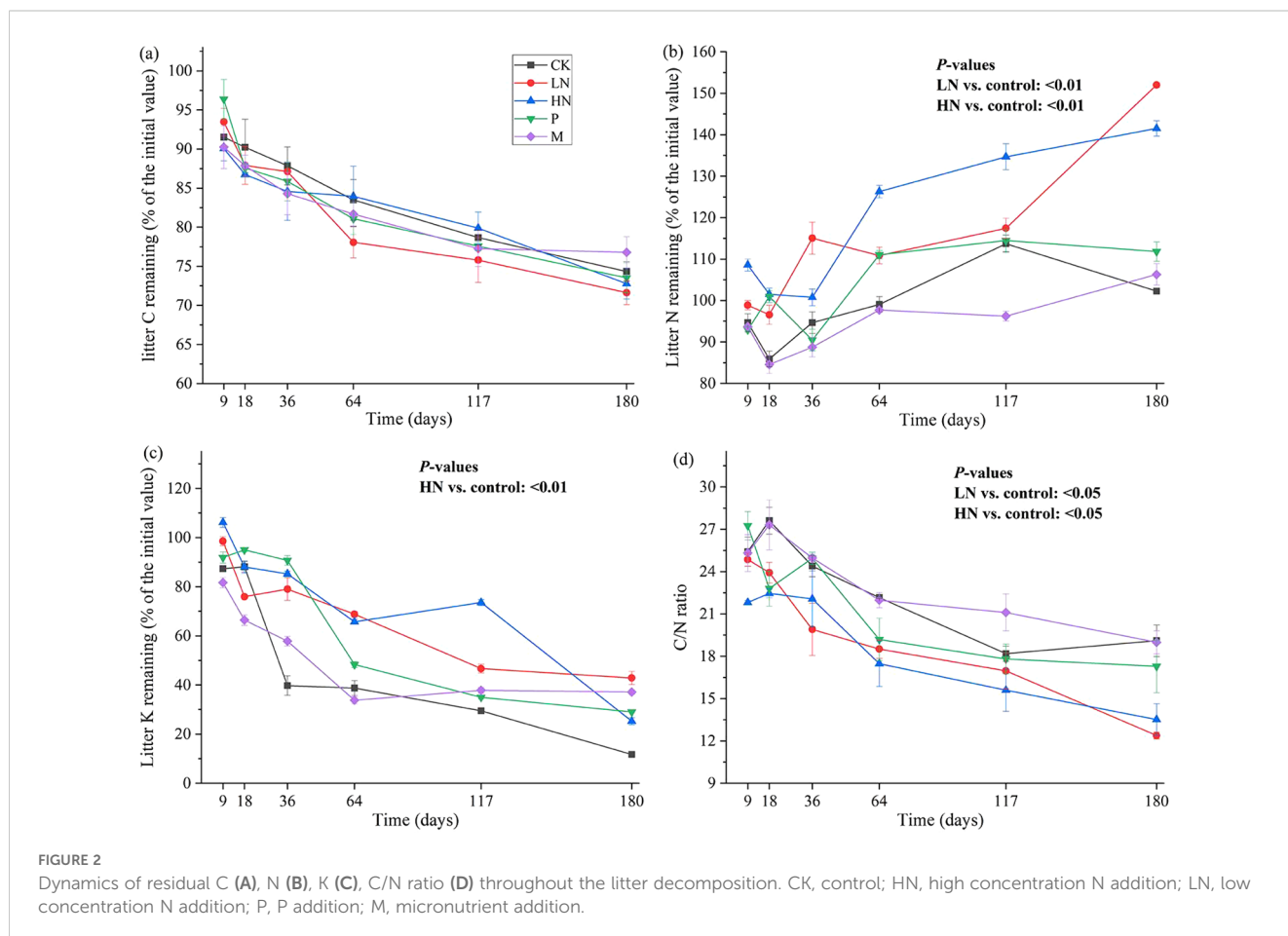
compared to the other treatments, while low N addition significantly decreased K release ($p < 0.01$) (Figure 2). Additionally, the findings of Pearson's analysis revealed a significantly negative correlation between the remaining mass and N content ($p < 0.01$) and a significantly positive

correlation between the remaining mass with C content, K content, and C/N ratio ($p < 0.01$) (Figure 3).

Impacts of nutrient addition on soil extracellular enzyme activity and microbial community

After the decomposition experiment, we found that the direct impacts of additional exogenous nutrients on PO, NAG, ACP, and BG activities during this study were significant. The results showed that exogenous nutrient input decreased soil enzyme activity (Figure 4). The high N fertilizer significantly decreased the activity of four soil enzymes. It is important to note that the CK group's soil enzyme activities were consistently higher than those of the treatments, including nutrient addition. As seen in Figure 5, the low N addition treatments did not influence the diversity of the soil bacterial community, but significantly negatively impacted fungal abundance. The addition of high N fertilization treatments significantly decreased the soil bacteria's Shannon and Chao indices. Low N fertilization treatments significantly decreased the Shannon indices of the soil fungal functional group ($p < 0.05$) (Figure 5). Other treatments had no appreciable impact on the diversity of the bacterial communities.

Actinobacteria, Acidobacteria, Proteobacteria, Bacteroidetes, and Firmicutes were the most prevalent bacterial phyla in all soils



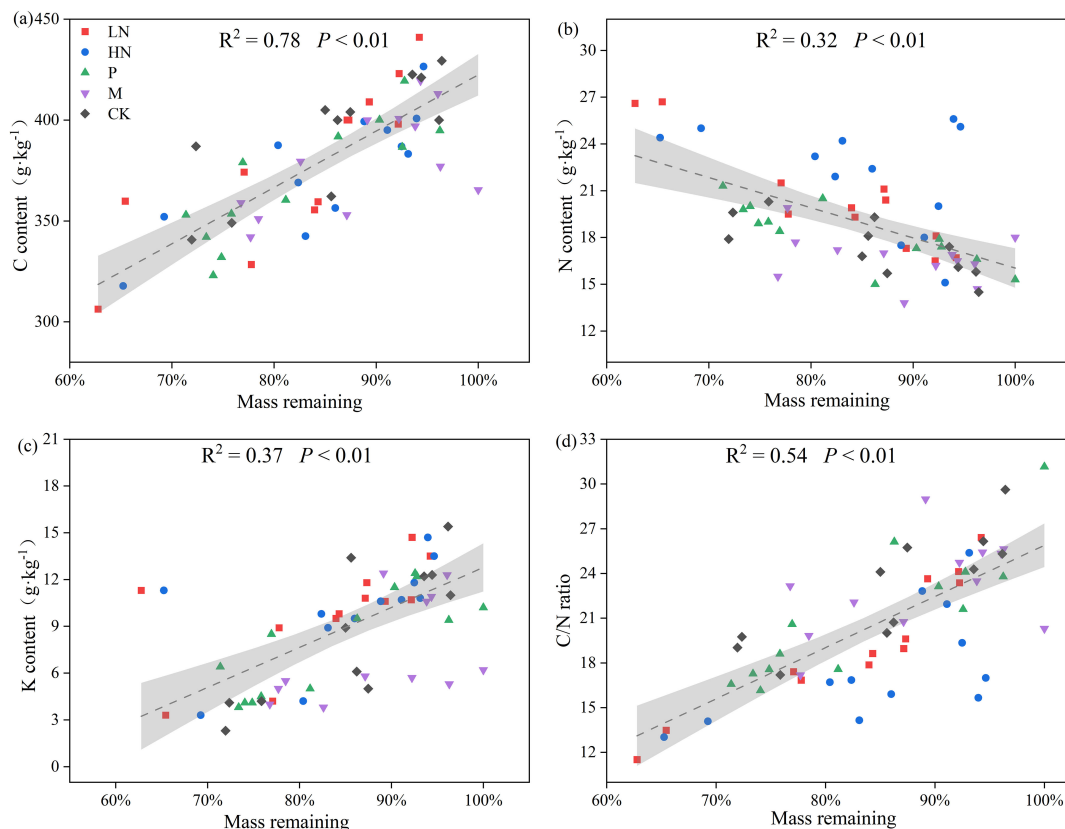


FIGURE 3

Relationships between remaining mass and C (A), N (B), K (C), C/N ratio (D) in all groups. CK, control; HN, high concentration N addition; LN, low concentration N addition; P, P addition; M, micronutrient addition.

included in this study (Figure 6). The addition of nitrogen and micronutrients reduced the abundance of Acidobacteria, while HN addition increased the abundance of Actinobacteria. The addition of micronutrients increased the abundance of Proteobacteria. The soil fungal community consisted primarily of Ascomycota, Mucoromycota, Basidiomycota, and unclassified fungi (Supplementary Figure S1). There was little difference between the CK and P addition treatments. The relationship between enzyme activity and decomposition rates was not found to be significantly different. Microbial diversity index and breakdown rate were not significantly correlated in this study, except for bacterial OTUs (Supplementary Figure S2). Supplementary Figure S3 displays the genus-level relative abundances of the soil community composition across all treatments.

Discussion

Changes in nutrient release and correlation with decomposition

As the most abundant element in the litter, C was often released continuously during the decomposition, as shown in many studies (Manzoni et al., 2010; Zhang et al., 2021). In contrast, N displayed a net accumulation in this study (Figure 3). Similarly, excessively high levels

of N addition significantly increased litter N content in *Stipa aliena* Keng and *Elymus nutans* Griseb (Song et al., 2019). Liu also found N enrichment in a study on the decomposition of litter in ecological tea gardens (Liu et al., 2023). These results may imply that adding N influences N cycling, but not C cycling, in orchard ecosystems. The N enrichment in our study could be attributed to *E. japonica* leaf litter's low initial N content, which was only 1.4%. Therefore, an increase in nitrogen content within a certain range will not lead to an increase in the total mass of litter. Decomposers typically immobilize N from the environment because litter has inadequate N, which causes decomposers to immobilize growth (Parton et al., 2007). N is released from the litter when its N content reaches a certain point (Berg and Staaf, 1981). A previous study has suggested that N release will occur in litters where the C/N ratio is between 25 and 34 (Chen et al., 2019). Additionally, the release of N from some litter may not be noticed for several years (Berg, 2000). In general, microorganisms were thought to be responsible for N enrichment. K was continuously released in this study because it was the most easily transferred element in the plant. It resided in the litter in ionic form and was released by osmosis.

Following the findings of this study, C content, K content, and C/N ratio were positively correlated with the remaining litter mass ($p < 0.01$), and N addition may influence decomposition by modifying litter element content. Low concentration N addition in this study altered the element release pattern by increasing litter N content and significantly decreasing the residual mass.

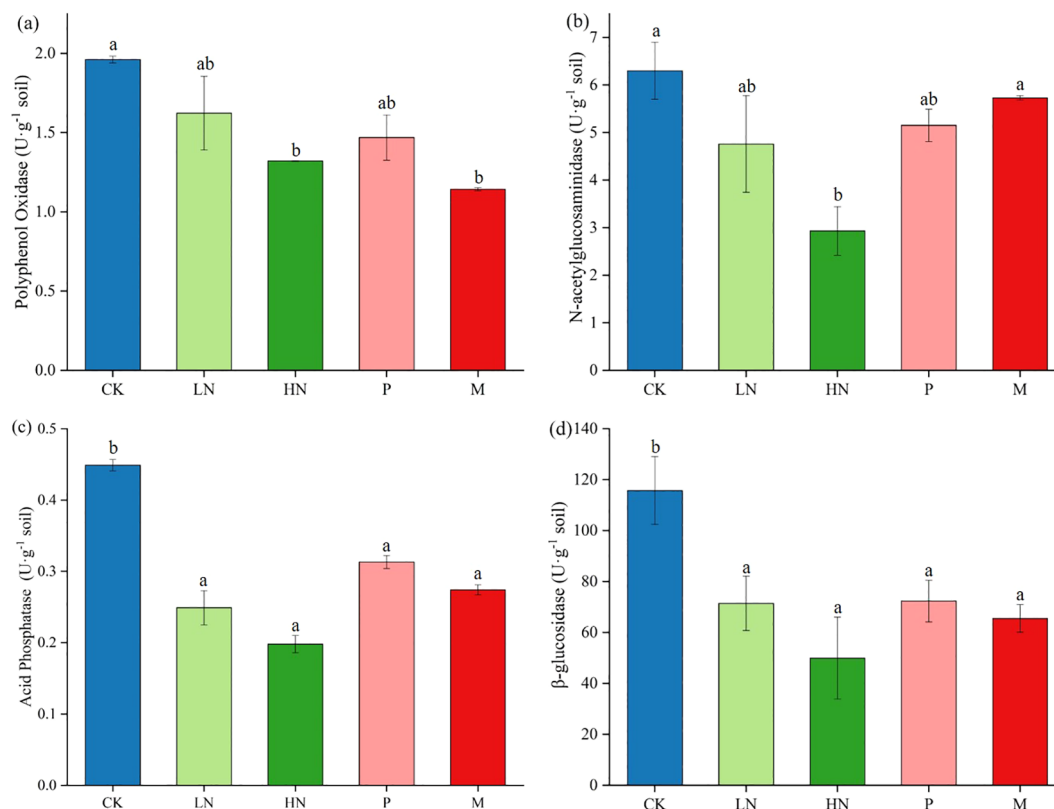


FIGURE 4

The soil enzyme activities of each treatment in the later phase of litter decomposition (A. Polyphenol oxidase, B. N-acetylglucosaminidase, C. Acid phosphatase, D. β-glucosidase). Different lowercase letters denote a significant difference between the treatment and control ($p < 0.05$). CK, control; HN, high concentration N addition; LN, low concentration N addition; P, P addition; M, micronutrient addition.

Effects of nutrient addition on soil enzyme activity and microbial structure

Enzyme activity is a key factor influencing the litter decomposition rate (Burns et al., 2013). ACP catalyzes the hydrolysis of organic P molecules, while oxidase primarily decomposes lignin (Tien and Kirk, 1983; Marklein and Houlton, 2012). BG activity directly affects the rate

of cellulose degradation (Sinsabaugh et al., 1993). In this study, the four enzyme activities significantly decreased after 180 days of nutrient application and decomposition. It has been reported that the decrease in C compounds was the reason for the decrease in oxidase activity caused by N addition (Hoyos-Santillan et al., 2018). In a study of N decomposition in mid-subtropical China, high N treatment decreased the activity of BG and ACP in the late phase of decomposition (Chen

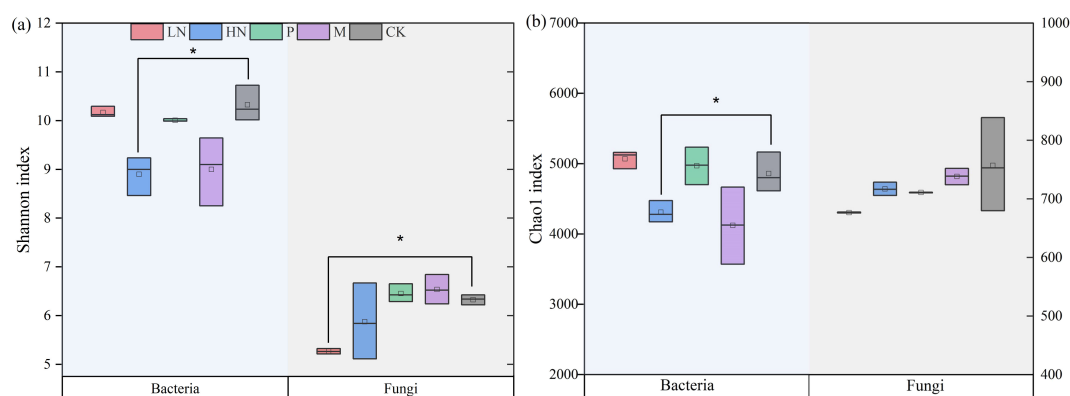


FIGURE 5

Soil microbial diversity index of each treatment in the later phase of litter decomposition (A. Shannon index, B. Chao1 index). Asterisk (*) denotes a significant difference between the treatment and control ($p < 0.05$). CK, control; HN, high concentration N addition; LN, low concentration N addition; P, P addition; M, micronutrient addition.

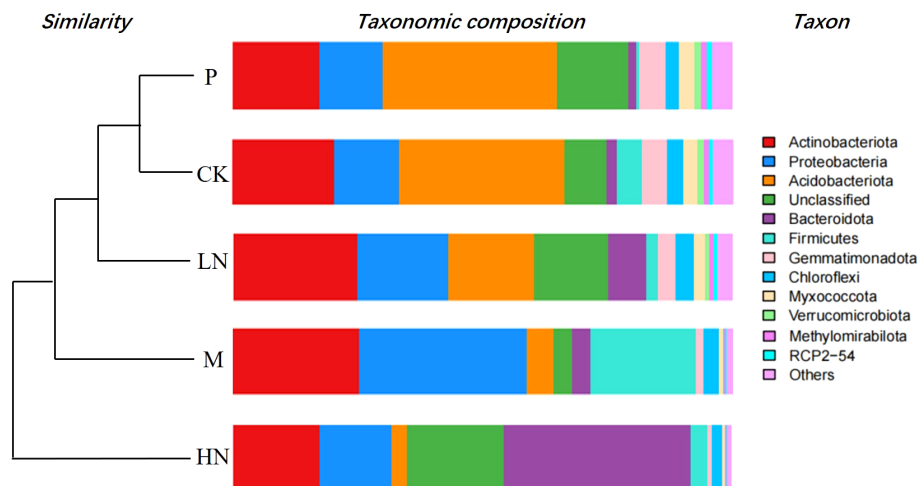


FIGURE 6

Phylum-level relative abundances of the soil bacterial community composition across all treatments. CK, control; HN, high concentration N addition; LN, low concentration N addition; P, P addition; M, micronutrient addition.

et al., 2012). In Hu's work, N administration also suppressed several enzyme functions (Hu, 2020). Microorganisms release oxidase to decompose lignin to obtain N (Moorhead and Sinsabaugh, 2006); however, bacteria may restrict enzyme activity when environmental conditions meet the nutritional requirement (Allison and Goulden, 2017). Additionally, exogenous N induces the formation of recalcitrant aromatic compounds that lower extracellular enzyme activity and stoichiometric interactions between polyphenols and amino complexes (Fog, 1988). In line with previous studies (Chen et al., 2013), adding P and micronutrients in this study decreased enzyme activity. Studies have demonstrated that P limitation stimulates microbial mineralization of P from the environment, while P addition inhibits the effect of "microbial P mining" and thus reduces enzyme activity (Moorhead and Sinsabaugh, 2006). It has also been demonstrated that bacteria reduce their investment in the production of enzymes when there is enough P (Zhang et al., 2021). This may be the reason why the addition of phosphorus decreased enzyme activity in this study.

In this study, nutrient addition decreased the diversity of soil microorganisms. N addition may harm microbial growth by decreasing soil acidity (Sun et al., 2018). Other studies had similar findings suggesting a deleterious relationship between fungal abundance and soil N availability (Bahram et al., 2012; Yao et al., 2017). P limitation may promote "microbial P mining" which P addition suppresses (Deforest, 2019). The expression of C and N cycling genes is reduced and there is a significant decrease in microbial activity when soil nutrients are available, as microorganisms use inactive substrates first (Fierer et al., 2010). Adding nutrients can impact microbial abundance by altering soil stoichiometry and the amount of fungal secretion, and by disrupting the initial nutritional balance (Wei et al., 2013). However, while microbial turnover efficiency may be increased, the decrease in abundance does not always imply that decomposition is inhibited (Li et al., 2022).

After 180 days of decomposition, the dominant species of soil microorganisms were the same as in many previous types of research (Tian et al., 2020; Xie and Yin, 2022). Acidobacteria and Proteobacteria

play significant roles in litter decomposition (Pankratov et al., 2011). Acidobacteria decompose complex macromolecules, including lignin and cellulose (Llado et al., 2016). Proteobacteria use the ammonia and methane produced during decomposition (Lv et al., 2014) to decompose simple organic matter (Wang et al., 2022). Through network analysis and subsequent culturing, Zheng revealed keystone taxa involved in the dynamics of microbial litter decomposition, including Actinobacteria, Bacteroidetes, and Chloroflexi (Zheng et al., 2021). Lu's research has shown that Gemmatimonadetes and Firmicutes are involved in litter decomposition of *Robinia pseudoacacia* Linn. and *Quercus acutissima* Carr (Lu et al., 2022). Basidiomycota and Ascomycota are the two primary groups of fungi that decompose the cell walls of leaf litter. Basidiomycetes decompose refractory compounds in litter by producing lignin-degrading enzymes (Castro and Freitas, 2000). Ascomycetes mainly decompose cellulose and hemicellulose (Baldrian, 2017). The reason for the change in microbial abundance may be that the input nutrients altered the growth strategy of microorganisms, and it is also related to the functional adaptability of microorganisms (Xie and Yin, 2022). The microbial diversity index and soil enzyme activity had almost no significant link with this study's decomposition rate and remaining mass (Appendix S2). The only factor that is significantly ($p < 0.5$) positively correlated with the rate of remaining mass is the number of 16S OTUs. However, it is possible that the study period was not long enough for short-term alterations to be significant.

Mechanisms of nutrient addition affecting litter decomposition

Adding exogenous nutrients can impact litter decomposition by altering the litter element content, soil enzyme activity (Li et al., 2011), and microbial growth or activity (Li et al., 2017; Yan et al., 2018). Low N addition in this study promoted decomposition by increasing N content, which significantly negatively correlated with the remaining

mass. High N addition increased N content but decreased K release, positively correlating with the remaining mass. The highest number of 16S OTUs positively correlating with the remaining mass was found in the micronutrient addition group. This may be the cause of the inhibition of decomposition caused by the addition of micronutrients.

As an economic fruit tree, *E. japonica* is widely planted in southern China. Therefore, this study provides a basis for the effects of fertilization on litter decomposition and nutrient cycling in orchards. However, the results are limited, as the study only focused on one type of litter. Furthermore, only soil enzyme activity and microorganisms in the final degradation phase were investigated in this study. The final results have limitations, and further research into the specific relationship between litter decomposition and soil microbial dynamics would require long-term monitoring of soil microbial dynamics.

Conclusion

The main conclusions of this study are as follows: 1) low N addition decreased residual mass, whereas the addition of micronutrients increased it. 2) Our findings showed that adding N increased the N concentration in the litter. The rate of the remaining mass was highly correlated with C concentration, K concentration, and the C/N ratio. N addition may affect how quickly litter decomposes by altering the content of the elements. 3) In the late stages of decomposition, nutrient addition also decreased soil enzyme activity and microbial diversity. Our findings could be used as a reference for researchers studying the mechanism of litter decomposition in fertile soil, and forecast element cycling of orchard ecosystem in the face of fertilizer through changes in nutrients during litter decomposition.

Data availability statement

Publicly available datasets were analyzed in this study. Data are available from Figshare: https://figshare.com/articles/dataset/Nie_xlsx/22954334.

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Author contributions

HN: Writing – original draft, Investigation, Methodology. CY: Formal analysis, Methodology, Writing – original draft. JG: Funding acquisition, Writing – review & editing.

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Conflict of interest

The authors declare the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fpls.2024.1467689/full#supplementary-material>

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Differential responses of soil C, N, and P ecological stoichiometric characteristics to different configurations of edge-locked forests in the Kubuqi Desert

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As a vital component of the desert ecological protection system, the edge-locked forests of the Kubuqi Desert play a crucial role in mitigating wind erosion, stabilizing sand, maintaining soil and water, and restricting desert expansion. In this paper, six types of standard protection forests in the Kubuqi Desert, namely *Salix psammophila* (SL), *Elaeagnus angustifolia* (SZ), *Salix matsudana* (HL), *Corethroedendron fruticosum*+*Salix psammophila* (YC + SL), *Caragana korshinskii* + *Populus simonii* (YYY + NT), and *Elaeagnus angustifolia* + *Salix matsudana* (SZ + HL), were investigated. Notably, the vertical differentiation patterns of soil carbon (C), nitrogen (N), phosphorus (P), and ecological stoichiometric ratios, as well as soil particle size features within the 0–100-cm soil layer under protection forests with different allocation modes, were systematically and comprehensively analyzed. The study's findings showed that: (1) Among the six configuration types, SZ, NT + YYY, and SL exhibited higher soil SOC and TN concentrations. Both soil SOC and TN content decreased with increasing soil depth, whereas soil TP content displayed no considerable variation among different stand types or soil depths. (2) Based on the N/P threshold hypothesis, N was the limiting nutrient element for the growth of edge-locked forests in the region. (3) The understory soils of different configurations of edge-locked forests mainly comprised sand. The silt and clay contents of SL and NT + YYY were substantially higher than those of the other four configurations. The vertical distribution patterns of particle size and parameter characteristics had variations. (4) Soil C, N, P, and stoichiometric characteristics are affected by vegetation type, soil depth, and soil texture. In conclusion, SZ and SL can be used as the dominant tree species in the edge-locked forests of the Kubuqi Desert, and the NT + YYY mixed forest configuration pattern displays the most apparent soil improvement effect. This study's findings

offer a scientific reference and foundation for restoring vegetation and enhancing the ecological environment in desert regions. In addition, they provide a theoretical foundation for establishing and managing edge-locked forests.

KEYWORDS

desertification, edge-locked forests, C, N, and P, ecological stoichiometry, particle size characterization, Kubuqi Desert

1 Introduction

Desertification is one of the biggest global environmental issues (Rivera-Marin et al., 2022). It exploits one-third of the worldwide land mass and is a prominent geochemical cycle component (Chen H. et al., 2024). However, climate change is primarily responsible for increasing the scope of desertification around the world. The latest data from the United Nations (the 2022 national reports of 126 Member States) show that 15.5 percent of the earth's land is already degraded, an increase of 4 percent over the past few years. The area ravaged by desertification has grown from 50,000 to 70,000 square kilometers annually, especially in regions near deserts (Kumari et al., 2023). Desert expansion destroys the biological potential of the land (Stiles, 1995) while causing a loss of ecological stability, a decline in biodiversity, and a reduction in carbon (C) sink capacity (Gupta, 2012). It threatens human survival, adult production, and life (Zhang et al., 2017). Therefore, effective desert expansion prevention is strategically significant for ensuring ecological security and realizing sustainable development in arid areas (Chen L. et al., 2024). According to pertinent research, vegetative measures seem to be the most effective approach to break off the spread of deserts (Wu et al., 2023). Essentially, edge-locking forests are one of the most standard and effective methods of preventing desert expansion. Desert edge-locked forests present a broad range of services by effectively reducing wind speeds, blocking sand particles, and curbing the spread of deserts. Meanwhile, edge-locked forests can maintain soil and water, refine soil, increase ground vegetation cover, regulate climate, and conserve water, which not only can effectively alleviate the deterioration of the regional ecological environment but is also crucial for the development of sustainable local desert ecosystems in terms of economy, society, and culture (Jenkins and Schaap, 2018; Olschewski et al., 2018).

Edge-locked forests cannot grow without the necessary environment in which they exist, and soil is a crucial site of energy and material exchange in the ecosystem (Chai, 2018). Soil serves as the fundamental material for plant survival. It can provide conditions such as nutrition and environment needed for plant growth (Hansjürgens et al., 2018; Xu et al., 2013). In addition to being critical for plant growth, soil C, N, and P are essential markers of soil nutrient fertility (Cheng and Guo, 2024). Furthermore, their

stoichiometric relationships generate valuable insights into biogeochemical cycling and equilibrium mechanisms, which are vital for assessing soil quality and recognizing the coupling relationship between soil nutrients (Chen Q. et al., 2022; Zhang et al., 2019). Relevant research has demonstrated that forest and grass vegetation types and densities should be rationally configured while developing a windbreak, sand-fixing desert-locked forest, and grass belt. Several configurations of plantation forests significantly impact soil C, N, and P and their ecological stoichiometry. Yu et al. (2024) demonstrated that pure forests of mountain poplar (*Populus davidiana*) should be prioritized in vegetation restoration in Luoshan, Ningxia. Yu et al. (2022) examined five degraded vegetation communities in Karst and demonstrated the critical role that N supply plays in restoring degraded forest vegetation. Furthermore, soil C, N, and P stoichiometric characteristics were appreciably affected by soil horizons. Typically, surface soils have higher C content and lower C/N/P ratios, whereas the opposite is true for deeper soils (Dong et al., 2024). For plantation forests in the western region of Guangdong Province, Wu et al. (2024) described the vertical distribution of soil carbon (C), nitrogen (N), and phosphorus (P) nutrients. They also revealed that soil horizons substantially influenced the stoichiometric characteristics of soil C, N, and P. In their study of central Himalayan vegetation, Joshi and Garkoti (2023) showed that SOC, TN, and TP content decreased with increasing soil depth. Although there are similarities between the existing related studies, no consistent conclusions have been drawn, indicating that there are still differences in the ecological stoichiometric characteristics of soil C, N, and P in various configuration types and soil depths at the regional scale.

Soil particle size is one of the most crucial physical properties of soil (Bayat et al., 2017). It is strongly correlated with the nutrients found in soil (Yuan et al., 2017), and variations in the coarseness and fineness of its particles directly affect soil nutrient changes (Nkheloane et al., 2012). Furthermore, soil particles are important indicators for classifying soil desertification (Bogunovic et al., 2017). Average particle size, sorting coefficient, kurtosis, skewness, and fractal dimension have emerged as crucial markers to assess soil particle changes in studies about the properties of soil particle size distribution (Pan et al., 2020). In an investigation of different types of *Populus alba*, Li et al. (2024) revealed that *Populus alba* considerably increased soil nutrients and fine particulate matter.

Li X. L. et al. (2022) examined the variation characteristics of the fractal dimension of soil particles in red sand scrub sandpiles. They discovered that the fractal dimension had the same trend as fine particles, such as soil nutrients and clay meal particles. Gui et al. (2010) found a relationship between soil particle size distribution and elevation, plant community, soil pH, and moisture. Based on the previous research on the relationship between soil nutrients and soil particle size characteristics, this study aims to provide a reference for in-depth investigations into the composition of soil particles, the fractal dimension characteristics of these particles, and their interrelationships with C, N, P, and stoichiometric properties in the understory of edge-locked forests.

The Kubuqi Desert is the seventh-largest in China. The sand control measures of “locking in the north, blocking in the south, and cutting in the middle” have been used because of the topographical characteristics of the Kubuqi Desert. The Kubuqi Desert is 400 kilometers long from east to west, with an average width of 50 kilometers from north to south, covering a total area of more than 18,000 square kilometers and flowing southeastward as a whole due to the impact of more northwesterly winds. The “northern lock” is in the Kubuqi Desert north of the wind mouth place, leading to the formation of edge-locked forests. This forest belt tightly locates the desert’s edge, blocks the wind, and reduces the source of sand, improving the soil structure. Due to its unique geographic location, which is affected by rainfall and climate, the vegetation type of the edge-locked forest belt is diverse. The Desert Edge-locked Forests Project has become one of the elements of the typical management model. In this paper, six configurations of protection forests (*Salix psammophila*, *Elaeagnus angustifolia*, *Salix matsudana*, *Corethroedendron fruticosum* + *Salix psammophila*, *Caragana korshinskii* + *Populus simonii*, and *Elaeagnus angustifolia* + *Salix matsudana*) within the edge-locked forests in Kubuqi Desert were used as research objects. Systematic and in-depth analysis of the vertical differentiation of soil C, N, P, and ecological stoichiometric ratio and soil particle size characteristics of the 0–100-cm soil layer under protection forests of different configuration modes, this study’s conclusions can provide a scientific foundation for the biogeochemical cycle of soil C, N, and P in the Kubuqi Desert edge-locked forests. Meanwhile, the findings provide a scientific reference for the desert area’s vegetation restoration and improvement of the ecological environment. They also present a guide for constructing the local edge-locked forest vegetation. At the same time, the results can serve as a scientific reference for restoring and improving the ecological environment in desert regions. In addition, they provide advice on how to maintain local vegetation in edge-locked forests.

2 Materials and methods

2.1 Study area

The northern edge of the Kubuqi Desert, located in Ordos City, Inner Mongolia Autonomous Region, was selected as the study area

(Figure 1). The region is semi-arid and has a temperate continental monsoon climate. Wind and sand activities prevail from March to May. The average yearly temperature fluctuates between 5°C and 8°C with an average annual precipitation of 144–366 mm. The geomorphology type is dominated by fixed sandy land with flowing and semi-flowing dunes. The central tree species include *Salix psammophila*, *Elaeagnus angustifolia*, *Caragana korshinskii*, *Salix matsudana*, *Corethroedendron fruticosum*, *Populus simonii*, and other native species. The understory vegetation is primarily *Artemisia desertorum*, *Salsola collina*, *Psammochloa villosa*, and *Elymus dahuricus*.

2.2 Sample collection

Six different configurations (*Salix psammophila*, *Elaeagnus angustifolia*, *Salix matsudana*, *Corethroedendron fruticosum* + *Salix psammophila*, *Caragana korshinskii* + *Populus simonii*, and *Elaeagnus angustifolia* + *Salix matsudana*) of protection forest sample plots were selected in the study area. Considering the uneven distribution of herbaceous plants in the sample plots, three sample squares of 30 m × 30 m were established in every sample plot, and five soil samples were taken at equal distances along the diagonal of each sample square and mixed as one representative soil sample. The soil samples were undertaken using a soil auger at various depths: 0–10 cm, 10–20 cm, 20–30 cm, 30–40 cm, 40–50 cm, 50–60 cm, 60–70 cm, 70–80 cm, 80–90 cm, and 90–100 cm. Soil samples from each depth were mixed and placed in self-sealing bags, resulting in 180 soil samples (6 × 3 × 10). The gathered samples were then separated into two sections: one for determining soil nutrients and the other for analyzing soil particle size.

2.3 Determination of soil parameters

The soil particle size was measured using a laser particle sizer (Mastersize 2000; Malvern Instruments Ltd.) ranging from 0.01 μm to 2000 μm. The soil particle size findings were classified according to the United States Department of Agriculture (USDA) grading criteria, defining particles as clay (0–2 μm), silt (2–50 μm), and sand (50–2000 μm).

Soil samples were dried naturally before being sieved through a 0.149-mm mesh. The potassium dichromate method was employed to ascertain the soil SOC content, the TN was assessed with an automatic Kjeldahl nitrogen tester, and the molybdenum blue colorimetric method was used to measure TP (Bao, 2000).

2.4 Calculating the parameters for soil particle size

The Folk-Ward graphical approach was applied to calculate particle size parameters, such as mean particle size (d_0), standard

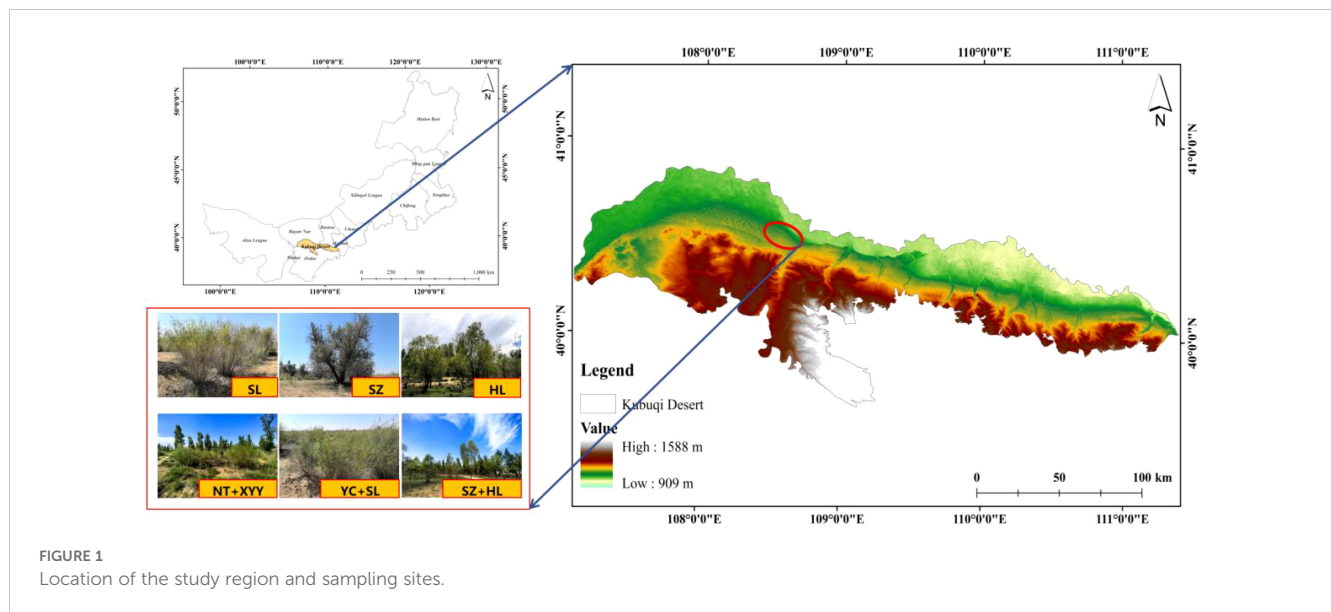


FIGURE 1
Location of the study region and sampling sites.

deviation (σ_0), skewness (SK), and kurtosis (K_g) (Folk and Ward, 1957). The calculation formula is expressed as follows:

$$\Phi = -\log_2 D$$

$$d_0 = \frac{1}{3} (\Phi_{16} + \Phi_{50} + \Phi_{84})$$

$$\sigma_0 = \frac{(\Phi_{84} - \Phi_{16})}{4} + \frac{(\Phi_{95} - \Phi_5)}{6.6}$$

$$SK = \frac{\Phi_{16} + \Phi_{84} - 2\Phi_{50}}{2(\Phi_{84} - \Phi_{16})} + \frac{\Phi_5 + \Phi_{95} - 2\Phi_{50}}{2(\Phi_{95} - \Phi_5)}$$

$$K_g = \frac{\Phi_{95} - \Phi_5}{2.44(\Phi_{75} - \Phi_{25})}$$

where D is the particle diameter, and Φ_x is the particle diameter corresponding to a cumulative volume fraction of $X\%$.

2.5 Parameters for soil fractal dimension (D) computation

Utilizing the method of Tyler and Wheatcraft (1989), the particle size volume distribution characterizes the soil fractal model, which is used to calculate fractal dimensions.

$$\frac{R_i^{3-D}}{R_{\max}^{3-D}} = \frac{V(r < R_i)}{V_T}$$

where R_i denotes the measured soil particle size; $R_{\max}$ is the maximum particle size; $V(r < R_i)$ is the soil's volume, which is smaller than the measured particle size; V_T is the sum of the volumes of the soil at each particle level; and D denotes the soil fractal dimension.

2.6 Data analysis

Microsoft Excel 2019 and SPSS 27.0 were used to organize the experimental data. Significant differences between soil nutrients and stoichiometric ratios under different configurations were analyzed via one-way ANOVA using Duncan's method for multiple comparisons. The LSD method was applied for multiple comparisons, with the significance level of the differences being $\alpha = 0.05$. R version 3.6.3 software "gplot2" package was applied to conduct the principal component analysis of soil factors under different configurations of edge-locked forests. The "stats" package was used to correlate soil C, N, and P contents and ecological stoichiometric ratios with particle size characteristics under different configurations of edge-locked forests. It was also used to draw correlation heat maps. Plotting was conducted using Origin 2021 software. The significance interval was defined as 95% level, and the graphs were reported as mean $\pm$ standard error.

3 Results

3.1 Characteristics of soil C, N, and P and their stoichiometry under different configurations of edge-locked forests

From the distribution of soil SOC, TN, TP and stoichiometric characterization levels under different configurations of edge-locked forests (Figure 2), soil SOC, TN, TP, C/N, C/P, and N/P in the study area were significantly different under different configuration types of edge-locked forests ($P < 0.05$). SOC and TN were considerably lower among the six configuration types. In contrast, SZ was significantly higher ($P < 0.05$) than others. Mixed forests (SL + YC, NT + XXY, HL + SZ), as well as SL, had higher TP ($P < 0.05$) than the other forest allocations. Overall, SOC was significantly higher ($P < 0.05$) under

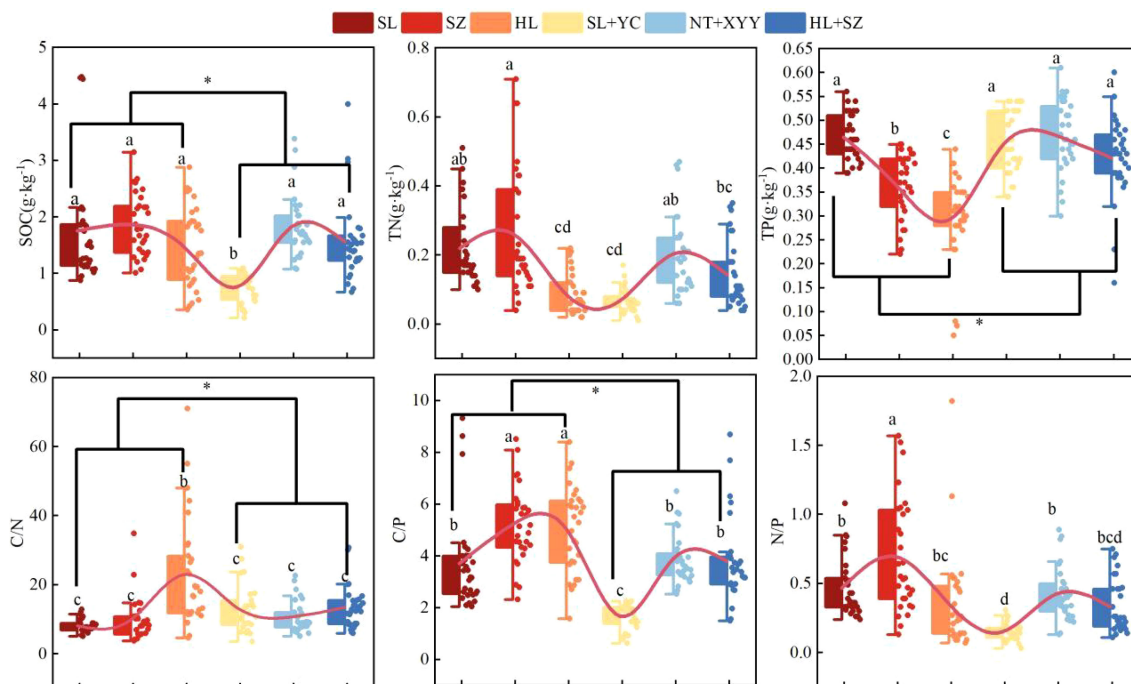


FIGURE 2

Changes in soil C, N, and P and their stoichiometric ratios among different configuration types. Different letters indicate significant differences ($P < 0.05$) in soil C, N, and P between different configuration types of lock-edge forests.

monocultures (SL, SZ, and HL) than under mixed forests (SL + YC, NT + XYY, HL + SZ). The higher SOC also caused significantly higher ($P < 0.05$) C/N and C/P under monocultures than in mixed forests. TN did not exhibit significant differences, and TP was considerably higher ($P < 0.05$) in mixed forests than in monocultures.

From the vertical distribution of soil SOC, TN, TP, and stoichiometric characteristics under different configurations of edge-locked forests (Figure 3), soil SOC, TN, TP, C/N, C/P, N/P, C/N, and N/P of the 0–100-cm soil layer under the six different configurations of edge-locked forests were all substantially different among different soil layers ($P < 0.05$). Furthermore, the overall content of SOC, TN, and TP gradually declined with increasing soil depth. However, the magnitude of the TP change was not evident. Soil SOC, TN, TP, and their stoichiometric ratios under different configurations demonstrated epimerization, where the nutrient content in the 0–20 cm surface soil was higher than that in the depth of 20–100 cm. In contrast, the epimerization of C/N was not as pronounced as that of C/P and N/P. Meanwhile, C/P and N/P under the different configurations of edge-locked forests reduced with increasing soil depth. In contrast, C/N displayed an opposite trend.

3.2 Characterization of soil particle composition and parameters under different configurations of edge-locked forests

The horizontal distribution of soil particle size under different configurations of edge-locked forests (Tables 1, 2) revealed that soil particle size composition in numerous edge-locked forest

configurations was basically the same, which primarily comprised sand, with the content of sand being about 76.13–99.09%. This trend was followed by silt with 0.64–23.16% and clay with the lowest content of 0.10–2.6%. From the distribution of silt and clay, SL, SZ, NT + XYY, and SZ + HL were substantially more abundant than HL and YC + SL, with SL and NT + XYY having the most silt and clay.

According to the vertical distribution of soil particle size under different configurations of edge-locked forests (Table 2), the vertical distribution patterns of soil particle size composition within the 0–100 cm soil layer varied among different configurations of edge-locked forests. These patterns can generally be categorized into three types. (1) As the soil layer becomes deeper, the content of clay and silt particles generally shows a change in decreasing, then increasing, and decreasing. Represented by SL and SZ + HL, clay and silt contents were significantly higher in the 50–70-cm layer than in all other layers, and the 20–30-cm layer has the lowest contents ($P < 0.05$). (2) There is no significant change in the grain levels with increasing soil layer depth. HL and YC + SL are represented. (3) As the soil layer becomes deeper, the content of coarse sand gradually increases, represented by SZ and NT + XYY.

From the characteristic-level distribution of soil particle size parameters under different configurations of edge-locked forests (Figure 4), the average soil M_z under the six configurations of edge-locked forests, SL, SZ, HL, YC + SL, NT + XYY, and SZ + HL, were 2.87, 2.51, 2.08, 2.38, 2.75, and 2.50, respectively. SL has a finer texture, and NT + XYY is second. The average S_d of the soil under the six configurations of SL, SZ, HL, YC + SL, NT + XYY, and SZ + HL in the edge-locked forests was 1.26, 0.75, 0.55, 0.57, 0.91, and 0.73, respectively. SL was poorly sorted, SZ, NT + XYY, and SZ + HL were moderately sorted, and HL and YC + SL were well sorted.

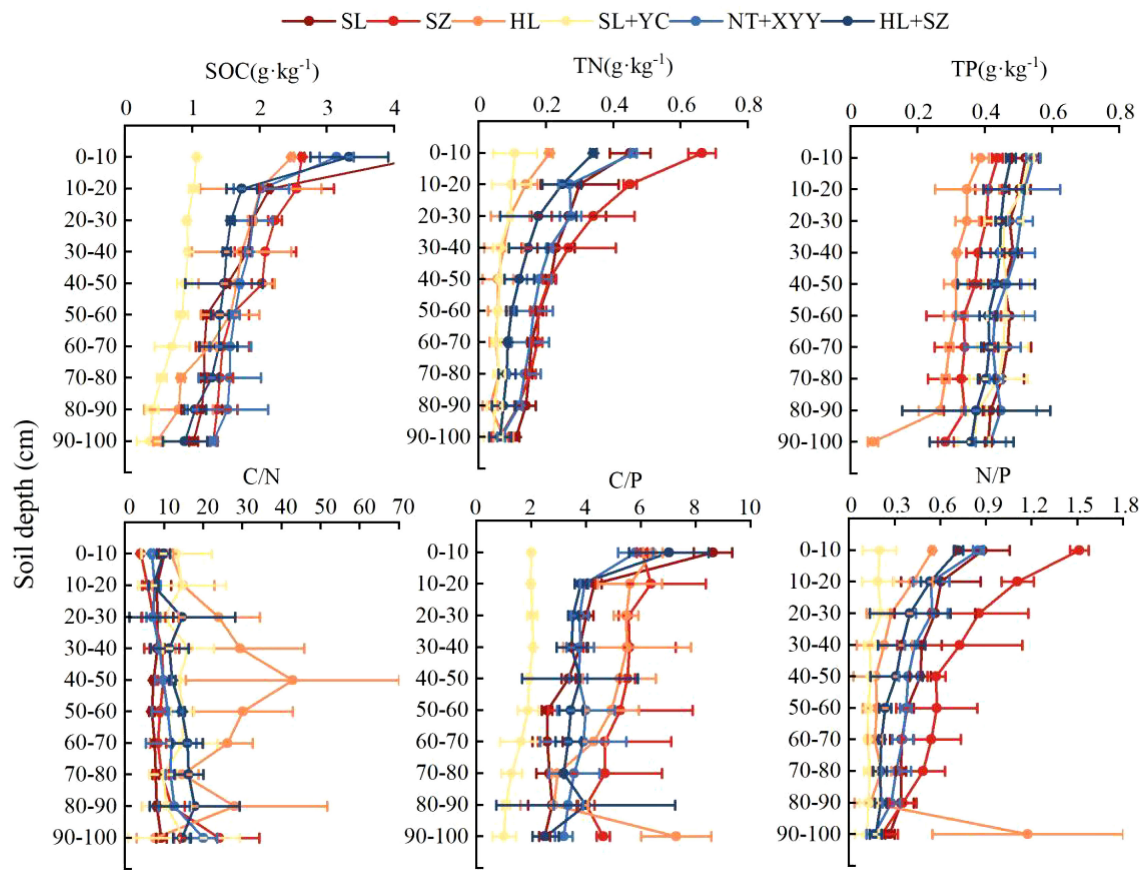


FIGURE 3 Distribution of soil C, N, and P and their stoichiometric ratios with soil depths in different configurations.

The average soil *K_g* values under the six configurations of SL, SZ, HL, YC + SL, NT + XYX, and SZ + HL edge-locked forests were 1.69, 1.34, 0.98, 0.98, 1.32, and 1.24, respectively. HL and YC + SL were moderate, SZ, NT + XYX, and SZ + HL were sharp and narrow, and SL exhibited very sharp and narrow. The average soil *SK* values under the six configurations of SL, SZ, HL, YC + SL, NT + XYX, and SZ + HL in the edge-locked forests were 0.43, 0.22, 0.07,

0.07, 0.26, and 0.19, respectively. HL and YC + SL were nearly symmetrical, HL, NT + XYX, and SZ + HL showed positive bias, and SL demonstrated very positive bias.

From the vertical distribution of soil particle size parameter characteristics under the different configurations of edge-locked forests (Figure 4), the average particle size and fractal dimension displayed the same change trend with an increase in soil depth. The

TABLE 1 Basic information on different configuration types of edge-locked forests.

Type	Latitude (N°)	Longitude (E°)	Main vegetation	Vegetation cover	Site conditions
SL	40°61′	108°58′	<i>Artemisia ordosica</i> , <i>Phyllostachys propinqua</i> , <i>Grubovia dasyphylla</i> , <i>Incarvillea sinensis</i> , <i>Sophora alopecuroides</i> , <i>Agriophyllum pungens</i>	>50%	fixed sandy land
SZ	40°58′	108°61′	<i>Corispermum mongolicum</i> , <i>Cynanchum chinense</i>	>50%	
HL	40°58′	108°60′	<i>Corispermum mongolicum</i> , <i>Artemisia ordosica</i> , <i>Phragmites australis</i> , <i>Echinops gmelini</i>	>50%	
YC+SL	40°51′	108°58′	<i>Amorpha fruticosa</i> , <i>Artemisia ordosica</i> , <i>Corispermum hyssopifolium</i> , <i>Artemisia desertorum</i> , <i>Phyllostachys propinqua</i>	>45%	
NT+XYX	40°53′	108°64′	<i>Setaria viridis</i> , <i>Corispermum hyssopifolium</i> , <i>Artemisia desertorum</i> , <i>Salsola collina</i>	>65%	
SZ+HL	40°55′	108°63′	<i>Corispermum mongolicum</i> , <i>Echinops gmelini</i> , <i>Artemisia ordosica</i>	>40%	

SL is *Salix psammophila*, SZ is *Elaeagnus angustifolia*, HL is *Salix matsudana*, YC + SL is *Corethroedron fruticosum*+*Salix psammophila*, NT + XYX is *Caragana korshinskii*+*Populus simonii*, and SZ + HL is *Elaeagnus angustifolia* + *Salix matsudana*.

TABLE 2 Characteristics of soil particle size distribution under different configurations of lock-edge forests.

Type		SL	SZ	HL	YC+SL	NT + XYZ	SZ + HL
Soil Depth (cm)	Soil Particle Size (%)						
0–10	Clay	0.37 ± 0.07 b	0.27 ± 0.07 c	0.17 ± 0.05 d	0.14 ± 0.04 d	0.61 ± 0.12 a	0.20 ± 0.04 cd
	Silt	13.20 ± 1.71 b	7.62 ± 0.93 c	2.00 ± 0.21 de	1.22 ± 0.18 e	23.26 ± 2.68 a	6.98 ± 0.55 c
	Sand	86.42 ± 1.74d	92.12 ± 1.00 c	97.83 ± 0.24 ab	98.64 ± 0.22 a	76.13 ± 2.75 e	92.82 ± 0.57 c
10–20	Clay	0.29 ± 0.08 c	0.39 ± 0.07 b	0.14 ± 0.05 d	0.11 ± 0.04 d	0.58 ± 0.13 a	0.16 ± 0.05 d
	Silt	4.89 ± 0.62 c	7.08 ± 0.49 b	1.19 ± 0.28 e	0.80 ± 0.12 e	17.47 ± 1.14 a	2.43 ± 0.57 d
	Sand	94.81 ± 0.7 d	92.54 ± 0.55 e	98.67 ± 0.33 ab	99.09 ± 0.16 a	81.95 ± 1.24 f	97.41 ± 0.61 b
20–30	Clay	0.31 ± 0.05 b	0.26 ± 0.07 bc	0.12 ± 0.04 e	0.13 ± 0.04 e	0.59 ± 0.09 a	0.16 ± 0.04 de
	Silt	3.25 ± 0.28 c	4.00 ± 0.58 b	0.77 ± 0.18 f	0.85 ± 0.16 f	15.04 ± 0.96 a	1.65 ± 0.22 e
	Sand	96.43 ± 0.32 c	95.73 ± 0.57 d	99.11 ± 0.22 a	99.02 ± 0.2 a	84.37 ± 1.01 e	98.19 ± 0.26 c
30–40	Clay	0.51 ± 0.08 a	0.43 ± 0.08 a	0.19 ± 0.05 a	0.21 ± 0.07 a	0.51 ± 0.08 a	0.35 ± 0.07 b
	Silt	5.25 ± 0.65 c	7.07 ± 1.19 b	1.07 ± 0.16 e	1.09 ± 0.19 e	12.73 ± 0.87 a	3.35 ± 0.51 d
	Sand	94.24 ± 0.71 c	92.5 ± 1.24 d	98.74 ± 0.20 a	98.69 ± 0.25 a	86.76 ± 0.9 e	96.3 ± 0.57 b
40–50	Clay	1.68 ± 0.32 a	0.50 ± 0.09 b	0.15 ± 0.03 e	0.33 ± 0.07 cd	0.47 ± 0.07 b	0.44 ± 0.08 bc
	Silt	19.55 ± 2.3 a	7.22 ± 0.48 c	0.80 ± 0.09 e	1.50 ± 0.20 e	7.68 ± 0.60 c	9.47 ± 1.97 b
	Sand	78.77 ± 2.53 e	92.28 ± 0.52 c	99.05 ± 0.12 a	98.17 ± 0.26 ab	91.85 ± 0.66 c	90.09 ± 2.00 d
50–60	Clay	2.6 ± 0.50 a	0.45 ± 0.10 b	0.10 ± 0.03 cd	0.19 ± 0.05 cd	0.37 ± 0.05 bc	0.30 ± 0.08 bcd
	Silt	22.34 ± 2.25 a	5.66 ± 0.98 b	0.64 ± 0.09 e	1.09 ± 0.14 e	3.73 ± 0.35 c	6.16 ± 2.08 b
	Sand	75.06 ± 2.60 e	93.88 ± 1.06 d	99.27 ± 0.12 a	98.72 ± 0.19 a	95.9 ± 0.39 c	93.54 ± 2.15 d
60–70	Clay	1.67 ± 0.24 a	0.42 ± 0.12 b	0.24 ± 0.05 c	0.20 ± 0.05 c	0.41 ± 0.07 b	0.47 ± 0.09 b
	Silt	18.99 ± 2.21 a	3.82 ± 0.77 c	1.50 ± 0.19 d	1.10 ± 0.14 d	3.81 ± 0.33 c	8.31 ± 1.83 b
	Sand	79.34 ± 2.41d	95.76 ± 0.89 b	98.26 ± 0.24 a	98.7 ± 0.19 a	95.78 ± 0.39 b	91.22 ± 1.90 c
70–80	Clay	1.05 ± 0.41 a	0.42 ± 0.11 b	0.24 ± 0.06 cd	0.15 ± 0.07 d	0.45 ± 0.10 b	0.33 ± 0.07 bc
	Silt	14.94 ± 6.69 a	3.06 ± 0.49 bc	1.57 ± 0.25 bc	1.00 ± 0.28 c	3.62 ± 0.87 bc	3.17 ± 0.43 bc
	Sand	84.01 ± 7.08 a	96.53 ± 0.59 a	98.2 ± 0.30 ab	98.86 ± 0.34 a	95.93 ± 0.95 b	96.50 ± 0.50 ab
80–90	Clay	1.01 ± 0.26 a	0.37 ± 0.07 b	0.16 ± 0.04 d	0.18 ± 0.05 d	0.28 ± 0.10 cd	0.27 ± 0.07 cd
	Silt	14.07 ± 3.34 a	2.46 ± 0.29 b	1.03 ± 0.16 c	1.08 ± 0.15 c	1.96 ± 0.39 bc	2.17 ± 0.32 bc
	Sand	84.91 ± 3.53 c	97.17 ± 0.35 b	98.81 ± 0.20 a	98.74 ± 0.19 a	97.77 ± 0.49ab	97.56 ± 0.38 ab
90–100	Clay	0.45 ± 0.13 b	0.59 ± 0.08 a	0.20 ± 0.05 d	0.20 ± 0.05 d	0.37 ± 0.08 c	0.66 ± 0.10 a
	Silt	11.71 ± 1.52 a	3.28 ± 0.25 c	1.06 ± 0.15 e	1.22 ± 0.16 e	2.33 ± 0.30 d	4.15 ± 0.40 b
	Sand	87.84 ± 1.64 e	96.13 ± 0.32 c	98.73 ± 0.20 a	98.57 ± 0.21 a	97.3 ± 0.38 b	95.19 ± 0.50 d

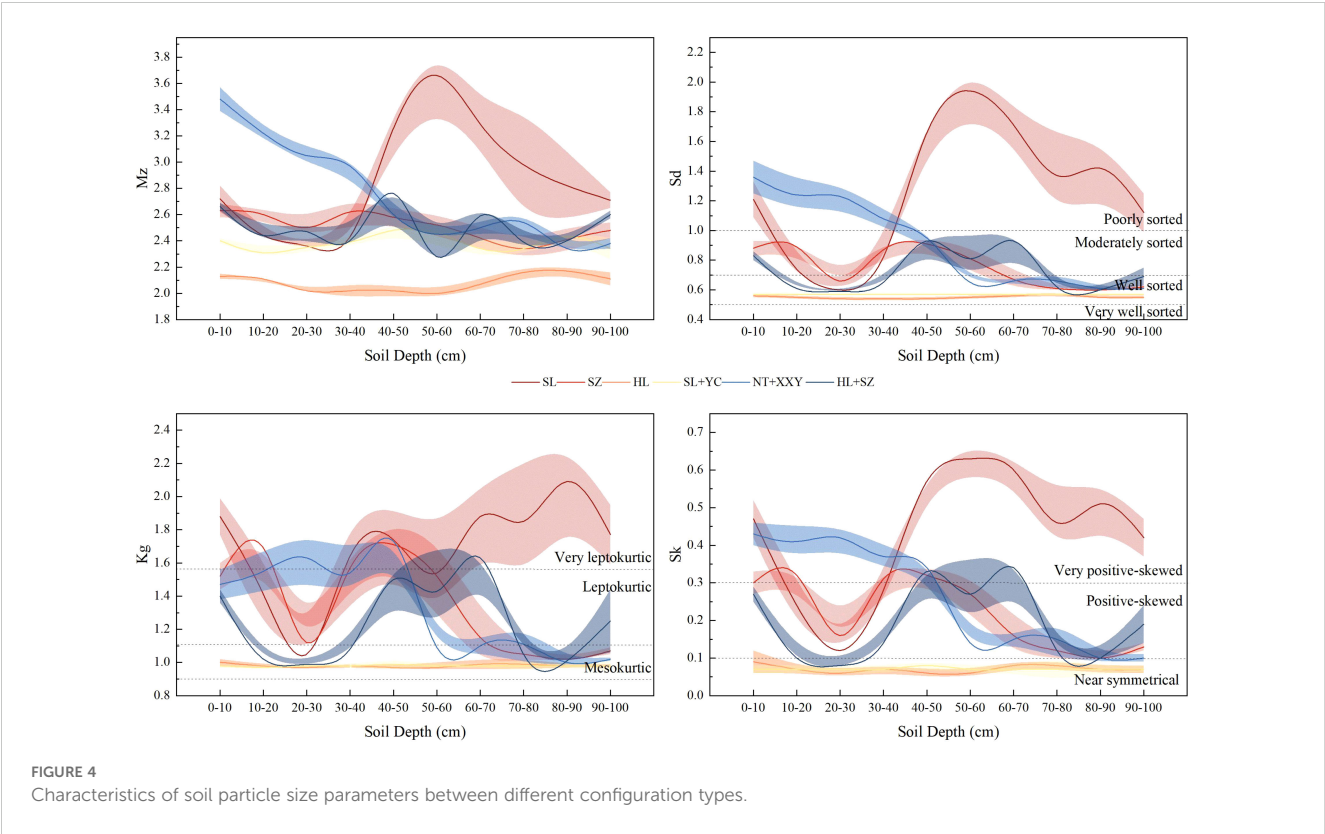
The average ± standard error is shown above. Different letters indicate significant ($P<0.05$) differences in grain size composition between different configuration types of edge-locked forests.

overall sortability of the soil profiles was moderately favorable, with nearly symmetrical positive skewness and moderately narrow kurtosis, except for SL. Notably, the HL, SL + YC skewness and kurtosis did not vary significantly ($p>0.05$) between the soil layers.

The characteristic-level distribution of the fractal dimension of soil particle size under the different configurations of edge-locked forests (Table 3), except for SL, reveals that the fractal dimension was highest in the NT + XYZ configuration type and lowest in the HL and YC + SZ configuration types. It was significantly different ($p<0.05$) from the other configurations. This outcome indicates that NT + XYZ has improved dramatically the soil structure and particle size distribution. Soil particle size fractal dimension varied on the vertical gradient in different configuration types of edge-locked forests but also displayed a certain pattern. The soil fractal dimension decreased with increasing soil depth in NT+XYZ edge-locked forests, while all other configurations of edge-locked forests showed a general trend of decreasing, then increasing and then decreasing with increasing soil depth, with a minimum in the 20-30 cm soil layer, increasing to a maximum and then decreasing around the 40-50 cm soil layer, and then increasing to the 90-100 cm soil layer.

3.3 Relationships between soil C, N, and P contents and ecological stoichiometric ratios and particle size characteristics in different configurations of edge-locked forests

In the principal component analysis, the 95% confidence interval distribution demonstrated differences in the effects of different configurations of edge-locked forests on soil indicators (Figure 5), with significant differences between SL and NT + XYZ and the other groups in the six groups and insignificant differences and similarities between HL, SL + YC, and HL + SZ stands. The first and second principal components explained 53.9% and 23.2%, respectively, which explained a total of 77.1% of the variation pattern of soil factors, and could comprehensively reflect the dominant factors affecting the status of each soil indicator. The largest contributions of PC1 were Sd, Mz, silt, and D, indicating that PC1 was primarily related to Sd, Mz, silt, and D of different configurations of edge-locked forest soils. N/P, SOC, and TN were the largest contributors to PC2, revealing that PC2 was



primarily related to N/P, SOC, and TN of different configurations of edge-locked forest soils. The different configurations of edge-locked forests overlapped on PC1 and PC2; therefore, the soil conditions of the six different configurations of edge-locked forests could not be completely differentiated by PC1 and PC2, and the various properties of the soils were closely related.

Correlations and asterisks respond to significance via color changes in the heat map. Pearson’s correlation analysis demonstrated (Figures 5, 6) that soil C, N, and P content and

ecological stoichiometric ratios differed in correlation degree between different configuration types and particle size characteristics. In addition, SOC positively correlated with Sk, Silt, *Sd*, and *Kg* ($P<0.05$) while demonstrating a negative connection with sand and C/N. Soil TN was highly associated with all indicators. Soil TP exhibited a highly significant positive correlation with TN and clay ($P<0.001$). In addition, TP presented a significant positive correlation with *Sd*, *D*, and *Mz* ($P<0.01$) while showing a highly significant negative correlation with the C/N

TABLE 3 Characteristics of soil fractal dimension distribution under different configurations of edge-locked forests.

Type		SL	SZ	HL	YC + SL	NT + XYY	SZ + HL
Soil Depth (cm)	D						
0-10		2.11 ± 0.03 d	2.03 ± 0.05 cd	1.88 ± 0.05 ab	1.83 ± 0.06 bcd	2.22 ± 0.03 a	1.99 ± 0.03 bc
10-20		2.01 ± 0.05 e	2.08 ± 0.03 ab	1.82 ± 0.06 c	1.78 ± 0.06 d	2.19 ± 0.04 ab	1.89 ± 0.07 d
20-30		2.00 ± 0.03 e	1.99 ± 0.04 cd	1.77 ± 0.06 d	1.80 ± 0.06 d	2.19 ± 0.02 ab	1.88 ± 0.04 d
30-40		2.10 ± 0.03 d	2.10 ± 0.03 a	1.86 ± 0.05 bc	1.89 ± 0.05 b	2.16 ± 0.03 b	2.02 ± 0.04 b
40-50		2.34 ± 0.03 b	2.12 ± 0.03 a	1.81 ± 0.04 c	1.97 ± 0.04 a	2.11 ± 0.02 c	2.12 ± 0.03 a
50-60		2.41 ± 0.03 a	2.09 ± 0.04 ab	1.73 ± 0.06 d	1.88 ± 0.04 b	2.04 ± 0.02 de	2.03 ± 0.06 b
60-70		2.34 ± 0.03 b	2.05 ± 0.07 bc	1.91 ± 0.04 a	1.88 ± 0.04 b	2.06 ± 0.03 d	2.11 ± 0.04 a
70-80		2.25 ± 0.08 c	2.04 ± 0.05 c	1.92 ± 0.05 a	1.81 ± 0.12 cd	2.06 ± 0.05 d	2.01 ± 0.04 b
80-90		2.25 ± 0.05 c	2.01 ± 0.03 cd	1.84 ± 0.05 bc	1.87 ± 0.05 bc	1.95 ± 0.07 f	1.96 ± 0.05 c
90-100		2.13 ± 0.05 d	2.10 ± 0.02 a	1.87 ± 0.04 ab	1.89 ± 0.04 b	2.01 ± 0.04 e	2.13 ± 0.03 a

The average ± standard error is shown above; different letters indicate that *D* differs significantly ($P<0.05$) between different configuration types of edge-locked forests.

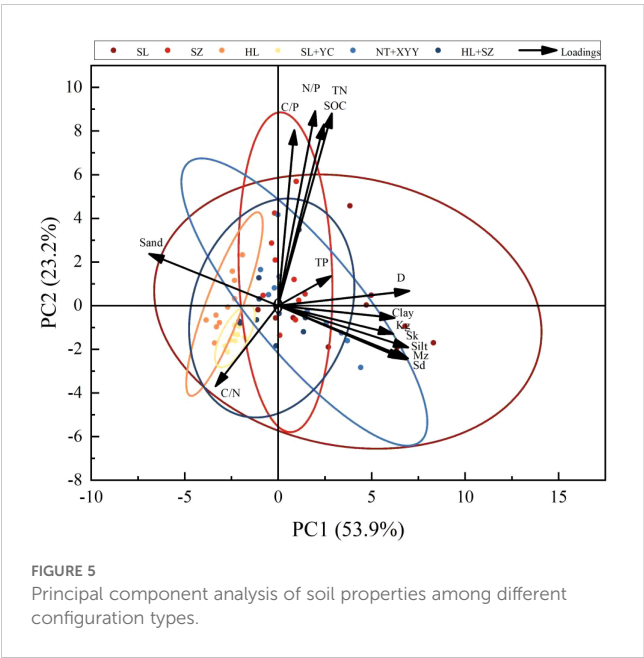


FIGURE 5
Principal component analysis of soil properties among different configuration types.

($P<0.001$). C/N was significantly and positively correlated with sand ($P<0.01$) and had no significant relationship with C/P. Furthermore, C/N exhibited a significant negative correlation with each of the other indices. C/P was significantly and

positively correlated solely with SOC. In contrast, N/P and TN exhibited highly significant positive correlations ($P<0.001$). N/P showed a highly significant negative correlation with sand and C/N ($P<0.001$), no significant relationship with Mz and TP, and a significant positive correlation with all other indicators.

4 Discussion

4.1 Effects of different configurations of edge-locked forests on soil carbon, nitrogen, and phosphorus and their stoichiometric characteristics

Soil C, N, and P content and stoichiometric ratios were strongly impacted by vegetation type (Huang et al., 2024). The average soil C, N, and P contents of the six configuration types of edge-locked forests ranged from 0.77 to 1.86 g·kg⁻¹, 0.07 to 0.26 g·kg⁻¹, and 0.2 to 0.6 g·kg⁻¹, respectively. According to the grading standard of the second soil nutrient census in China (National Soil Census Office, 1998), the soil C, N, and P contents were grade 4~5 (0.2~0.6 g·kg⁻¹), grade 6 (<6.0 g·kg⁻¹), and grade 6 (<0.5 g·kg⁻¹), respectively. This result suggests that in the lock border forests in this study area, the soil was relatively deficient in C and N, the organic C sequestration capacity of the soil was low, and the P content of the soil was

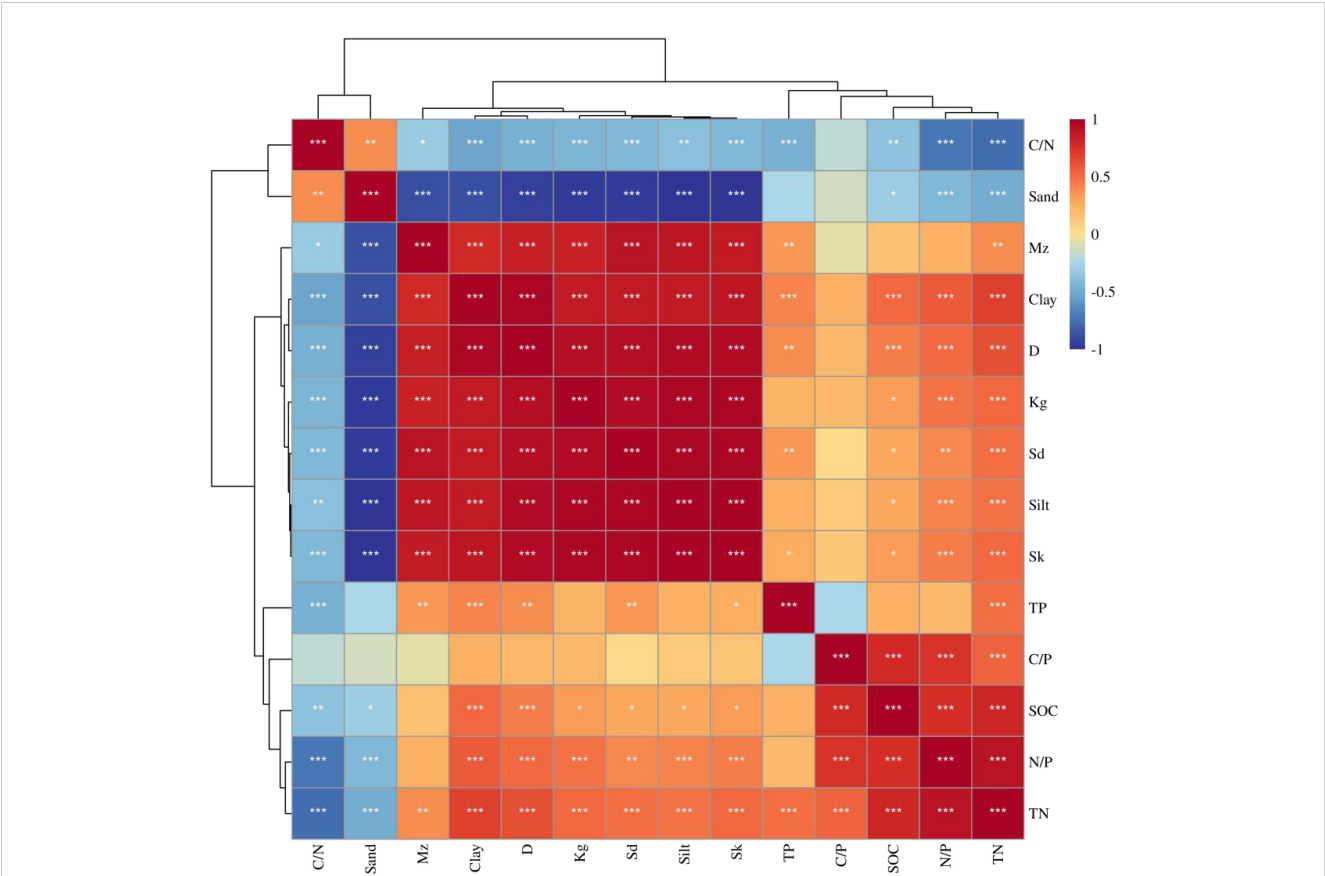


FIGURE 6
Heat map of Pearson correlation between soil properties among different configuration types. (At the 0.05, 0.01, and 0.001 levels, respectively, significant correlation is indicated by the symbols *, **, and ***).

average. This phenomenon may be caused by the site being a fluvial sandy area with sandy and fragile soils, greatly affecting soil organic C sequestration. Meanwhile, the main component analysis results indicated that soil SOC and TN exerted the greatest influence on the PCA2 axis (Figures 5, 6), suggesting that the soil in this research area is more likely to be limited by C and N elements.

In previous studies, soil C, N, and P soil nutrients are important components primarily affected by apoplastic decomposition, root secretions, soil mineralization, and microbial activities (Gao et al., 2014). There were differences in the C, N, and P contents of soils under six different configuration types of lock-edge forests in the Kubuqi Desert. The SOC and TN contents of SZ, NT + XYY, and SL soils were considerably higher than those of other configuration types. This trend is consistent with the results of Wang et al. (2022) and Li et al. (2022) in the transition zone along the Yellow River. This phenomenon is primarily attributed to differences in the quantity and quality of root secretions in different configuration types, as well as the varying rates of decomposition of apoplastic material in other vegetation, which causes differences in the impact on nutrients (Yang et al., 2021; Angst et al., 2017). At the same time, climate change and human activities can also lead to changes in the quality and quantity of apoplastic and root inputs, which in turn can affect below-ground biogeochemical processes in forest ecosystems (Abay et al., 2024). The root system of SL has strong sprouting power and a wide distribution range. The decomposition of its apoplastic material is relatively slow, and it gradually accumulates on the soil surface to create an organic layer and increase the organic C content of the soil. Its root secretion comprises N compounds, which can provide a nitrogen source for soil microorganisms and enhance the soil (Yang et al., 2018). SZ is also affected by plant apoplastic decomposition, root secretions, and larger biomass and more C fixed by photosynthesis compared to SL (Shi et al., 2022). In NT + XYY, NT rhizobacteria play a crucial role in nitrogen fixation, and the pairing of the two significantly affects soil improvement (Wen et al., 2024). Another essential factor is the abundance of plant species, high biomass, and high vegetation cover in SZ, NT + XYY, and SL (Table 1). Related studies have shown that increased herbaceous biomass and vegetation cover can enable soil C and N biological processes and surface soil microbial activity, leading to higher surface soil SOC and STN contents (Lu et al., 2023). The study findings demonstrated that the soil mixtures under the six configuration types of lock-edge forests were higher in total P than the single species, with NT + XYY being the most pronounced. Li et al. (2022) are consistent with this research's results because the synergistic effect of mixed forests can more effectively convert insoluble P into effective P in the soil than a single tree species (Qin et al., 2024). In addition, the complementary distribution of root systems in mixed forests can fully use P at different levels in the soil and increase the soil's total P content through root turnover and apoplastic return (Du et al., 1995).

The C, N, and P ratios of the soils under six different configuration types of lock-edge forests in the Kubuqi Desert showed variations. The average C/N, C/P, and N/P contents of the soils of the six configuration types of lock-edge forests ranged from 8.14 to 22.95 g·kg⁻¹, 1.68 to 5.22 g·kg⁻¹, and 0.15 to 0.69 g·kg⁻¹. C/N

fluctuated around the national average (11.90), and the C/P and N/P ranges were considerably lower than the national average (61 and 5.2) (Tian et al., 2010). It indicates that nitrogen is the restricting nutrient element for the growth of edge-locked forests in the region, but P is more effective. The C/N indicator primarily evaluates C and N cycling in the soil. When the mean C/N ratio is high, the decomposition rate of its organic matter is slow; conversely, when the mean C/N ratio is low, soil decomposition releases N pigments, which increase the N elemental content of the soil (Wang et al., 2020). HL, HL + SZ, and SL + YC soil C/N were higher than the average among the six configuration types, probably because of the slow decomposition of soil organic matter in these three edge-locked forests, limiting the rate of nutrient cycling. Although SL, SZ, NT + XYY soil C/N was lower than the mean value, these three configurations of lock-edge forest soil nitrogen transformation and accumulation efficiency were higher. Generally, vegetation growth is N-limited when N/P < 10 (Tyler and Wheatcraft, 1989). Vegetation at this site may have been constrained by soil N during growth. Of the six types, SL + YC soil C/P and N/P were considerably lower than the other configurations, indicating that the soil P effectiveness of SL + YC forest was much higher than that of the different tree species. At the same time, the degree of limitation by N was stronger compared to the other five forest stands. This is also consistent with the Wu et al. (2024). Therefore, nitrogen fertilizers and exogenous nitrogen inputs should be rationally applied to improve nutrient limitation and increase soil fertility for ecological restoration of the area's edge-locked forests.

The SOC and TN of the understory soil of the edge-locked forests at this site were associated with the C/P and N/P contents (Figure 5). The soil SOC and TN exhibited highly significant positive associations with both soil C:P and soil N:P, as well as with soil TN. This phenomenon is similar to the findings of Chen Y. et al. (2022) because of the synchronized response of C and N in the understory soil of this site to the same environmental factor, and there is a close coupling relationship (Zhang et al., 2024). It reveals that the soil C/N of the edge-locked forests at this site is relatively spatially stable, confirming the dynamic equilibrium theory of ecological stoichiometry.

4.2 Changes in soil C, N, and P and their stoichiometry with soil depth in different configurations of edge-locked forests

Soil depth significantly impacts soil C, N, and P levels and stoichiometric ratios (Li et al., 2021). In this research, the C and N contents of the soil under six different types of edge-locked forests in the Kubuqi Desert decreased with the increase of soil depth and exhibited the phenomenon of "surface aggregation." The primary reason behind this was that the surface soil was subjected to the return of nutrients by the external environmental factors and the vegetation litter, as well as the aggregation of plant and animal microbial residues, which resulted in an accumulation of nutrients in the surface soil (Chapin et al., 2011; Logah et al., 2020). There was no discernible variation in P concentration with increasing depth.

This trend agrees with the findings of Sun et al. (2023) in a previous investigation in Southwest China. Similar conclusions were obtained for related studies in the northern grasslands of China (Lu et al., 2023). Relative to soil C and N content, the P content did not vary much in different soil horizons, primarily because the slow biotransformation rate during the cycling of P. Microbial activities in the soil have less influence on P. The biological role of P in the soil is relatively small (Da Silva et al., 2022).

Soil C/P and N/P steadily dropped with the increase in soil depth, agreeing with the findings of Zhang et al. (2020). This outcome may be ascribed to the decrease of soil SOC and TN contents caused by soil microbial activity and the downward leaching migration of organic matter (Wang et al., 2021). The opposite pattern of C/N variation was consistent with Yang et al.'s vertical profile pattern of soil in Jinji'er forest in Maowusu Sandland (Yang and Liu, 2019). Except for HL, the differences in C/N among the various soil layers were insignificant, indicating that the C/N values were relatively stable, reflecting the synergistic response of C and N elements to changes in the external environment. This is similar to the findings of Ma et al.'s investigation in the Baiyu Mountain area (Ma et al., 2023).

4.3 Effect of different configurations of edge-locked forests on soil particle composition and parameter characteristics

The soil particle size was primarily sand under the different configurations of edge-locked forests. At the same time, the silt and clay contents of SL and NT + XYY were considerably higher than the other four configurations due to the depositional effect of the protective forests (Chen et al., 2020). It has been shown that silt and clay can be suspended over long distances by wind (Qin, 2009). The site is windy, and the silt and clay grain size is small and susceptible to wind transport (Lou et al., 2022). This finding indicates that SL and NT + XYY have the best protective effects. The vertical distribution characteristic pattern of soil particle size composition differs, SZ and NT + XYY, with the increase in soil depth, soil clay, powder, average particle size, and the gradual decrease in sorting coefficient. The decrease in fine particles with soil deepening is due to the ability of the edge-locked forest canopy to intercept wind-sand movement, resulting in the accumulation of fine particulate debris in the event of blocked settlement (Hupy, 2004). This finding is consistent with the study's results by Dong et al. (2022). Tao and Zhang (2015) demonstrated that soil particle size fractal dimension can be used to reflect soil fertility status and the degree of soil exposure to wind and sand. The fractal dimension of soil particle size and mean particle size revealed positive connections with clay and silt concentration but negative associations with sand content (Ya et al., 2019). Similar findings were obtained in the present study (Figure 5), which indicated that fractal dimension and mean particle size could reflect the particle coarseness and fineness of the soil in the edge-locked forests, and fractal dimension increased with clayey and powdery grain content and decreased with sandy grain content. At the same time, higher soil silt and clay can keep SOC accumulating and increase the nitrogen input.

Furthermore, the characteristics of soil C, N, and P and their stoichiometric relationships are significantly influenced by soil texture (Wang et al., 2009). A correlation study found that SOC and TN had a substantial positive correlation with silt and clay but a negative correlation with sand. This is comparable to the findings of Tian et al., who concluded that soil texture significantly affects SOC and STN content (Tian et al., 2017) and that higher soil silt and clay can lead to the continual buildup of SOC (Wu et al., 2017). Plant production is stimulated by improving soil water-holding capacity and increasing soil C and N inputs. Soil C/N in the understory of the edge-locked forests was strongly and positively connected with powder grain content and considerably and negatively correlated with sand grain content, a finding contrary to the study of Marty et al. (2017). In comparison, the correlation of soil N/P with chalk and sand in the understory of the edge-locked forests was the opposite, suggesting that rough soil texture increases soil N/P.

5 Conclusions

In this paper, the following main conclusions were drawn through an in-depth analysis of the soil C, N, and P contents of six configuration types of edge-locked forests in the Kubuqi Desert, as well as their ecological stoichiometric characteristics and the vertical distribution characteristics of particle size.

1. The limiting nutrient element for the growth of edge-locked forests in the region is N. Of the 6 configuration types, the SOC and TN contents in the top 3 are SZ, NT + XYY, and SL. With the increase of soil depth, the soil C, N, C/P and N/P under the lock-edge forest gradually decreased, and the decrease of P content was not obvious. C/N showed the opposite pattern. and the phenomenon of epimerization of C and N contents was evident.

2. The area primarily comprised sand. The silt and clay contents of SL and NT + XYY are significantly higher than the other four configurations. Vertical distribution patterns of soil particle size varied under different configurations of edge-locked forests. SOC, TN, D, and Mz had substantial positive correlations with silt and clay concentration but negative correlations with sand content.

In summary, vegetation type, soil depth, and soil texture affect soil C, N, P, and stoichiometric characteristics. SZ and SL can be used as the dominant tree species in the Kubuqi Desert edge-locked forests, and the NT + XYY mixed forest configuration pattern has the most evident soil improvement effect.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

Author contributions

XC: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Software, Validation,

Writing – original draft, Writing – review & editing. HZ: Funding acquisition, Project administration, Resources, Validation, Methodology, Supervision, Writing – review & editing. MY: Methodology, Supervision, Validation, Writing – review & editing. HW: Conceptualization, Methodology, Supervision, Visualization, Writing – review & editing. CX: Investigation, Methodology, Software, Writing – review & editing. YC: Investigation, Software, Writing – review & editing.

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Rainfall distribution variability controls surface but not belowground litter decomposition in a semi-arid shrubland

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Introduction: Rainfall patterns are expected to become increasingly erratic as a result of global climate change, with more intense but less frequent rainfall events leading to an increased occurrence of drought events. This process may lead to significant declines in vegetation cover and subsequent increases in soil erosion, consequently accelerating the bury of detached litter by soil deposition and the mixture of residues from different plant species. Responses of litter decomposition to increasing rainfall variability in distribution and subsequent litter mixing or soil cover have scarcely received attention.

Methods: To fill this gap in our knowledge, we analyzed the influence of rainfall variability, soil cover, and litter mixing on shrub-species litter decomposition in a semi-arid shrubland. We explored the effects of redistributing the frequency and amount of precipitation on surface and belowground decomposition of litter from two separate or mixed predominant shrubs.

Results: Decomposition of belowground litter was consistently higher than that of surface litter over the entire field-incubation process. Mass loss significantly decreased in surface litter but not in belowground litter due to the lower frequency and larger amount of precipitation compared to the control treatment. Furthermore, exclusion of 30% precipitation had no significant effects on decomposition of either surface or belowground litter. We observed stronger synergistic effect for belowground litter mixture relative to surface litter mixture of the two shrubs, especially in the hotter months over the 5-month incubation.

Discussion: These findings support that rainfall variability in terms of distribution pattern rather than in the amount controls the litter decomposition on the soil

surface in the semi-arid shrubland. Meanwhile, soil burial or litter mixing have greater effects on litter decomposition, individually or jointly. Together, our results highlight the need to consider rainfall distribution variability and incorporate soil-covering and litter-mixing as driving factors of organic matter turnover in drylands.

KEYWORDS

decomposition constant, precipitation frequency, precipitation amount, mass loss, mixed effect

1 Introduction

The decomposition of plant material in arid and semi-arid ecosystems plays an important role in regulating carbon storage and nutrient cycling because global drylands account for approximately 30% of net primary production (Field et al., 1998; Austin et al., 2004). A notable characteristic of drylands is the relative shortage of natural rainfall which is considered to constrain plant material decomposition (Throop and Archer, 2009). However, a growing body of evidence suggests that responses of litter decomposition are inconsistent with changes in rainfall at the local scale (Yahdjian et al., 2006; Dirks et al., 2010; Li et al., 2016). Some previous observations suggested that litter decomposition rates correlate well (Yahdjian et al., 2006; Brandt et al., 2007) or do not correlate with seasonal or annual precipitation (Vanderbilt et al., 2008; Gallo et al., 2009). This discrepancy was partially attributed to the fact that current studies in drylands have mostly focused on the effects of cumulative rainfall rather than rainfall variability, which is one of the dominant components of climate change (Joly et al., 2019). Rainfall variability is usually exhibited as a complex pattern including annual or seasonal variations in the total amount of the precipitation, intensity, interval, and timing of rainfall events, etc (Smith, 2011; Beier et al., 2012). In terms of a given cumulative precipitation quantity, it is unknown whether the effects of large and infrequent precipitation events on inducing and sustaining litter decomposition are equivalent to smaller but more frequent rainfall events. However, responses of litter decay to rainfall variability scarcely received attention, because of the difficulty in simulating the complexity of natural rainfall regimes in drylands (Joly et al., 2019).

Ongoing global rainfall changes in arid regions are expected to become more variable, with less frequent rainfall events and subsequent increases in the durations of drought (Easterling et al., 2000; IPCC et al., 2013). One of the predictable consequences of high rainfall variability in arid and semi-arid ecosystems is that surface litters and upper soils undergo longer periods of drying before being rewetted by a following rainfall pulse (Austin et al., 2004). These extended durations of dry periods between pulses thereby may constrain litter decomposition by shortening accumulative time that litter has adequate moisture for activities of microbial decomposers and detritivores. Such response patterns

have been demonstrated that large and infrequent rainfall pulses reduce litter decomposition (Whitford et al., 1986); but may vary with rainfall pulse sizes, as, for example, has been shown for the non-linear responses of decomposition to increasing cumulative rainfall quantity under low rainfall frequencies (Joly et al., 2017b). However, robust evidence of the interaction between pulse size and frequency on decomposition in drylands remains limited to a very small number of microcosm experiments with restricted scope for generalizability and validity (Whitford et al., 1986; Austin et al., 2009; Joly et al., 2017a, 2019).

Extended durations of dry periods induced by high rainfall variability can have a direct impact on plant growth in drylands, and, hence, can lead to significant declines in vegetation cover and subsequent increases in soil erosion (Austin et al., 2004; Austin, 2011). This process no doubt accelerates the covering of detached litter by soil deposition and the mixing of litters from different plant species (Hewins et al., 2013; Lee et al., 2014), especially under the shrub canopy or in some aeolian accumulation areas (Garner and Steinberger, 1989; Austin, 2011). Several studies have demonstrated that litter mixtures often decompose at a different rate relative to the average rate of the individual litters (Berglund and Ågren, 2012). A synthesized study concluded that 67% of studies on litter mixture decomposition was non-additive, namely, the decomposition rate of the mixture is either faster or slower than the average rate of the individual litters (Gartner and Cardon, 2004). These non-additive effects mainly resulted from accelerated or decelerated decomposition of certain species litters. Simultaneously, decomposition of litter was considered to be accelerated after soil-covering (or soil-mixing) because such process may buffer litter from high frequency moisture oscillations in the soil relative to that on the surface, thereby increasing the opportunity for microbially-mediated decomposition (Hewins et al., 2013; Lee et al., 2014; Joly et al., 2017a). Moreover, moisture oscillation in soil is heavily dependent upon rainfall pulse size and frequency (Austin et al., 2009). Unfortunately, little is currently known about how increases of rainfall variability affects litter decomposition under conditions of soil-covering or litter mixtures, and uncovering these processes can provide new insights into how litter decay responds to ongoing rainfall changes in arid regions.

In this study, we quantified the effects of rainfall variability on surface and belowground (simulated soil-covering) litter

decomposition in semi-arid shrubland of northern China. Litters of two dominant shrubs and their litter mixture were incubated in the field, where the frequency and amount of natural rainfall was artificially altered in a growing season. The specific objectives of the present study were to address three guiding research questions: 1) How does increased rainfall variability or decreased rainfall amounts affect dry mass loss of litter in semi-arid shrubland? 2) Does belowground litter decompose faster than surface litter under conditions of simulated soil-covering? 3) If the decomposition rate of the litter mixture is consistent with the sum of the individual litter?

2 Materials and methods

2.1 Study site

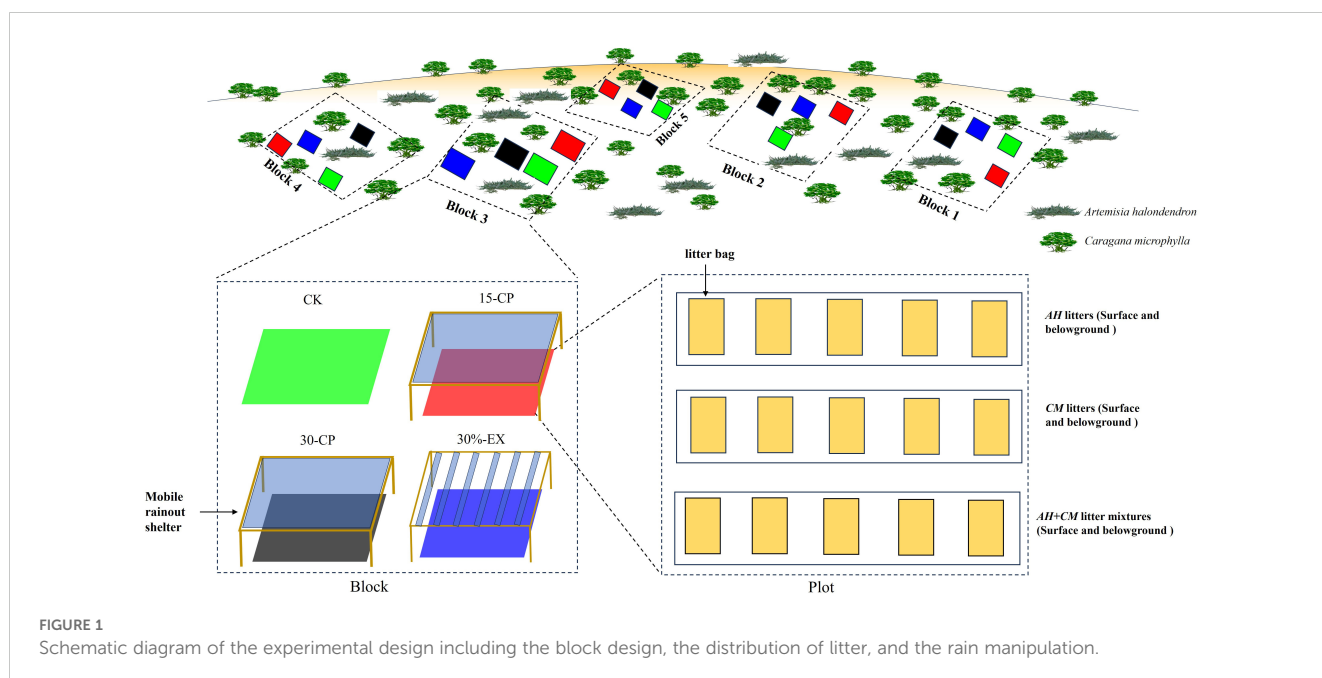
The study was carried out at Naiman Desertification Research Station in Horqin Sand Land, Chinese Academy of Sciences (NDRS, Inner Mongolia, China, 42°56'26"N, 120°43'05"E, 358 m altitude). Mean annual temperature in the area is 6.4°C, with monthly averages ranging from a minimum of -13.1°C in January to a maximum of 23.7°C in July. The yearly average solar radiation is 5200 MJ/m², while the total yearly sunshine duration is about 2946 h. The mean annual precipitation is 362 mm, nearly 70 - 80% of which falls between April and October. During the growing season, approximately 58.7% of rainfall events are ≤ 5 mm and contribute only 12.6% of the total rainfall amount, while 9.6% of large events with rainfall > 20 mm account for 45.0% of the total rainfall (Yue et al., 2016). The soils are light yellow in color, very infertile, and sandy with a coarse texture and loose structure (Su et al., 2006). In general, the maximum sand content (1 - 0.05 mm) in the soils of the study site is 90%, with organic matter and total N contents of less than 1.0 g kg⁻¹ and 0.13 g kg⁻¹, respectively (Zhou et al., 2008). The

vegetation is characterized by shrubland of *Artemisia halodendron* and *Caragana microphylla*, with scattered trees and windbreak tree belts of *Populus* spp.

2.2 Experimental design, treatments, and sampling

The incubation experiment was performed in a relatively flat shrubland of NDRS, using the litterbag method from May to October 2016. Twenty plots of 1.5×1.5 m² were scatteredly set up in bare soil areas between shrubs with a 1-m wide buffer zone at least around each plot to avoid the shade by shrubs. The herbaceous plants in the plots were artificially pulled up to minimize soil disturbance prior to the beginning of the experiment. A random block design was used in which there were five blocks subjected to each of four rainfall repackaging treatments, including CK, 30%-EX, 15-CP, and 30-CP (Figure 1). CK treatment was remained naturally with ambient precipitation. 30%-EX treatment means 30% of the ambient precipitation was intercepted by mobile rainout shelters. In treatment 15-CP, the ambient precipitation was totally intercepted by mobile rainout shelters but collected in a container. When the amount of collected precipitation equal to or exceed 15 mm, it was artificially sprinkled into the soils under the corresponding shelter of 15-CP treatment. Similar method was carried out in 30-CP treatment where the amount of collected precipitation was managed to equal to or exceed 30 mm. Prior to the experiment, soils in all the blocks were wetted to 75% of field capacity to avoid any initial differences in soil moisture. Soil moisture (0 - 15 cm) was monitored about every 15 days using a portable Time-Domain Reflectometry (TDR) during the experimental period.

We performed precipitation repackaging treatments with two types of mobile rainout shelters (1.8 m × 1.8 m, 0.60 m mean height, 20° inclination), which had roofs made of transparent



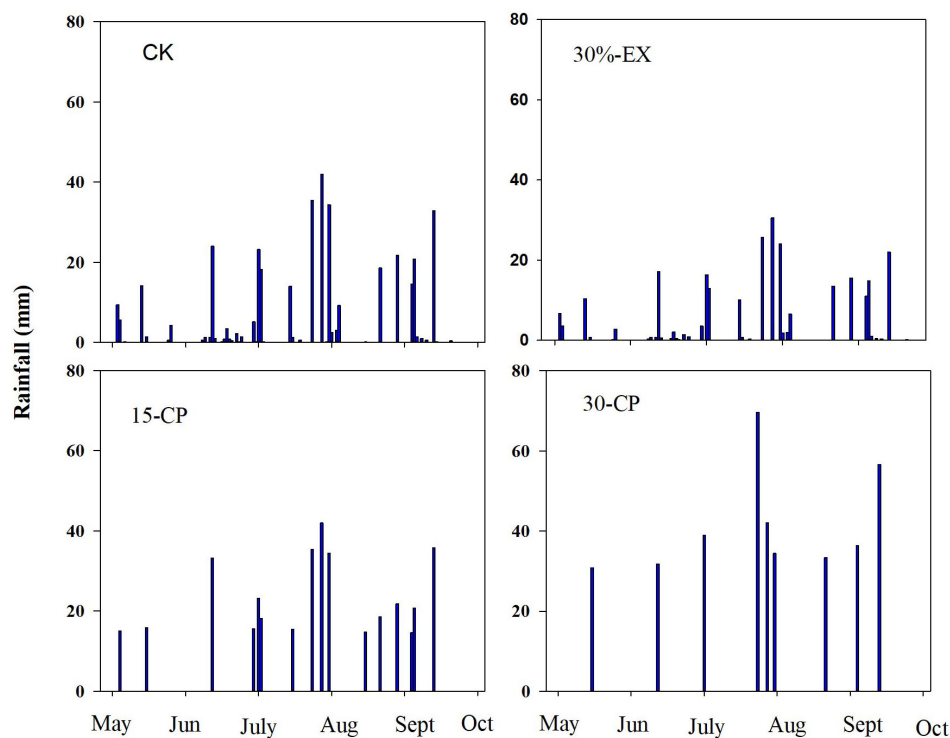


FIGURE 2

Rainfall distribution and amount in repackaging precipitation treatments during the experimental period. 15-CP, pulse size of repackaged ambient precipitation ≥ 15 mm; 30-CP, pulse size of repackaged ambient precipitation ≥ 30 mm; 30%-EX, 30% of the ambient precipitation was intercepted by rain-exclusion shelters; CK, untreated ambient precipitation.

polycarbonate sheets for 15-CP and 30-CP treatments but V-folded transparent polycarbonate bands (with 1.8 m length and 0.09 m width) for 30%-EX treatment, respectively (Figure 1). For the rainout shelters above the plots of 30%-EX treatment, we used six bands of V-folded transparent polycarbonate as the roof at a distance from each other of 25 cm to intercept 30% of natural rainfall. For the rainout shelters above the plots of 15-CP and 30-CP treatments, we used a 1.8 m $\times$ 1.8 m transparent polycarbonate sheet as the roof to totally intercept the natural rainfall (Yahdjian and Sala, 2002). Shelter sides remained open always to maximize air movement and minimize temperature and relative humidity artefacts. To minimize the solar radiation interception above the plots, rainout shelters were set up only before rainfall events and removed instantly after rain. Meanwhile, shelters were put on the target plots at night or on overcast days to avoid the adverse impacts of off-guard rainfall.

Throughout the experimental period, ambient accumulation precipitation in the study area was 375 mm. Under repackaging precipitation treatments, incoming rainfall varied from 0.2 mm to 42 mm (46 events and 375 mm of total precipitation) in the CK treatment, from 0.1 mm to 31 mm (46 events and 262.5 mm of total precipitation) in the 30%-EX treatment, from 15 mm to 42 mm (16 events and 375 mm of total precipitation) in the 15-CP treatment, and from 31 mm to 70 mm (9 events and 375 mm of total precipitation) in the 30-CP treatment (Figure 2).

In October 2015, freshly senesced leaf litters of *A. halondendron* (AH) and *C. microphylla* (CM) were collected directly from the

plants instead of on the soil surface. To minimize heterogeneity in litter chemistry, all plants of the two species were sampled in a small area of the shrubland. The litters were cleaned and dried at 60°C to a constant weight. Then, 15.0 g of each leaf litter of the two individual species and a litter mixture with equal proportions of the two species (AH-CM mixture, 7.5 g AH and 7.5 g CM) were enclosed in 10 $\times$ 15 cm nylon net bags. Litterbags on the soil surface were sewed with a 5-mm mesh size on the upper layer and a 1-mm mesh size on the lower layer, while belowground litterbags were sewed with a 1-mm mesh size on both layers. This combination maximized solar radiation interception aboveground and minimized soil contamination and loss of litter material (Austin et al., 2009). In May 2016, leaf litterbags of each type were buried belowground at an 8-cm depth (simulating the cover of detached litter by soil deposition in the Horqin Sand Land) and placed on the soil surfaces of the 20 plots. A total of 600 litterbags (five replicates $\times$ four treatments $\times$ three litter types $\times$ five collections $\times$ two positions) were prepared for this experiment (Figure 1). Litterbags were collected regularly every 30 days from May to October 2016. At each collection date, 120 bags were collected from the 20 plots for three litter types and transported to the laboratory where litters were separated from the bags, cleaned to remove any extraneous organic material, and weighed after drying at 60°C for 48 h. After the dry weight was measured, the samples were finely ground in a laboratory mill, and a portion of the litter was converted to ash to determine the ash-free dry weight of each sample. The ash-free dry mass was used for statistical analyses.

2.3 Chemical analysis of initial litter

Leaf litters were dried at 70°C and finely ground in a laboratory mill prior to chemical analysis. Carbon was determined by oxidation with a mixture of potassium dichromate and sulphuric acid, while nitrogen was measured by the semi-micro Kjeldahl method. P concentrations were determined colorimetrically using the ammonium molybdate method, after acid digestion (Sparks, 1996) and lignin was measured gravimetrically following extraction with 72% H₂SO₄ and ashing of acid detergent fiber residue (Dence, 1992). Condensed tannin concentration (% in dry matter) was extracted by adding butanol-HCl and ferric reagents to yield red anthocyanidins, and measuring absorbance at 550 nm (Porter et al., 1986). Ash was determined by a muffle furnace with litter samples burning at 550°C to a constant weight (Wang et al., 2019).

2.4 Data calculation and analysis

The remaining dry mass was calculated as the percentage of initial litter mass. The decomposition constant, k , was determined for all the treatments using the following equation:

$$\ln(M_t/M_0) = -kt$$

where M_0 is the initial mass, M_t is the mass remaining at given collection date t , and k represents an integrated measure of decomposition over a certain period time. We examined the non-additive effects of the AH-CM litter mixture by comparing the measured (MMR) and expected (EMR) litter mass remaining. EMR was calculated as the means of weighed mass remaining of individual species by their mass proportion in litter mixture for corresponding treatment. The relationship between MMR and EMR was compared with 1:1 line, with deviations from the 1:1 line indicating non-additive effects. The litter mixing effect (LME) was quantified as $(MMR-EMR)/EMR \times 100\%$. Positive or negative LME values indicate antagonistic or synergistic effects, respectively.

One-way ANOVA was performed for multi-comparisons of the significant differences in initial litter chemistry among different litters. We used four-way ANCOVA to detect differences between precipitation repackaging, positions, litter types, collection dates, and their interactions in the remaining mass, with the block number as a covariate. For all ANOVAs, R^2 values were computed for each term by dividing the sum of squares by the total sum of squares. One-way ANOVAs were performed to detect the decomposition constant (k) variations for precipitation repackaging, positions, and litter types, followed by Duncan's *post hoc* tests. Differences between MMR and EMR for the AH-CM litter mixture were detected by paired sample T-tests. We used three-way ANCOVA to detect the effects of precipitation repackaging, positions, collection dates, and their interactions on EMR of the AH-CM mixture, with the block number as a covariate. Prior to analysis, data were tested for normality using Shapiro-Wilk's test. Response variables that did not show a normal distribution were log transformed. A level of $P < 0.05$ was accepted as significant. Data are presented as means $\pm$

standard errors. All statistical analyses were conducted using SPSS 17.0 for Windows (SPSS Inc., Chicago, Illinois, USA).

3 Results

Generally, dry mass loss of leaf litter was significantly affected by rainfall repackaging, collection dates, positions, and litter types, which explained a total of 82.8% of the variance ($p < 0.001$, Supplementary Table S1). Over the 5-month incubation period, the mean mass loss across litter types and positions for the 15-CP and 30-CP treatments did not differ from each other but both were significantly lower than that in control treatment (Figure 3A). In contrast, we observed minimal effects of precipitation exclusion on mass loss. The mean mass remaining across litter types and positions was 34.2% in control plots and 31.7% in 30%-EX plots at the 5-month collection. Accordingly, no significant differences were detected in decomposition constant, k , between the control and 30%-EX treatments. The interaction of rainfall repackaging and litter position was also significant, indicating that the effects of rainfall repackaging on decomposition were position independent ($p < 0.01$, Supplementary Tables S1, S2). Belowground decomposition was unaffected by rainfall repackaging, while surface litter decomposition was significantly inhibited, by 4.68% and 8.07% in the 15-CP and 30-CP treatments, respectively, relative to the control treatment.

We observed that belowground leaf litters decomposed more quickly than surface litters (Figure 3B). The averaged mass of belowground remaining litters across litter type and rainfall repackaging treatments was 14.6% lower than that of surface litters over the 5-month incubation period. As a result, the mean decomposition constant, k , of belowground litters was significantly higher than that for surface litters (Figures 4A, B, Supplementary Table S2). Furthermore, interactions between litter position and collection dates were significant ($p < 0.001$, Supplementary Table S1), suggesting that litter decomposition rates between surface and belowground varied asynchronously with time. The mass loss of belowground litter collected at 1 month was a mean of 19.6% higher, but was 10.6% higher than those on the surface after 5-month incubation.

Decomposition rates were significantly different among litter types (Figure 3C). CM litter decomposed more slowly than AH litter. CM litter has higher nitrogen contents, lignin and condensed tannin content than AH litter, and lower C:N ratios than AH litter (Table 1). Additionally, the litter type significantly interacted with the position ($p < 0.05$, Supplementary Table S1). We observed that k values of AH and AH-CM mixture for belowground litter decomposition were significantly higher than that of CM (Figure 5), whereas no significant difference were detected in the decomposition constant, k , for surface litter decomposition among litter types.

The measured mass remaining was significantly lower than the expected mass remaining of AH-CM litter mixtures as paired sample T-test ($t = -9.46$, $n = 199$, $p < 0.001$), suggesting a non-additively

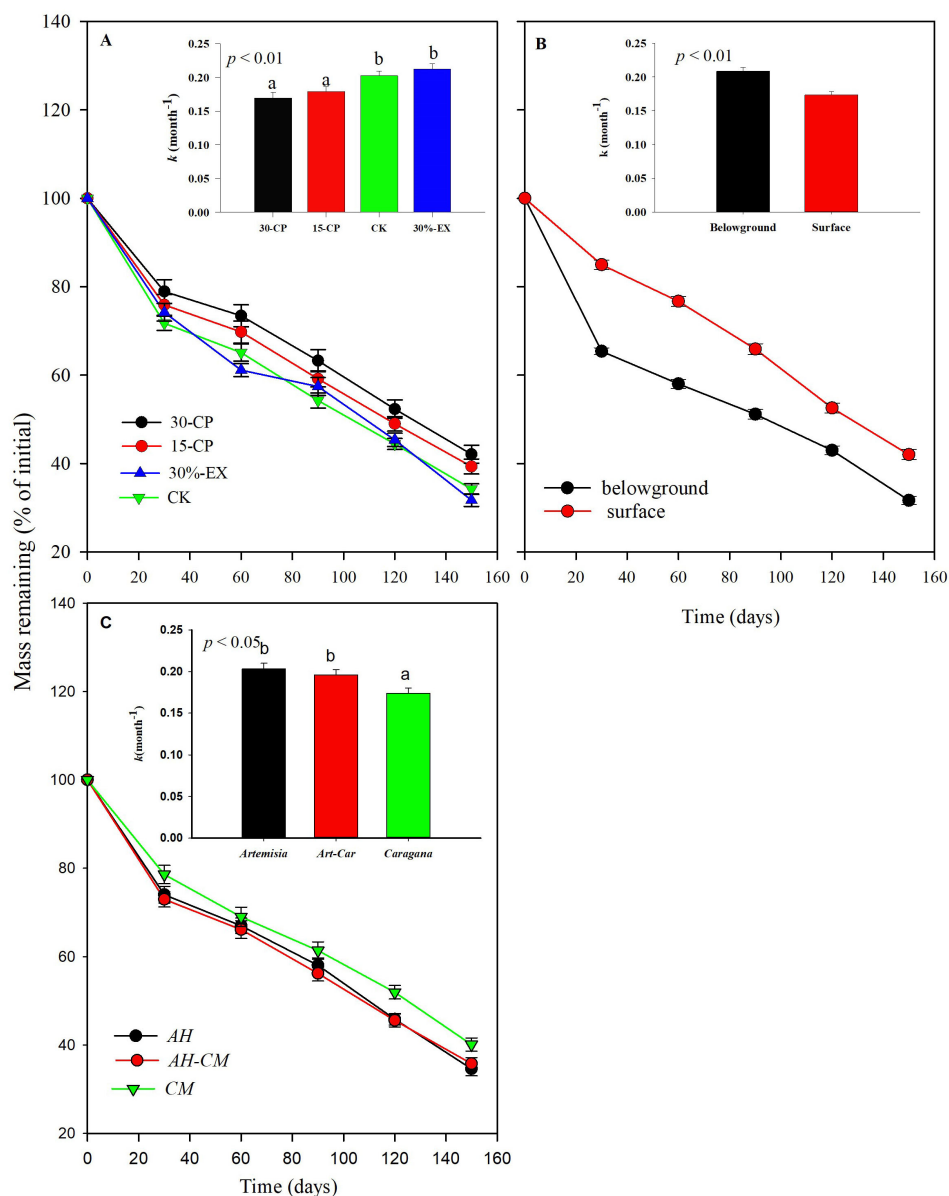


FIGURE 3

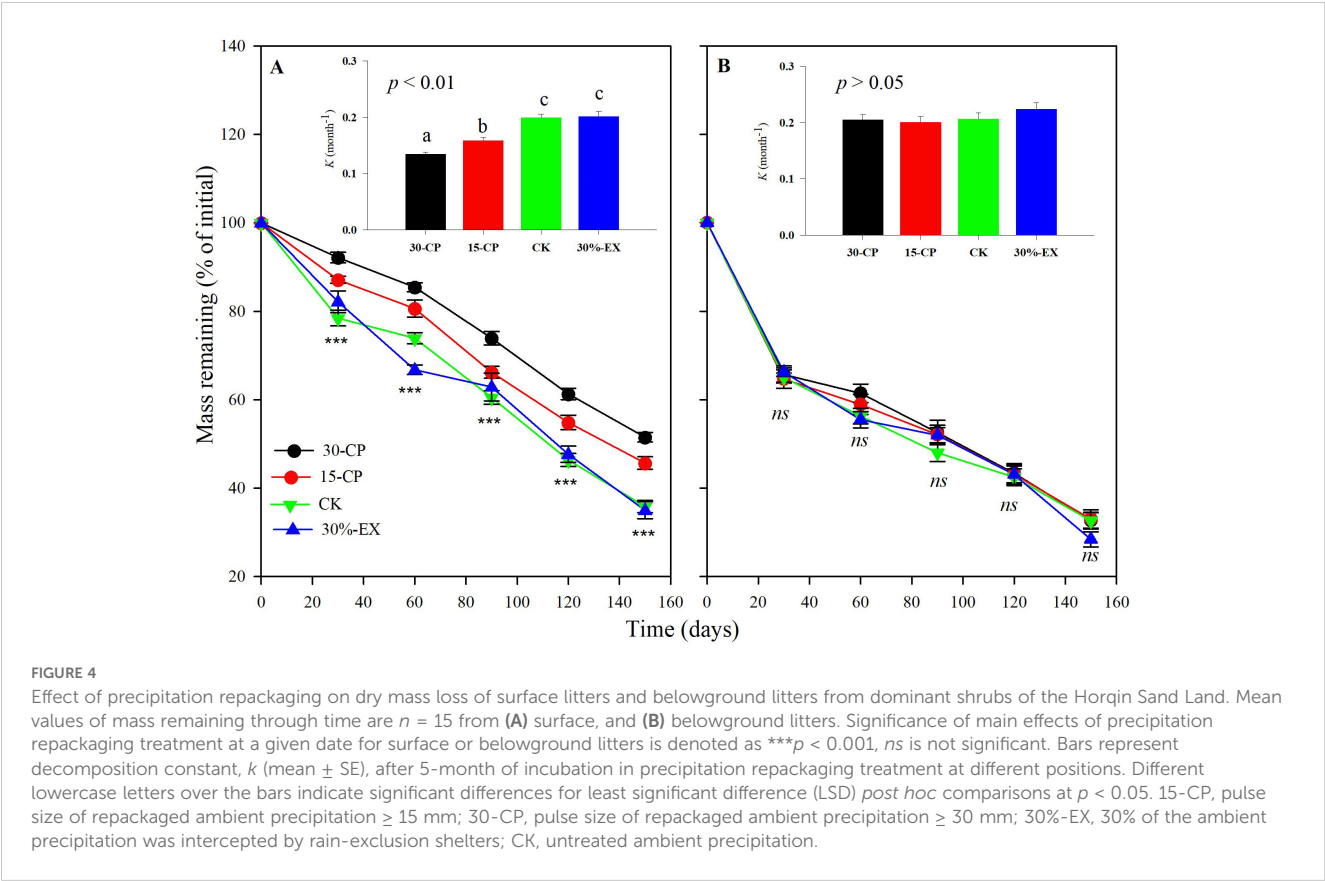
Mass of leaf litters from dominant shrubs in Horqin Sand Land remaining (mean $\pm$ SE) over time, for precipitation repackaging (A, $n = 30$), litter position (B, $n = 60$), and litter type (C, $n = 40$) treatments. Bars represent the decomposition constant, k (mean $\pm$ SE), after 5-month of incubation for a given treatment. Different lowercase letters over the bars indicate significant differences determined by least significant difference (LSD) *post hoc* comparisons at $p < 0.05$. 15-CP, pulse size of repackaged ambient precipitation ≥ 15 mm; 30-CP, pulse size of repackaged ambient precipitation ≥ 30 mm; 30%-EX, 30% of the ambient precipitation was intercepted by rain-exclusion shelters; CK, untreated ambient precipitation.

synergistic effect of litter mixing on decomposition. Although only 29.4% of variance was totally explained by the main effects and their interactions, ANCOVA analysis with the block number as a covariate revealed that litter-mixing effects were significantly affected by litter position, and the interaction between litter position and collection date (Supplementary Table S3). More synergistic effects were frequently found for the belowground litter mixture, with 84% of AH-CM mixtures decomposing faster than expected over the 5-month incubation. In contrast, approximately 73% of AH-CM mixtures on the soil surface decomposed faster than expected over the 5-month incubation. Additionally, significant differences were

detected in litter-mixing effect between surface and belowground litters at 2-, 3-, and 4-month collection times (Figure 6).

4 Discussion

Litter decomposition is a fundamental process of biogeochemical cycles (Cusack et al., 2018; Vitousek, 1982), which are influenced by both extrinsic factors (temperature, precipitation and disintegrators) and intrinsic factors (litter quality) (Robinson, 2002; Luo et al., 2010). As expected, we observed significant differences in dry mass loss in



leaf litter among the three litter types in the present study. With higher lignin and condensed tannin contents, CM litter had the lowest decomposition rate among the three litter types over the entire incubation period, suggesting that decomposition was primarily inhibited by litter recalcitrant compounds. However, litter type explained a limited amount of variance (1.53%). Regardless of collection dates which accounted for 60.33% of the variance, rainfall variability and litter position explained 3.74% and 17.22% of the variance, respectively. Although several researches suggested that litter quality plays a more important role in regulating litter

decomposition than environmental factors (Aerts et al., 2003; Cornwell et al., 2008), our results indicated that extrinsic factors (e.g., precipitation and soil-covering) probably exerted a great influence on litter decomposition in the semi-arid shrubland.

4.1 Variation between surface and belowground decomposition

Consistent with previous studies (Austin et al., 2009; Liu et al., 2015), belowground decomposition was more rapid than surface decomposition for the three litter types studied here, indicating that soil-covering enhanced litter decomposition in the semi-arid shrublands to some certain degree. However, the result contrasts with the reports that litter decomposition on the soil surface is equal to or faster than that of soil-covered litter in drylands (McBride et al., 2023). Photodegradation was considered as the main drive to facilitate litter decomposition on the soil surface in arid regions. Regardless, soil-covering may physically abrade litter and buffers litters from temperature and moisture oscillations following rain pulses. Several studies have demonstrated that plant litters covered by mineral soil may be subject to milder temperature and moisture compared to the surface litters (Lee et al., 2014; Zhou et al., 2016). This process may facilitate the growth of bacterial decomposers by altering the microclimate around litter material, as suggested by Hewins et al. (2013), who found increases in bacterial lipid biomarkers and decrease in the relative importance of the fungal biomarker around buried litters. Consequently, a lower frequency of

TABLE 1 Initial chemical composition of the three litter types used in decomposition experiments Data are means ± SE, n = 5.

	<i>A.halodendron</i>	<i>C. microphylla</i>	AH-CM
C%	45.6 ± 0.13c	47.0 ± 0.04a	46.4 ± 0.1b
N%	1.9 ± 0.04c	2.5 ± 0.3a	2.2 ± 0.03b
P%	0.22 ± 0.04a	0.14 ± 0.00c	0.17 ± 0.05b
Lignin%	9.9 ± 0.3c	16.0 ± 0.21a	13.1 ± 0.13b
condensed tannin%	0.89 ± 0.02c	1.89 ± 0.01a	1.38 ± 0.03b
N:P	9.0 ± 0.2c	17.8 ± 0.2a	12.9 ± 0.3b
C:N	23.6 ± 0.5a	18.8 ± 0.2c	20.9 ± 0.3b
Lignin:N	5.1 ± 0.1c	6.4 ± 0.1a	5.9 ± 0.1b

AH-CM denote mixed leaf litter in a 1:1 ratio of *A. halodendron* and *C. microphylla*. Different lowercase letters within rows indicate significant differences ($p < 0.05$) among different litter sources.

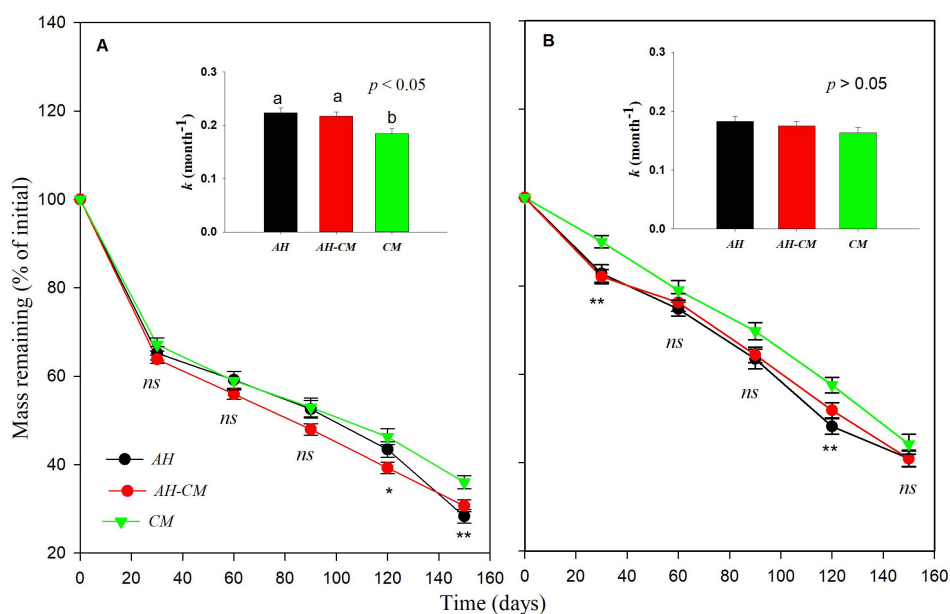


FIGURE 5

Effect of litter types on dry mass loss of surface litters and belowground litters from dominant shrubs of the Horqin Sand Land. Mean values of mass remaining through time are $n = 20$ from (A) surface and (B) belowground litters, respectively. AH represent leaf litter of shrub *Artemisia halodendron*, CM represents leaf litter of shrub *Caragana microphylla*, and AH-CM represents litter mixture of *A. halodendron* and *C. microphylla*. Significance of main effects of litter type treatment at a given date between surface or belowground litters is denoted as $*p < 0.05$, $**p < 0.01$, ns is not significant. Bars represent surface and belowground litters decomposition constant, k (mean $\pm$ SE), after 5-month of incubation in litter type treatments. Different lowercase letters over the bars indicate significant differences for least significant difference (LSD) *post hoc* comparisons at $p < 0.05$.

moisture oscillations may sustain relatively higher microbial activity, resulting in rapid decomposition rates of litters covered by soil.

Our results suggested that the differences in the magnitude of dry mass loss between surface and belowground litters varied greatly with time, with larger differences at 1-month collection (19.6% difference) and smaller differences at 6-month collection (10.3% difference). This may be attributed to poor leaching of water-soluble compounds in surface litter owing to minimal precipitation prior to the 1-month collecting date (Figure 2). In contrast, dried litters in mineral soil ostensibly obtained water from soil solution, which likely facilitated leaching of water-soluble compounds and, thus, may promote microbial activity. The decrease in differences between surface and belowground mass loss at the 6-month collection likely reflect compensatory leaching of water-soluble compounds and breakdown by UV radiation in surface litters relative to belowground litters (Gaxiola and Armesto, 2015).

4.2 Rainfall variability controls

Several previous researches have showed that the size and temporal distribution of rainfall pulses likely induce and sustain litter decomposition in drylands (Anaya et al., 2012; Li et al., 2016; Schuster, 2016). Our results confirmed that mean decomposition constant, k , in 15-CP and 30-CP treatments were significantly lower than that in control (Figure 3A), suggesting that the increase in rainfall variability strongly inhibited litter decomposition in the shrubland. Specifically, we observed that large and infrequent

rainfall events inhibited surface litter decomposition relative to smaller but more frequent events for a given cumulative rainfall quantity. This result contrasts with previous findings which show that surface litter decomposition is irrespective to pulse size and frequency (Joly et al., 2017a), however, it supports the report in which small weekly pulses accelerated litter decomposition relative to larger monthly pulses for a given 25 mm cumulative precipitation (Whitford et al., 1986). Regardless, we observed insignificant differences between rainfall repackaging treatments on decomposition of soil-covered litter, which is in contrast to previous reports that showed small and large rainfall event treatments demonstrated large differences in their effects on decomposition (Austin et al., 2009; Anaya et al., 2012). Under field conditions of arid ecosystems, strong evapotranspiration usually accelerates losses of moisture from the soil surface. Topsoil is consequently subjected to frequent dry-wet cycles, whereas the underlying soil is less often influenced by rapid losses of the topsoil moisture (Austin et al., 2004). This may explain the different responses between surface and belowground decomposition to increases in rainfall variability observed in our study. In the present study, similar trends in soil moisture (0–15 cm) were detected across four rainfall treatments over the entire experiment although significant differences in soil moisture among rainfall repackaging treatments were observed on 7 of the 11 sampling dates (Figure 7). This results directly indicates that rainfall distribution variability alters dry-wet cycles of soil moisture, and, thus, influence microbial activity in dryland systems. However, moisture of topsoil and underlying soil are greatly modified by soil properties that influence runoff,

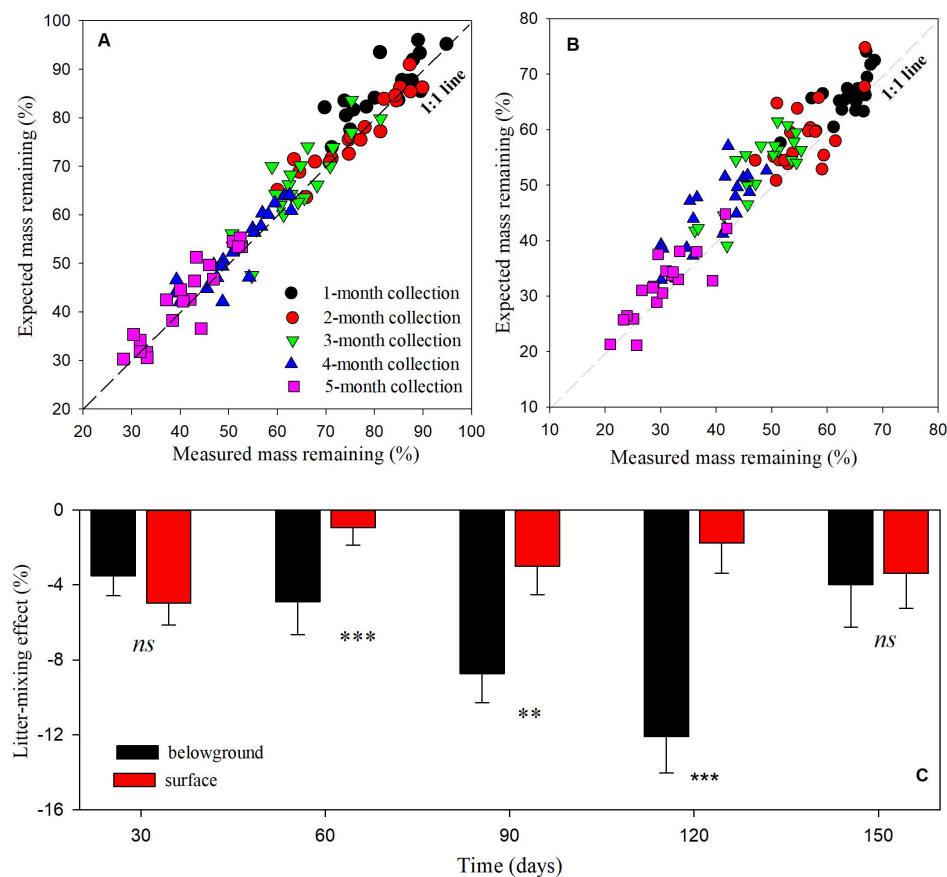


FIGURE 6

Expected vs. measured mass remaining in (A) surface and (B) belowground litters, and (C) mixing effects over time in mixture of shrub *AH* and *CM*. The relationship between expected vs. measured mass remaining are compared with the 1:1 line, with deviations from the 1:1 line indicating antagonistic or synergistic effects and an overlap of the 1:1 line indicating additive effects. Means of litter-mixing effects through time are $n = 20$ from surface and belowground litter mixtures. Significance of soil-covering on litter-mixing effects at a given date are denoted as ** $p < 0.01$, *** $p < 0.001$, *ns* is not significant.

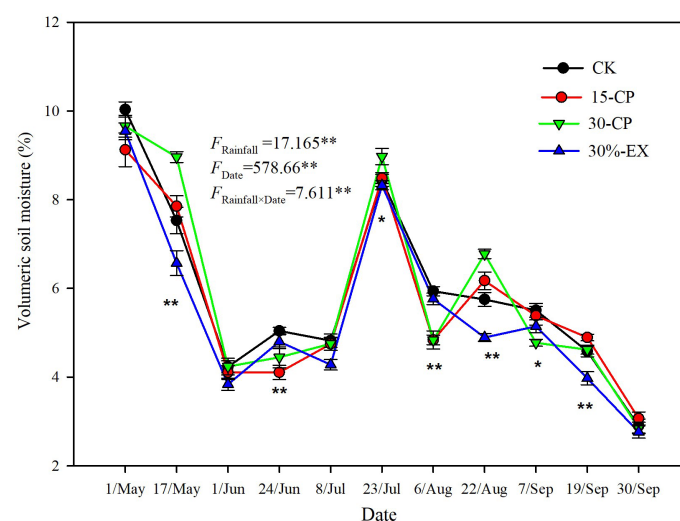


FIGURE 7

Volumetric soil moisture (0–15 cm) in repackaging precipitation treatments during the experimental period. 15-CP, pulse size of repackaged ambient precipitation ≥ 15 mm; 30-CP, pulse size of repackaged ambient precipitation ≥ 30 mm; 30%-EX, 30% of the ambient precipitation was intercepted by rain-exclusion shelters; CK, untreated ambient precipitation. Significant differences in soil moisture among the four treatments on each sampling date are indicated by * ($p < 0.05$) and ** ($p < 0.01$).

infiltration, and water holding capacity (Lee et al., 2014). To validate this conjecture, further studies are needed to specifically clarify the response of hydrological process in the soil, and consequently microbial activity, to rainfall variability.

We observed insignificant effects of exclusion of 30% precipitation on mass loss in both surface and belowground litters, suggesting that variations in rainfall amount scarcely affected litter decomposition in the study site. The observation presented here coincided with the result that litter mass loss was not decreased by a 35% decrease in precipitation amount in a peatland (Bell et al., 2018). However, some opposing evidence suggests that litter decomposition rates are positively correlated with incoming annual precipitation in semi-arid ecosystems. Yahdjian et al. (2006) observed that the litter decomposition rates of *Stipa speciosa* were negatively correlated with the amount of intercepted precipitation in a semi-arid steppe. In the present rainfall exclusion experiments, temporal rainfall amount, but not frequency, was purposefully altered by rainout shelters. According to Borken and Matzner (2009), rainfall intensity has only a limited effect on C turnover while the duration of the dry period will influence cumulative C mineralization. Additionally, soil microorganisms have different thresholds of soil water availability, and some resistant groups may maintain vigorous activities even under conditions of low water availability (Treonis et al., 2000; Schwinning and Sala, 2004). This may explain the insignificant effects of rainfall exclusion on litter decomposition in the present study.

4.3 Litter-mixing effects

Some researchers have concluded that when different litters are mixed, litter that is more easily decomposed can stimulate the decomposition of litter that is less easily decomposed, and a synergistic effect is exhibited (Wardle et al., 2003; Liu et al., 2007). Consistent with these previous results, we observed 80.5% of AH-CM litter mixtures had synergistic effect on litter decomposition in the present study, indicating that decomposition was often stimulated by mixing leaf litters of two dominant shrubs. Moreover, our results showed synergistic effect in belowground AH-CM mixture was relatively stronger than that in surface mixture, suggesting that soil-covering stimulate nonadditive effects of litter mixtures on decomposition of leaf litters. Probable differences in moisture oscillations between topsoil and the underlying soil may attribute to the stimulation of synergistic effect in belowground AH-CM mixture. Despite the difficulties in prediction, water availability has been considered as one of the predominant drivers to regulate non-additive effects of litter mixtures (Makkonen et al., 2013). Some robust evidence has demonstrated that drought reduces synergistic effects on litter decomposition (Santonja et al., 2015; Schuster et al., 2017).

In addition, our results showed that magnitudes of the synergistic effect between surface and belowground differed temporally, especially in the hotter months. Relative to the 1- and 5-month collections, LMEs were much stronger in the belowground AH-CM mixture than in the surface AH-CM mixture at 2-, 3-, and 4-month collections (Figure 6). Rainfall in the study site is unimodal, with a

considerable amount occurring in the hotter summer months (June–August). This suggests that seasonal changes in precipitation and temperature may regulate the synergistic effect of belowground mixture litters. Large precipitation amounts along with high temperatures were considered to improve the microenvironmental conditions for litter consumers (e.g., fungi and detritivores) in soils, which in turn stimulates the litter fragments (Makkonen et al., 2013; Wu et al., 2013). This highlights the need to consider environmental conditions such as precipitation, temperature, and soil-covering when predicting the direction and magnitude of LMEs in dryland systems.

5 Conclusions

Our results showed that variations in rainfall amount have no effect on litter decomposition. By contrast, variations in rainfall distribution exert a great influence on litter decay process. Specifically, repackaging natural precipitation into large and infrequent rainfall events inhibited surface litter decomposition in the study. It implies that increasing rainfall variability in the current context inevitably affects organic matter turnover in dryland system. Additionally, we found that belowground litters decomposed more quickly than surface litters in the semi-arid shrubland, indicating that soil covering may buffer litter from rainfall variability by maintaining milder soil moisture and, thus, sustain microbial activity in dryland systems. There also exhibited significant litter-mixing effects in litter mixtures of two dominant shrubs, especially in the soils in the hotter months. Such results suggest that litter mixing and soil covering jointly drive litter decomposition in the context of increasing rainfall variability in distribution. In summary, these findings highlight the role of increasing rainfall variability and subsequent soil-covering or litter-mixing in driving organic matter turnover in drylands.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

YL: Writing – original draft, Writing – review & editing. LC: Data curation, Writing – review & editing. HY: Formal Analysis, Writing – review & editing. RZ: Writing – original draft. ZN: Formal Analysis, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fpls.2025.1455170/full#supplementary-material>

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Coupling relationships between vegetation and soil in different vegetation types in the Ulan Buh Desert and the Kubuqi Desert

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Introduction: Desertification is a globally recognized ecological issue that poses severe threats to the environment, economic and social systems. Revegetation is the primary means to combat desertification, yet the effectiveness of revegetation practices requires reasonable quantification.

Methods: To identify appropriate planting patterns for revegetation in different deserts and provide a basis for vegetation reconstruction in deserts, we conducted a comprehensive survey in the Ulan Buh Desert and the Kubuqi Desert of the Northern China. Data on vegetation and soil were collected from 54 representative sites, covering both natural and revegetation communities.

Results: The findings revealed that the diversity of herbaceous and woody species, and soil nutrient content increased after revegetation, in comparison to adjacent moving sand dunes. Additionally, the species diversity and soil conditions in revegetation areas, gradually approached those of natural vegetation communities, indicating a succession towards a state resembling natural conditions. Variations in the coupling of vegetation-soil systems were observed among different community types in both deserts. Notably, the communities dominated by *Caragana korshinskii* and *Artemisia ordosica* exhibited the strongest coupling in the vegetation-soil system, driven primarily by soil water and nutrients, as well as vegetation growth.

Discussion: Evaluation of vegetation-soil system coupling effect was used to evaluate the effectiveness of vegetation restoration and species selection in the two deserts, which can serve as a reference for vegetation reconstruction and ecological restoration in desert areas.

KEYWORDS

revegetation, natural vegetation, vegetation-soil system, coupling coordination, revegetation construction

1 Introduction

Desertification is an increasingly severe ecological problem worldwide due to climate change, soil erosion, natural disasters, and unreasonable human activities (Cao et al., 2009; Yang and Wu, 2010; Odjugo and Isi, 2003; Kar, 2018; Meng et al., 2021). The vegetation-soil system is a dynamic equilibrium ecosystem based on the reciprocal effects of vegetation, soil, and the complex biogeochemical process (Zeng et al., 2006; Chi et al., 2022). Vegetation-soil system coupling refers to the interactive and interdependent relationship between vegetation and soil (Wang et al., 2021). This coupling is fundamental to the functions and services of ecosystems and is of great significance for the study of ecological restoration (Ma et al., 2023). Desertification not only causes the vegetation destruction and soil degradation, but also weakens the coupling effects between vegetation-soil systems (Fu et al., 2011). China is also influenced by desertification, which exerts significant impacts on ecological, economic, and social systems (Wang et al., 2002; Bao et al., 2017; Zhang and Huisingh, 2018). To combat desertification, China has initiated a series of key ecological projects (He et al., 2015; Hu et al., 2021; Zhai et al., 2023). Numerous studies have focused on the ecological effects of these projects and paid excessive attention to the impacts of isolated indicators like vegetation characteristics, while overlooking a comprehensive assessment that includes the ecosystem health, biodiversity, and soil quality (Zhang et al., 2016; Dou et al., 2024).

In desert ecosystems, vegetation restoration plays a significant role in reducing wind erosion and stabilizing the mobility of sandy soils. Consequently, selecting appropriate plant species is crucial during the process of vegetation restoration (Zhang et al., 2016). In order to scientifically quantify the effectiveness of revegetation, it is necessary to set the adjacent natural communities and highly degraded moving sand dunes as control. The purpose of this approach is to assess the ecological restoration effectiveness of revegetation on the structure of vegetation and soil properties (Li et al., 2018; Zhou et al., 2023). Building on this foundation, the present study will conduct a scientific quantitative analysis of the ecological restoration effects of vegetation restoration in improving vegetation coverage and soil properties, using adjacent natural plant communities and highly degraded moving sand dunes as controls.

The common method assessing the effects of revegetation is to compare changes in vegetation cover, species diversity, soil properties after revegetation (Courtney et al., 2009). But rarely consider the coupling effects between them (Zhao et al., 2022). The traditional methods tend to consider vegetation and soil properties separately (Pan et al., 2019), but rarely consider the coupling effects between them (Zhao et al., 2022). Separate analysis of vegetation and soil considers their respective characteristics and changes individually, whereas vegetation-soil system coupling analysis takes into account the interactions between the two subsystems, enabling more accurate predictions of the ecosystem's response to environmental changes. The vegetation-soil system coupling evaluates the restoration status of both vegetation and soil (Li et al., 2020; Zhang et al., 2013). Likewise, vegetation-soil coupling models offer theoretical foundations for ecological

restoration (Du et al., 2013; Wang et al., 2021; Puyang et al., 2021). Therefore, understanding evaluation of vegetation-soil system coupling effect in desert ecosystems provides scientific evidences for species selection and configuration, and further ensures the sustainability of ecological restoration.

This study selected the Wulan Buhe Desert and the Kubuqi Desert as the research areas, with survey points chosen based on the different vegetation types in the two deserts. These two deserts exhibit significant spatiotemporal heterogeneity in terms of geographical location, climatic conditions, dune morphology, vegetation coverage, and the impacts of human activities (Zhu et al., 2025). Additionally, different regions of the two deserts are characterized by various types of vegetation restoration. Therefore, different vegetation restoration models should be adopted for revegetation construction and ecological restoration in these two deserts. Effect value is used to quantify the magnitude of the effect of an experiment or intervention, describing the average difference between two or more groups on a specific variable. In this study, we compared the effect values of revegetation with natural vegetation and moving sand dunes in the Ulan Buh Desert and Kubuqi Desert to investigate the influence of revegetation on species diversity and soil nutrient content. Furthermore, we conducted an investigation into the vegetation and soil characteristics of different vegetation types in the two deserts and explored appropriate strategies for vegetation restoration, with the aim of determining the most suitable replanting patterns for these two deserts. To achieve these objectives, we posited the following hypotheses: 1) Compared to the adjacent moving sand dunes, revegetation would improve the plant and soil conditions, which were similar to the adjacent natural vegetation community. 2) Different community types will exhibit varying degrees of vegetation-soil system coupling, and the extent of recovery of vegetation and soil will differ following the planting of different revegetation types.

2 Materials and methods

2.1 The study area

The study area is located at the critical area for mitigating desertification in the Ulan Buh Desert and Kubuqi Deserts. The Ulan Buh Desert is located in the middle reaches of the Yellow River and belongs to a transitional zone from warm-temperate semi-arid to arid climate (Li et al., 2018). The annual average precipitation is about 140 mm, and the annual average evaporation ranges from 2110 to 2995 mm (Li et al., 2024). The predominant soil type is aeolian sand (Tian et al., 2019), and the vegetation is dominated by xerophytic herbaceous plants and shrubs. The Kubuqi Desert is located at the northern edge of the Ordos Plateau, falling within the temperate arid and semi-arid regions. The annual precipitation is about 249 mm, and the annual average evaporation ranges from 2100 to 2700 mm (Yang et al., 2016; Chen et al., 2022). The predominant soil types are aeolian sand and gravelly sand (Dong et al., 2020; Sun et al., 2023), and the vegetation consists of steppe-like desert vegetation dominated by perennial grasses and small shrubs (Figure 1).

2.2 Vegetation survey, soil samples collection and measurement

We collected data from 24 survey plots in the Ulan Buh Desert and from 30 survey plots in the Kubuqi Desert from July and August in 2022 and 2023 (Figure 1). In the Ulan Buh Desert, the main survey line was established along the east-west sand-crossing highway from Jilantai to Wuhai, where ten survey points were set up. An additional line extended from Jilantai through Dengkou to Wuhai, with fourteen survey points established along this route. In the Kubuqi Desert, the main survey line was laid out along the east-west direction of the Expressway, with branch lines set up in the north-south direction. The north-south branch line was divided into three regions: east, middle, and west, with 11, 7, and 12 survey points, respectively. At each survey point, we established a transect line of 100 to 200 meters. In each survey site, a nested design was implemented along the transect line, consisting of three 10 m × 10 m quadrats for moving sand dunes, six for revegetation, and three for natural woody vegetation. Within each of these larger woody vegetation quadrats, a smaller 0.5 m × 0.5 m

quadrat was nested for the purpose of studying herbaceous vegetation. When survey points were distant from moving sand dunes or lacked revegetation, only natural vegetation plots were established. In the Ulan Buh Desert, a total of 99 quadrats were established (N=33 for revegetation, 57 for natural vegetation, and nine in moving sand dunes), and in the the Kubuqi Desert, a total of 185 quadrats were established (98 for revegetation, 60 for natural vegetation, and 27 in moving sand dunes) (Figure 1; Supplementary Figure S1).

In each woody vegetation quadrat, we recorded the species, density and cover of woody plants, as well as the planting methods, row spacing (to evaluate the initial density of revegetation), and types of revegetation. In each herbaceous quadrat, we counted the number of species and estimated the vegetation cover. The above-ground biomass was collected using envelopes in each herbaceous quadrat, and then was dried at 80°C in the laboratory for 48 hours, finally was weighed. The above-ground biomass was collected using envelopes in each herbaceous quadrat, and then was dried at 80°C in the laboratory for 48 hours, finally was weighed. For both woody and herbaceous quadrats, we measured species richness (R) and

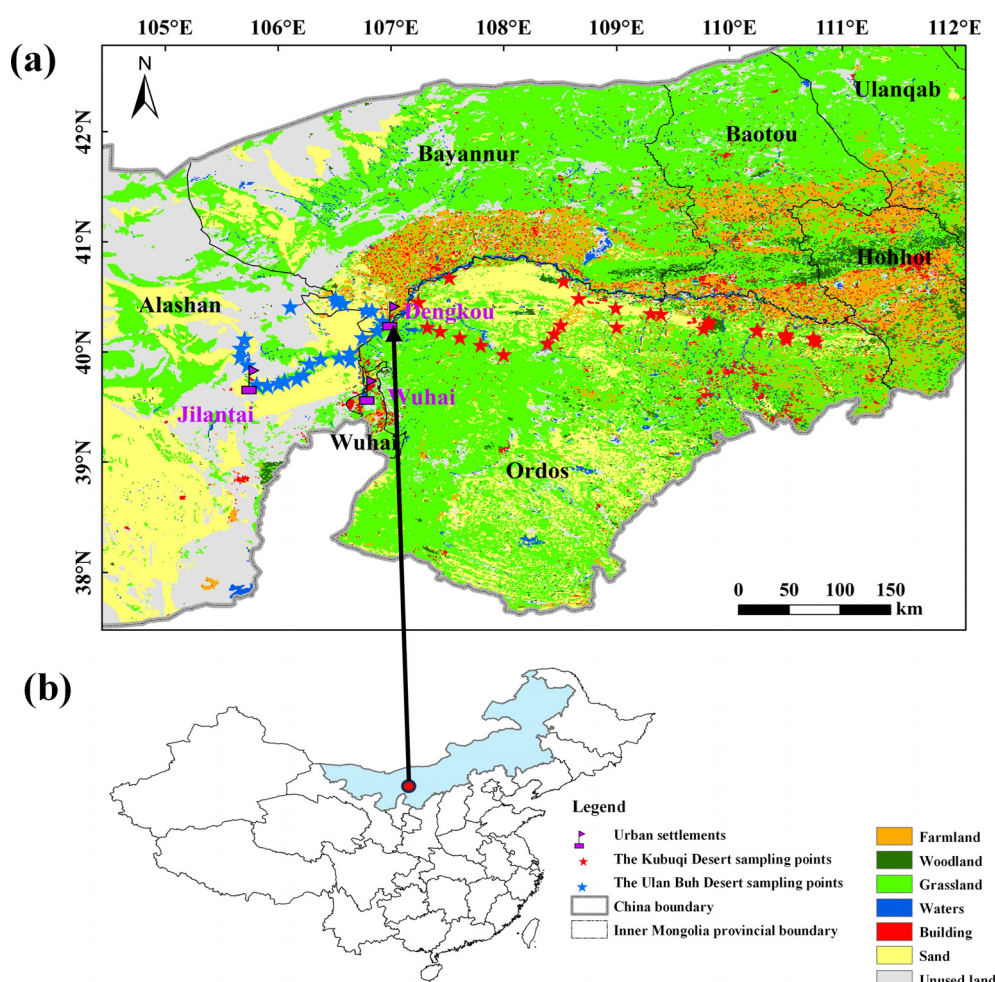


FIGURE 1

Location of the study area and distribution of the sampling points. (a) Distribution of sampling points in the Ulan Buh Desert and Kubuqi Deserts (b) Location of research areas on the map of China.

calculated the Shannon-Wiener index (H') and Simpson index (D) (Whittaker, 1972; Magurran and McGill, 2010; Tuomisto, 2010).

We collected latitude, longitude and altitude data of each sample plot using a GPS device. Meteorological data for the local area was obtained from the spatial interpolation dataset of China's average meteorological elements using ArcGIS Desktop 10.8 software, based on the latitude and longitude of the sample plots (Spatial Interpolation Dataset of Average Conditions of Chinese Meteorological Elements: <https://www.resdc.cn/DOI/DOI.aspx?DOIID=39>). The acquired meteorological data mainly includes annual evaporation, annual average ground temperature, annual precipitation, annual average atmospheric pressure, annual average relative humidity, annual sunshine hours, annual average temperature, and annual average wind speed. We collected soil samples at nine depths (0, 0.1, 0.2, 0.4, 0.6, 0.8, 1.0, 1.2, 1.5 m) in the center of each woody quadrat. We placed the fresh soil into sealed bags and weighed them *in situ*. The soil samples were dried at 105°C for 24 hours and were weighed to get their dry weight in the laboratory. The gravimetric soil water content at different soil depths could be calculated. We collected surface (0–5 cm) soil samples using a $1 \times 10^{-4} \text{ m}^3$ core in each quadrat and measured soil bulk density in the laboratory. To measure soil saturated water content, we soaked the soil samples in water for 24 hours and then weighed them before and after drying at 105°C for 24 hours. We collected soil samples from 0–20 cm using a $1 \times 10^{-4} \text{ m}^3$ cutting ring and then divided them into two parts after air-drying. One part was passed through a 2 mm mesh sieve for measuring soil mechanical composition using the wet sieve and pipette method. The other part was passed through a 1 mm sieve to measure soil organic carbon, total carbon, total nitrogen, total phosphorus content, pH and conductivity. We tested the pH of a solution with a soil to water ratio of 1: 2.5 (g/ml) using a pH meter, and measured the electric conductivity of a solution with a soil to water ratio of 1:5 (g/ml) using a conductivity meter. Total carbon, total nitrogen, and total phosphorus contents were measured using an external heating-potassium dichromate method, a semi-micro Kjeldahl method, a sodium hydroxide melting-molybdenum antimony anti-colorimetric method, respectively (Pal, 2013; Haluschak, 2006).

2.3 Data analysis

2.3.1 Comparison of vegetation and soil characteristics

We calculated effect values ($\ln RR$) of vegetation and soil indicators (ratios of indicators in revegetation to those in natural vegetation, and ratios of indicators in revegetation to those in moving sand dunes) as follows (Equation 1; Hedges et al., 1999):

$$\ln RR = \ln (X_t/X_c) = \ln (X_t) - \ln (X_c) \quad (1)$$

Where X_c represents the value of the indicator of the revegetation community, X_t represents the indicator of the natural vegetation community or moving sand dunes.

We used one-way ANOVA to test the differences in vegetation and soil indicators among different community types, and used the Duncan test for multiple comparisons ($\alpha=0.05$).

2.3.2 Evaluation of vegetation-soil system coupling

The selection of indicators for vegetation-soil system coupling evaluation followed the principle of representativeness, scientificity and independence. The evaluation system for vegetation-soil system with different vegetation community types in Ulan Buh Desert and Kubuqi Desert was divided into a vegetation subsystem and a soil subsystem, here in seven indicators were selected in each subsystem, after removing strongly correlated indicators (Supplementary Figure S2). The vegetation subsystem was comprised of herbaceous and woody indicator. The herbaceous indicator selected included herbaceous abundance, richness, coverage and biomass, as well as the woody abundance, richness and coverage. The soil subsystem consisted of soil physical property indicator and soil nutrient indicators, the former included soil water content, sand, silt and clay contents; the latter included organic carbon, total carbon and total phosphorus. Finally, we employed the entropy weight method (Zou et al., 2006) to determine the weights of vegetation and soil indicators and constructed an evaluation indicator system for vegetation-soil coupling (Table 1).

We standardized the vegetation and soil indicators (Equation 2; Zeng et al., 2006; Guo et al., 2021) using the following formula:

$$N_i = \begin{cases} \frac{x_i - \min(x_i)}{\max(x_i) - \min(x_i)} & (\text{Positive effect}) \\ \frac{\max(x_i) - x_i}{\max(x_i) - \min(x_i)} & (\text{Negative effect}) \end{cases} \quad (2)$$

Where N_i is the standardized value of each indicator, x_i is the value of the different indicators. Positive indicators included herbaceous abundance, richness, coverage, and biomass, woody abundance, richness, and cover, soil water content, organic carbon, total carbon, total phosphorus, clay and silt content. Negative indicators included sand content.

We calculated a comprehensive evaluation indicator of vegetation and soil as follows (Equations 3, 4; Zeng et al., 2006; Peng et al., 2011; Zhang et al., 2013; Zhao et al., 2022):

$$CCE(x) = \sum_{i=1}^n p_i x_i \quad (3)$$

$$PCE(y) = \sum_{i=1}^n q_i y_i \quad (4)$$

Where CCE is the vegetation evaluation indicator; PCE is the soil evaluation indicator; p_i and x_i are the weights and standardized values corresponding to the i -th indicator in the vegetation evaluation function, respectively; q_i and y_i are the weights and standardized values corresponding to the i -th indicator in the soil evaluation function, respectively. Higher CCE and PCE values indicate better vegetation growth status or soil properties.

TABLE 1 Evaluation indicator system and indicator weight of vegetation-soil coupling.

Goal layer	Criterion layer	indicator layer				Comprehensive weight
		First grade indicators	Weight	Second grade indicators	Weight	
Evaluation of vegetation-soil coupling coordination degree	Vegetation comprehensive evaluation function (CCE)	Herbaceous indicator	0.5	Abundance	0.3758	0.1879
				Richness	0.1388	0.0694
				Coverage	0.2183	0.1091
				Biomass	0.2671	0.1336
		Woody indicator	0.5	Abundance	0.4159	0.2080
				Richness	0.1539	0.0770
	Soil comprehensive evaluation function (PCE)	Soil physical property indicator	0.75	Coverage	0.4302	0.2151
				Soil water content	0.2205	0.1329
				Sand	0.3252	0.0690
				Silt	0.3764	0.0481
				Clay	0.0780	0.2439
		Soil nutrient indicator	0.25	Organic carbon	0.5315	0.2823
				Total carbon	0.2762	0.0585
				Total phosphorus	0.1923	0.1653

We calculated the coupling coordination degree (C_d) of the vegetation-soil system as follows (Equations 5–7; Zeng et al., 2006; Peng et al., 2011; Zhang et al., 2013):

$$C_d = \sqrt{C \cdot T} \tag{5}$$

$$T = aCCE(x) + bPCE(y) \tag{6}$$

$$C = \sqrt{\frac{CCE(x) \cdot PCE(y)}{(CCE(x) + PCE(y))^2}} \tag{7}$$

Where C_d is the coupling coordination degree of vegetation-soil system, which ranges between 0 and 1. The greater the C_d value, the more harmonious the coupling relationship of vegetation-soil system. T is the comprehensive harmonic indicator of vegetation-soil system, which reflects the synergistic effect of vegetation-soil system. C is the coupling degree of the vegetation-soil system, which ranges between 0 and 1, where C approaches 1, the relationship between vegetation and soil is more benign. a and b are coefficients of the CCE and PCE comprehensive evaluation functions, respectively. Because vegetation and soil both play important roles in ecological restoration, we set a and b both to 0.5. Finally, we used the coupling results to determine a reasonable vegetation construction mode (Table 1).

We used redundancy analysis (RDA) to analyze the factors that influence the coupling indicator, which we analyzed and plotted with Canoco5.

3 Results

3.1 The effect values of vegetation and soil indicators

In the Ulan Buh Desert, we found that revegetation led to an increase in the abundance, diversity and richness of herbaceous species, but a decrease in herbaceous biomass and woody abundance compared to natural vegetation. Similarly, compared to moving sand dunes, revegetation resulted in higher herbaceous abundance, richness, coverage and biomass; in addition, the soil water content in both shallow (0–0.3 m) and deep (0.4–1.5 m) layers decreased, while soil organic carbon, total nitrogen, total carbon, silt, clay, and electrical conductivity increased in both natural and revegetation communities (Figure 2).

In the Kubuqi Desert, revegetation led to lower herbaceous abundance, richness, diversity cover, and biomass, but higher woody cover compared to the natural vegetation. There were higher herbaceous abundance, richness, and diversity, as well as higher woody abundance and cover in revegetated areas compared to moving sand dunes. In revegetated areas, the soil organic carbon, total nitrogen, total carbon, silt, clay contents, and electrical conductivity were lower than those in natural vegetation areas, while the organic carbon, total nitrogen, total carbon, clay content, and electrical conductivity were higher than those in moving sand dunes (Figure 2).

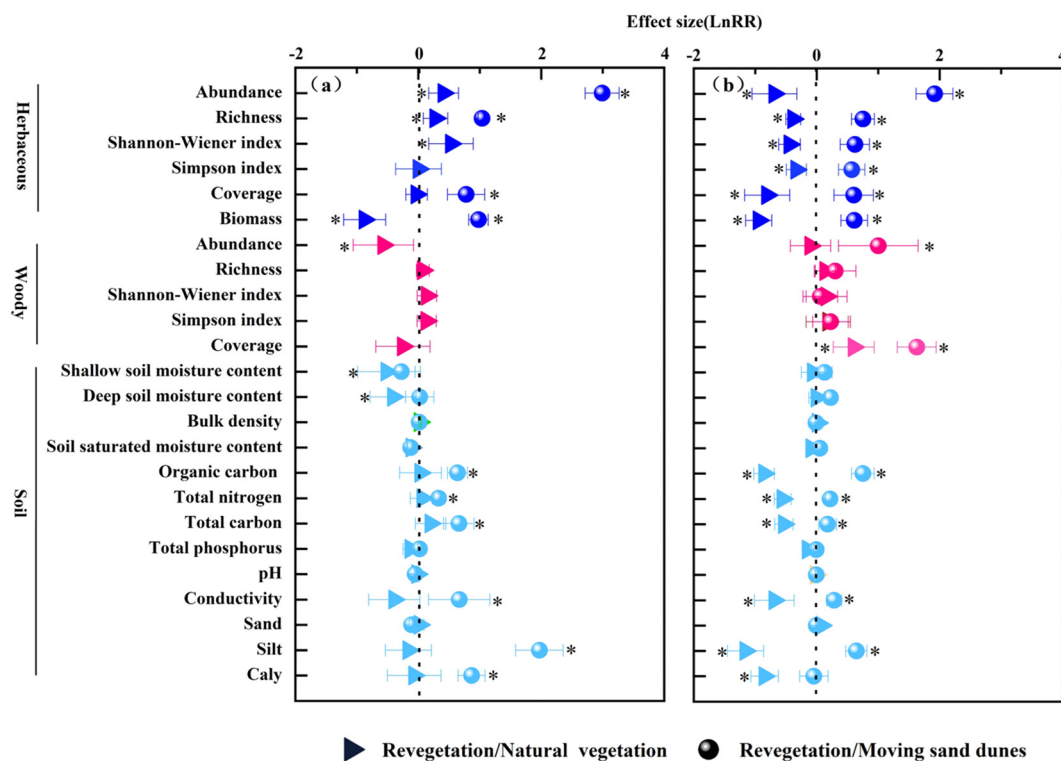


FIGURE 2

Vegetation and soil indicator effect values of different community types in Ulan Buh Desert (a) and Kubuqi Desert (b). * represents significant effect size at $p=0.05$ level. (Effect value >0 indicates an increase in the indicator, and effect value <0 indicates a decrease in the indicator).

3.2 Vegetation-soil system coupling of different community types in two deserts

We found that the natural *Caragana korshinskii* community, the *Artemisia ordosica* community and the *Nitraria tangutorum-Haloxylon ammodendron* community exhibited stronger vegetation-soil system coupling among the natural vegetation communities in the Ulan Buh Desert, and the coupling degree values (C) were 0.496, 0.492 and 0.486, respectively. Likewise, the natural *Kalidium foliatum* community, *N. tangutorum* community and *N. tangutorum-H. ammodendron* community exhibited better vegetation-soil system coupling and coordination. Their respective coupling coordination degree values (C_d) were 0.594, 0.515, and 0.471. In the revegetation community, the vegetation-soil system coupling was highest in the *H. ammodendron*, followed by the *Hedysarum scoparium* community, and the worst in the *C. korshinskii* community. Their respective C values were 0.495, 0.469 and 0.440. The vegetation-soil system coupling coordination state was highest in the *C. korshinskii* and *H. ammodendron* communities, but lowest in the *H. scoparium*, their C_d values were 0.494, 0.412, and 0.324, respectively. Compared to the natural *C. korshinskii* community, the coupling relationship between vegetation and soil of the revegetation *C. korshinskii*

community was improved, and the vegetation-soil system also showed a good coupling state (Table 2).

The coupling between vegetation communities and soil was higher in natural vegetation communities of the Kubuqi Desert. This included higher C values of natural *Achnatherum splendens*, *Caragana tibetana*, and *A. ordosica* communities were 0.500, 0.499 and 0.498, respectively. Likewise, the natural *N. tangutorum-Tamarix chinensis*, *C. tibetana* and *A. ordosica* communities had higher coupling coordination states of the vegetation-soil system, with high C_d values of 0.753, 0.694 and 0.682 respectively (Table 2). In revegetated areas, the vegetation-soil system coupling in the *A. ordosica*, *C. korshinskii*, and *Populus przewalskii-Salix psammophila* revegetation communities was relatively higher, and the C values of them were 0.500, 0.498, and 0.490, respectively. The revegetated communities of *A. ordosica*, *C. tibetana* and *P. przewalskii* had the relatively higher vegetation-soil system coupling coordination states, with C_d values of 0.763, 0.612, and 0.484, respectively. The vegetation-soil system coupling and its coordination states of revegetated *A. ordosica* community were higher than those of natural *A. ordosica* community (Table 2).

We found that the first axis (RDA1) and the second axis (RDA2) explained 56.2% and 17.5% of the influence of environmental factors on the vegetation-soil system coupling,

respectively. Specifically, we found that vegetation-soil system had strong correlations with total nitrogen, total carbon, the cover, abundance, richness, and biomass of herbaceous species, as well as woody cover and richness, while it was negatively correlated with soil pH, sand content, wind speed and temperature. Furthermore, water status, vegetation growth and soil nutrient contents also influence the vegetation-soil system coupling (Figure 3).

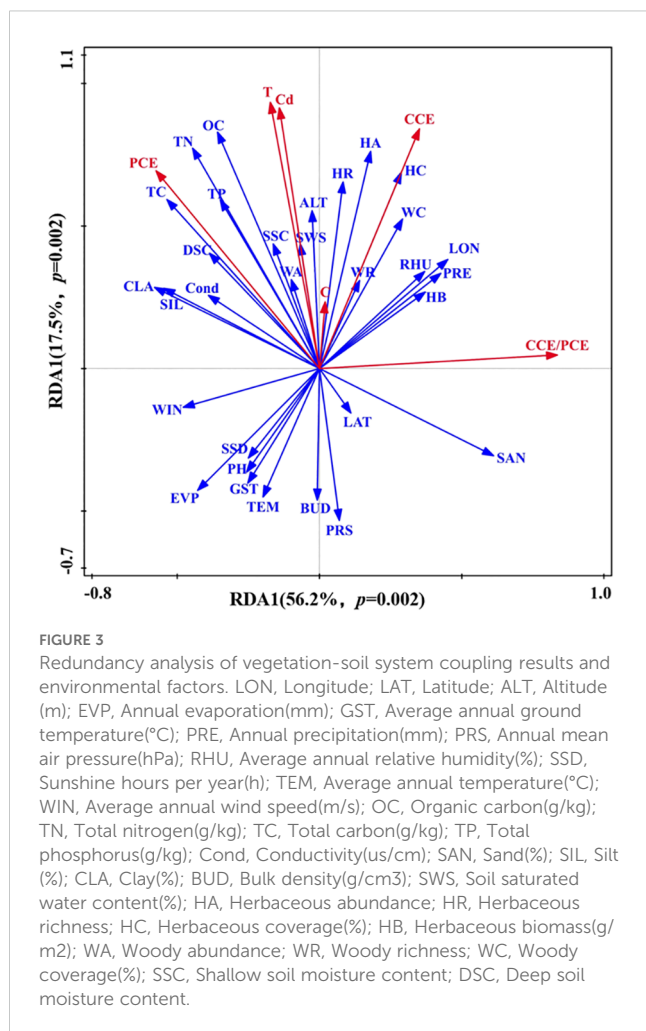
3.3 Identification of optimal revegetation species in Ulan Buh Desert and Kubuqi Desert

We compared vegetation and soil indicators, and vegetation-soil system coupling to select the proper revegetation species and configurations. In the Ulan Buh Desert, compared to the natural C.

TABLE 2 Coordination of vegetation-soil system coupling in different desert community types.

Desert	Area	Community category	CCE	PCE	C	T	C _d	CCE/PCE
Ulan Buh Desert	Natural	Pha	0.380	0.135	0.440	0.258	0.337	2.820
		Nit	0.260	1.082	0.395	0.671	0.515	0.240
		Kaf	0.308	1.613	0.367	0.960	0.594	0.191
		Amm	0.259	0.596	0.460	0.428	0.443	0.435
		Aro	0.259	0.372	0.492	0.315	0.394	0.695
		Cos	0.557	0.211	0.447	0.384	0.414	2.635
		Aro-Ars	0.251	0.076	0.423	0.164	0.263	3.293
		Nit- Haa	0.350	0.563	0.486	0.457	0.471	0.621
		Cak	0.436	0.333	0.496	0.384	0.436	1.309
	Revegetation	Haa	0.296	0.389	0.495	0.342	0.412	0.759
		Cos	0.302	0.147	0.469	0.224	0.324	2.055
		Cak	0.292	0.817	0.440	0.554	0.494	0.357
	Moving sand dunes	Moving sand dune	0.004	0.159	0.153	0.082	0.112	0.025
Kubuqi Desert	Natural	Aro-Nit	0.557	1.012	0.479	0.784	0.613	0.551
		Aro	0.828	0.692	0.498	0.760	0.615	1.197
		Krc	0.527	0.960	0.478	0.744	0.596	0.549
		Cab	0.836	0.702	0.498	0.769	0.619	1.191
		Cat	0.907	1.023	0.499	0.965	0.694	0.886
		Nit-Tac	1.021	1.260	0.497	1.140	0.753	0.811
		Nes	0.939	0.920	0.500	0.930	0.682	1.021
		Aro-Cof	1.005	0.287	0.416	0.646	0.518	3.498
		Cof	0.751	0.429	0.481	0.590	0.533	1.750
	Revegetation	Cof	0.739	0.284	0.448	0.511	0.478	2.606
		Haa	0.277	0.417	0.490	0.347	0.412	0.664
		Cam	0.532	0.162	0.423	0.347	0.383	3.279
		Sac	0.559	0.276	0.471	0.418	0.443	2.024
		Aro	1.140	1.192	0.500	1.166	0.763	0.956
		Pop	0.594	0.369	0.486	0.481	0.484	1.608
		Pop-Sac	0.256	0.172	0.490	0.214	0.324	1.485
		Cak	0.824	0.675	0.498	0.750	0.611	1.220
	Moving sand dunes	Moving sand dunes	0.145	0.231	0.487	0.188	0.302	0.626

Pha, *Phragmites australis*; Nit, *Nitraria tangutorum*; Kaf, *Kalidium foliatum*; Amm, *Ammopiptanthus mongolicus*; Aro, *Artemisia ordosica*; Cos, *Corethroedendron scoparium*; Ars, *Artemisia sieversiana*; Haa, *Haloxylon ammodendron*; Cak, *Caragana korshinskii*; Krc, *Krascheninnikovia ceratoides*; Cab, *Caragana brachypoda*; Cat, *Caragana tibetica*; Tac, *Tamarix chinensis*; Nes, *Neotrinia splendens*; Cof, *Corethroedendron fruticosum*; Cam, *Calligonum mongolicum*; Sac, *Salix cheilophila*; Pop, *Populus przewalskii*.



korshinskii community, the woody abundance, richness, and coverage of revegetated *C. korshinskii* community increased by 2.90%, 18.4%, and 15.8%, respectively; the soil organic carbon, total nitrogen, total carbon, silt, and clay contents increased by 39.5%, 31.3%, 30.7%, 70.8%, and 61.3%, respectively; the vegetation-soil system coupling also increased; while the sand contents decreased by 20.7%. Therefore, in the Ulan Buh Desert, we recommend two replanting species and their densities: *C. korshinskii* with 18-44 individuals per 100 m⁻², and *H. ammodendron* with 24-30 individuals per 100 m⁻² (Table 2; Supplementary Table S1).

In the Kubuqi Desert, compared to the natural *A. ordosica* community, the herbaceous abundance, woody abundance, herbaceous coverage, and woody coverage of the revegetated *A. ordosica* community increased by 3.63%, 72.2%, 18.6%, 58.5%, respectively; the soil organic carbon, total nitrogen, total carbon, total phosphorus, silt, and clay contents increased by 57.7%, 27.6%, 10.7%, 21.7%, 27.7%, and 22.5%, respectively; the vegetation-soil system coupling also increased; while the sand content decreased by 4.83%. As a result, in the Kubuqi Desert, we recommend two replanting species and their densities: *A. ordosica* with 60-70 individuals per 100 m⁻² and *C. korshinskii* with 20-45 individuals per 100 m⁻² (Table 2; Supplementary Table S1).

4 Discussion

4.1 The selection and establishment of revegetation ameliorate the conditions for plant survival

Consistent with our first hypothesis, plant and soil conditions improved compared to those of the moving sand dunes and became similar to those in natural vegetation areas following revegetation. This study finds that herbaceous species diversity significantly increased comparing to adjacent natural vegetation communities after the establishment of revegetation in the Ulan Buh Desert, whereas herbaceous biomass, woody richness, and soil water content significantly decreased. This may be due to shrub planting effectively stabilizing the surface of sandy soil and improving soil nutrient conditions, thus providing a suitable environment for the settlement and germination of herbaceous plant seeds (Angers and Caron, 1998; Miao et al., 2015; Zhong et al., 2018). Meanwhile, the root turnover of woody plants also provides essential nutrients for the growth of herbaceous plants. Therefore, the abundance, richness, and diversity indices of herbaceous plants have increased (An, 2019). However, the growth of woody species also competed for some soil nutrients and water resources, leading to the reduction in the herbaceous biomass and woody richness (Rossatto et al., 2014). In addition, the root water uptake of woody vegetation resulted in the decline soil water content (Pellissier et al., 2008). The establishment of revegetation in the Kubuqi Desert, herbaceous indicators, soil nutrients, silt, and clay contents all declined when compared to natural vegetation communities, whereas woody abundance increased. These might be illustrated that the introduction of woody vegetation increased the abundance of woody species. Meanwhile, the competition for nutrients and water among these woody plants was relatively intensive, attenuating the resource availability and thus inhibiting the growth of original herbaceous plants (Cui et al., 2019; Zheng, 2022).

In the present study, we found that the establishment of revegetation significantly increased the diversity of herbaceous plants, biomass, and soil nutrients, which is attributed to the woody vegetation creating more suitable growth conditions for herbaceous plants and increasing the content of silt and clay in the soil, thereby improving soil structure and stability (Ou et al., 2020; Scotton and Andreatta, 2021; Kumar et al., 2022). Vegetation restoration enhanced soil organic matter content through the input of roots and residues, which in turn increased soil fertility, beneficial for the growth of woody plants, and reduced wind erosion, providing a more stable growth environment for plants and promoting their reproduction and spread (Lajtha et al., 2014; Mitchell et al., 2018; Zhang et al., 2020; Zhu et al., 2010; Mensah, 2015; Maiti et al., 2021; Luo et al., 2020). Meanwhile, vegetation restoration improved the physical, chemical, and biological characteristics of the soil, increased soil nutrient content and water retention capacity, and enhanced species diversity (Xu et al., 2010; Chen et al., 2023; Zhou et al., 2023; Sheoran et al., 2010; Ploughe et al., 2021). In the early stages of vegetation restoration, effective soil coverage reduced water evaporation and

soil erosion, helping to maintain soil nutrients (Li et al., 2004; Zhang et al., 2018). Overall, the vegetation subsystem, soil subsystem, and the vegetation-soil system coupling all increased after restoration, and these improvements collectively promoted the favorable status and interaction of the vegetation and soil systems (Li and Liber, 2018; Guo et al., 2021).

Our findings provided scientific evidence for windbreak and sand-stabilization in these two deserts, and gave important guidance to future vegetation restoration in deserts. Traditionally, the success of restoration was determined by monitoring plant cover, individual counts, and soil characteristics after revegetation (Cudjoe, 2011; Song, 2018) as well as by selecting suitable species by greenhouse, field experiments, and seedling survival tests (Jusaitis and Pillman, 1997; Gastauer et al., 2020). Here, we considered not only the vegetation and soil systems, but also the vegetation-soil coupling in different vegetation types to select the most suitable revegetation strategy.

4.2 Coupling coordination of vegetation-soil system in two deserts

Consistent with our second hypothesis, we found that different community types exhibited variations in the vegetation-soil system coupling in these two deserts, which indicated that species selection was extremely important for the sustainability ecological restoration in deserts. The consistence of the changes between vegetation and soil indicators elucidated that plant growth and soil properties were closely correlated. There is a feedback mechanism between vegetation and soil. The plants exert a huge influence on soil conditions, which in turn support plant growth (Bever et al., 1997; Ehrenfeld et al., 2005; Miki, 2012; Maiti and Ghosh, 2020). Vegetation alters soil properties through physical and chemical processes during the restoration process (Cao et al., 2008; Ghestem et al., 2011; Wu et al., 2019). Meanwhile, vegetation roots increase soil porosity, and the decomposition of plant material adds organic matter to soil (Wu et al., 2016). In a word, different community types have varying impacts on soil properties, leading to disparities in the vegetation-soil systems coupling of different community types. The improvements of soil properties and vegetation growth enhance soil aggregate stability and resistance to wind erosion (Dou et al., 2020), thereby creating a positive feedback loop within the vegetation-soil system.

In this study, we found that soil nutrient content, herbaceous and woody indicators were positively correlated with the coupling degree of the vegetation-soil system. These were consistent with our hypothesis that the vegetation-soil system coupling was mainly affected by vegetation and soil characteristics. Generally, superior soil conditions promote plant growth, which in turn improves soil structure and nutrient cycling, thus forming a positive feedback loop. The mutual promotion and dependence between vegetation and soil constituted a well-coupled ecosystem, demonstrating a positive coupling state between vegetation-soil systems (Van der Putten et al., 2013; Hobbie, 2015; Lehman et al., 2015; Wang et al., 2020;

Aqeel et al., 2023). Simultaneously, this feedback loop suggests that healthy soil and abundant vegetation maintain ecosystem stability and functionality (Powelson et al., 2011; Mensah, 2015). Our findings indicated that unsuitable soil pH, high sand content, high wind speed, and high temperature adversely influenced plant growth and soil conditions (Zuo et al., 2012). These factors can also lead to soil degradation, nutrient loss, and reduce water availability, which in turn reduce plant growth and survival. The plant degeneration subsequently reduced vegetation cover and richness, exacerbating soil degradation (Duniway et al., 2019; Huang and Hartemink, 2020; Zhang et al., 2021; Ferreira et al., 2022). Taken together, coupling coordination of vegetation-soil system is crucial for maintaining the stability of ecosystems after the establishment of revegetation, as it directly affects the normal functioning of ecological processes and the long-term health of the ecosystem.

5 Conclusion

In our study, revegetation significantly improved the vegetation and soil conditions in the Ulan Buh Desert and Kubuqi Desert of Northern China. Water conditions, vegetation growth, and soil nutrients all influenced the vegetation-soil system coupling. We propose a method could be used for evaluating the effects of different revegetation types on the vegetation subsystem, soil subsystem, and the vegetation-soil system coupling. This method can select optimum plant species and its density, as well as evaluate the effects of revegetation on global desertification prevention. Our findings provide important guidance for vegetation reconstruction and ecological restoration in deserts.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

GH: Data curation, Formal analysis, Investigation, Writing – original draft. JH: Funding acquisition, Investigation, Writing – review & editing. HR: Investigation, Writing – review & editing. XG: Investigation, Writing – review & editing. YN: Investigation, Writing – review & editing. YL: Investigation, Writing – review & editing. ZZ: Funding acquisition, Investigation, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declare that no Generative AI was used in the creation of this manuscript.

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Unravelling the combined effects of drought and nitrogen addition on carbon assimilation and reserves in Korean pine saplings

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Climate change profoundly impacts the physiological processes and adaptation strategies of plants. However, the physiological mechanisms of coniferous species responding and adapting to combined drought and nitrogen (N) addition remain unclear. Here, based on 2-year multi-level N addition and drought experiments, we investigated the responses of carbon assimilation (net photosynthetic rate A_n , stomatal conductance g_s and intrinsic water use efficiency WUE_i) and carbon reserves (non-structural carbohydrates, NSC) of 7-year-old Korean pine (*Pinus koraiensis*) saplings. Our results showed that: (1) Drought decreased A_n and g_s , while N addition increased A_n and decreased g_s . N addition decreased A_n and WUE_i but increased g_s in plants under drought conditions, indicating that N addition under drought stress will maintain gas exchange by increasing stomatal opening, but failed to mitigate the reduction of A_n . (2) Both drought (moderate and severe) and N addition reduced leaf NSC concentrations. Under moderate drought stress, however, N addition led to an increase in leaf NSC concentrations. (3) The interconversion between leaf starch and soluble sugars slowed the decrease in carbon assimilation caused by drought. *P. koraiensis* saplings adopted a conservative strategy of increasing leaf mass per area (LMA) to adapt to reduced water use efficiency. The study highlights the coordinated relationship between carbon assimilation and carbon reserves of Korean pine saplings under combined drought and N addition, which improves our understanding of the diverse carbon dynamics of different species under climate change.

KEYWORDS

drought, nitrogen deposition, combined abiotic stress effects, conifers, nonstructural carbohydrates

1 Introduction

Forest ecosystems are the largest terrestrial carbon sink on Earth (Pan et al., 2011), and they are also critical habitats for biodiversity (Hisano et al., 2018). However, forest ecosystems are facing big challenges posed by climate change, such as prolonged severe droughts with warming (Anderegg et al., 2019; Sánchez-Pinillos et al., 2022) and increasing nitrogen (N) deposition due to large anthropogenic emissions of reactive N (Davidson, 2009; Roth et al., 2022), potentially limiting forest development and persistence, and thus on forest ecosystem services.

The ability of trees to assimilate carbon through photosynthesis is mostly highly sensitive to soil water-stress condition. During soil water stress, trees typically reduce water loss through transpiration by regulating leaf stomatal conductance (g_s). This, in turn, leads to a decrease in the net photosynthetic rate (A_n) as the rate of CO_2 diffusion decreases, ultimately resulting in reduced CO_2 assimilation (Rowland et al., 2015; Zhang et al., 2023). Excessive environmental stress can lead to a depression in photosynthesis, resulting in a diminished production of non-structural carbohydrates (NSC) that are crucial for respiration, growth, and defense. When the availability of NSC falls below the threshold required to sustain these vital functions, trees may succumb to carbon starvation (McDowell and Sevanto, 2010). Water stress can also alter the relationship between carbon assimilation and carbon storage in trees, reflecting the coordination of carbon acquisition and expenditure (Tsuji et al., 2022; Zhang et al., 2021b), the tree's metabolic growth and survival ability (Li et al., 2022; Peltier et al., 2023), and its buffering capacity to withstand external stressors (Piper and Paula, 2020).

Unlike the negative impacts of soil water stress, N deposition often has positive impacts on trees, mainly by altering the N nutrient status of the soil. Recent meta-analyses have indicated that, in terms of carbon assimilation, N addition significantly increased leaf photosynthetic rate and intrinsic water use efficiency (WUE_i), resulting in gross photosynthetic carbon gain (Liang et al., 2020; Zhang et al., 2018). In terms of carbon reserves, N addition also affects NSC concentrations and the allocation of photosynthetic assimilates in tree tissues, showing that carbon allocation for growth and respiration is stronger than that for NSC storage, and carbon allocation to aboveground parts is more than to belowground parts (Li et al., 2020). However, under N-saturated conditions, additional N input may attenuate this positive effect. For instance, studies have indicated with the accumulation of continuous N addition, there is a non-linear increase in carbon assimilation of conifer species such as Chinese fir *Cunninghamia lanceolata* (Li et al., 2022), and angiosperm species such as *Fraxinus mandshurica* (Wang et al., 2018). Furthermore, the NSC allocation of angiosperm and coniferous tree species to N addition differ, where *Pinus massoniana* allocates more NSC to roots, while *Castanopsis chinensis* to branches (Huang et al., 2021).

Although the responses of tree carbon assimilation and carbon storage to independent water stress or N addition have been extensively addressed, there is no clear consensus on their combined effects. Some studies have shown that N addition can offset the negative impacts of drought, for both coniferous and broadleaf tree species. For example, N addition ($46 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) improved carbon

exchange and reserves traits (such as A_n , g_s , and leaf NSC) in two broadleaf species (*Quercus mongolica* and *Fraxinus mandshurica*), mitigating the negative impacts of drought (Zhang et al., 2021a). Under drought conditions, N addition ($50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) positively affected A_n and WUE_i in the coniferous species of *Abies fabri* (Yang et al., 2012). On the other hand, some studies have suggested that the vulnerability of trees to drought will increase under N addition. For example, N addition ($50 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) increased aboveground biomass investment in European beech seedlings (*Fagus sylvatica*), but enhanced drought sensitivity, as evidenced by higher tissue mortality (Dziedek et al., 2017). The comprehensive effects depend on the combined levels of drought and N addition. For instance, N addition ($80 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) increased xylem soluble sugar and starch of two broadleaf species (*Ormosia pinnata* and *Schima superba*) under moderate drought (60% of soil field capacity), but decreased the xylem soluble sugar under severe drought (40% of soil field capacity) (Li et al., 2021). Recent study showed that the negative effects of droughts on the mortality of Norway spruce (*Picea abies*) would be enhanced with a critical threshold for N deposition of $10.9 \text{ kg N ha}^{-1} \text{ yr}^{-1}$ (Tresch et al., 2023).

Tree species with different drought tolerances also experience different combined impacts of water stress and N addition. On the one hand, the ability of plants to maintain carbon balance also depends significantly on the differences in stomatal regulation to drought stress (Henry et al., 2019), whereas gymnosperms and angiosperms have different response mechanisms. Leaf abscisic acid (ABA) levels play a major role in stomatal closure in angiosperms' response to drought stress, while effective stomatal closure in gymnosperms is driven by a combination of leaf ABA levels and water potential (Brodrribb and McAdam, 2013; McAdam et al., 2014). However, most studies have been focused on the responses of angiosperm tree species to the combined effects of different water stresses and N addition levels, with little attention on conifer tree species (Dulamsuren and Hauck, 2021).

In this study, in order to examine the physiological mechanisms underlying the responses of the temperate conifer tree species *Pinus koraiensis* to soil water stress and N deposition, we designed a field manipulation experiment with independent and combined drought and N addition. Leaf gas exchange (A_n , g_s , and WUE_i), carbon reserves (NSC concentrations and its composition) and physicochemical characteristics of stem and leaf were measured. The study aimed to answer three questions: (1) What are the differences between the independent and combined treatments of soil water stress and N addition on gas exchange and carbon reserves of *P. koraiensis*? (2) Will the same effect exist at different combined levels of water stress and N addition? (3) Will the reduction in carbon assimilation be regulated by carbon reserves underlying interactive stresses?

2 Materials and methods

2.1 Description of study site

The experiment was conducted in Changbai Mountain Forest Ecosystem Research Station of Chinese Academy of Sciences ($128^\circ 28'E$, $42^\circ 24'N$), which has a temperate continental mountain

climate affected by monsoon. Average annual temperature is 3.6°C, and the average annual precipitation is 745 mm. The growing season is from late May to early October. Broadleaved Korean pine forest is a typical forest in the area, and *Pinus koraiensis*, *Fraxinus mandshurica*, *Acer mono*, *Quercus mongolica* and *Tilia amurensis* are its dominant species. The soil in the forest is mainly dark brown soil with a soil field capacity of 85% (0–10 cm depth) (Peng et al., 2019). Average annual atmospheric N deposition in the Changbai Mountain region is 23 kg N ha⁻¹ yr⁻¹, and the rate of N deposition is expected to double by 2050 (Dong et al., 2022).

2.2 Experimental design and treatments

Seven-year-old *P. koraiensis* saplings of similar height (approximately 90 cm) were selected from field in 2017, and then transplanted in pots (diameter 41 cm × height 28 cm) in April of the same year for a two-year (from May to October in 2017 and 2018) multi-level N addition and drought experiment. The soils inside the pots were natural topsoil collected from the broadleaved Korean pine forest. There were three drought treatments: well-watered (maintained at soil field capacity), moderate drought (40–50% of soil field capacity) and severe drought (20–30% of soil field capacity). Under each drought treatment four N addition (urea solutions with different N addition concentrations were sprayed once a month) levels were conducted to simulate the atmospheric N deposition ranging from no N (N0, 0 kg N ha⁻¹ yr⁻¹), low N (N1, 23 kg N ha⁻¹ yr⁻¹), medium N (N2, 46 kg N ha⁻¹ yr⁻¹) and high N (N3, 69 kg N ha⁻¹ yr⁻¹) additions, respectively. A total of 36 tree saplings, representing 12 treatments in total, were used in the experiment. For each treatment, there were three replicates (n = 3) per species, with saplings randomly placed under a transparent rain shelter. Each sapling was measured three times with measurements averaged within each replicate to avoid pseudoreplication. Soil moisture in the pots was monitored at 30-min intervals automatically using soil moisture sensors (Stevens Hydraprobe, Stevens Water Monitoring Systems, Inc., Portland, OR, USA). The changes in soil water content during the experiment are shown in Supplementary Figure S1. In order to distinguish the independent and combined effects of drought and N addition on plants, we defined the single N addition treatment as four N addition gradients under well-watered conditions, and the single drought treatment as three drought gradients without N addition.

2.3 Gas exchange

In late July 2018, the instantaneous values of leaf gas exchange parameters such as A_n and g_s of each pot were measured from 09:00 to 11:00 using a portable photosynthetic system (LI-6400XT, LI-COR Inc., Lincoln, NE, USA). Each sapling was measured three times with three different randomly selected needles. The average of these three measurements represents the measurement data for this plant. During the measurements, chamber CO₂ concentration was set at environmental 400 ppm, photosynthetically active radiation was maintained at 1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$, the flow rate was 500 $\mu\text{mol s}^{-1}$,

and the leaf chamber temperature was maintained at 25 ± 1.5°C. Intrinsic water use efficiency (WUE_i) was calculated using A_n and g_s ($\text{WUE}_i = A_n/g_s$).

2.4 Physicochemical characteristics and non-structural carbohydrates

After gas exchange measurements, measured needles were collected and scanned for leaf area using ImageJ software, and then dried to constant weight at 65°C to obtain leaf dry mass. Leaf mass per area (LMA, g m⁻²) was calculated as leaf dry mass/leaf area. Total C and total N (%) were determined using an elemental analyzer (Elementar Vario MACRO Cube, Hesse, Germany). The contents of soluble sugar (%) and starch (%) were determined by anthrone method described in Zhang et al., (2021a). NSC (%) is the sum of soluble sugar and starch concentrations.

2.5 Statistical analysis

The least significant difference method (LSD) of one-way ANOVA was used to compare the mean values to test the differences in gas exchange, carbohydrate characteristics and physicochemical characteristics under the same drought treatment or N addition level. Two-way ANOVA was used to analyze the effects of different levels of independent N addition, drought stress and their interaction on functional traits. Linear regression was used to analyze the relationships between parameters. Data are provided as mean ± SE. SPSS 21 was used for statistical analysis.

3 Results

3.1 Responses of gas exchange

Drought and N addition treatments had different effects on gas exchange (Figure 1; Supplementary Table S1). Single drought treatments significantly reduced A_n and g_s , reaching minimum values ($1.139 \pm 0.077 \mu\text{mol m}^{-2} \text{s}^{-1}$, $0.019 \pm 0.001 \text{mol m}^{-2} \text{s}^{-1}$) at severe drought and moderate drought respectively (Figures 1A, B). WUE_i showed a trend of increasing and then decreasing with the increase of drought stress, reaching maximum values ($94.677 \pm 9.935 \mu\text{mol mol}^{-1}$) at moderate drought (Figure 1C). Single N addition treatments significantly increased A_n and WUE_i but decreased g_s . Under drought stress, N addition treatments decreased A_n and WUE_i , but increased (the already quite low) g_s (Figure 1). Medium N (N2) and low N (N1) addition had the strongest promoting effects on g_s under moderate and severe drought, respectively (Figure 1B).

3.2 Responses of carbon reserves

Single drought and N addition treatments did not significantly affect the leaf soluble sugar concentrations, but significantly reduced

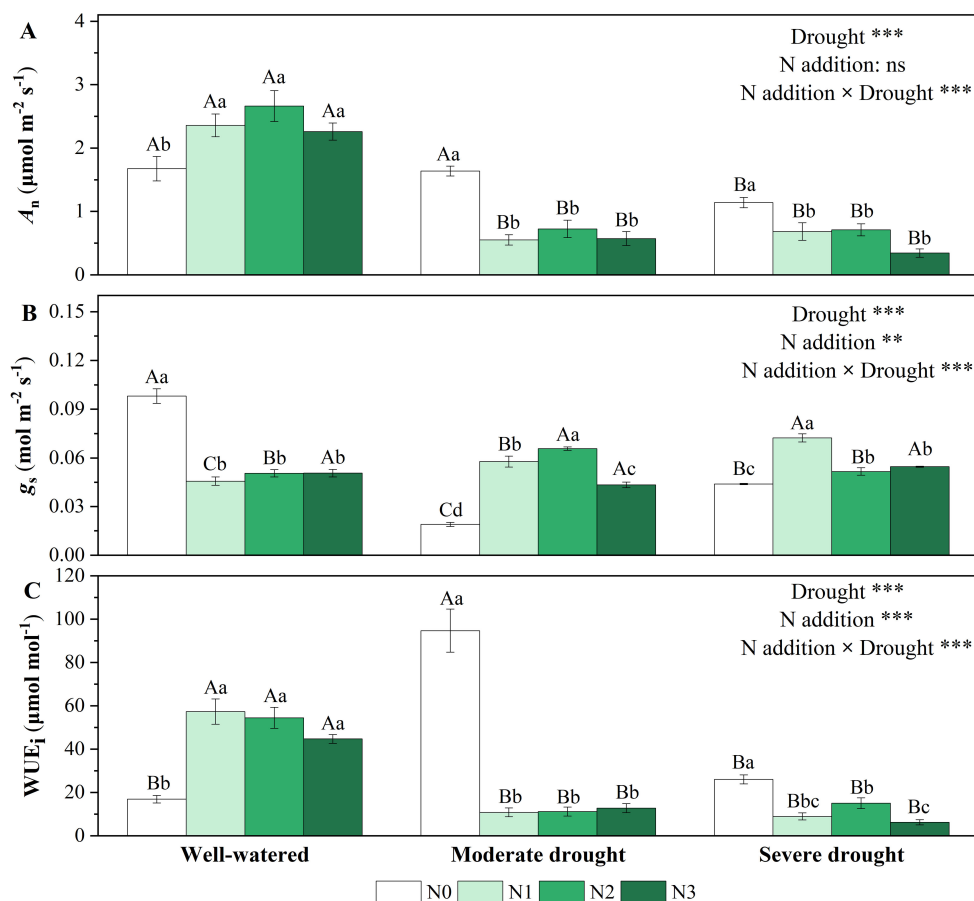


FIGURE 1

Responses of net photosynthetic rate [(A), A_n , $\mu\text{mol m}^{-2} \text{s}^{-1}$], stomatal conductance [(B), g_s , $\text{mol m}^{-2} \text{s}^{-1}$], and intrinsic water use efficiency [(C), WUE_i] of *P. koraiensis* to different treatments of soil water stress and N addition. Different uppercase letters indicated significant differences among different drought treatments at the same N addition level, and different lowercase letters indicated significant differences among different N addition levels in the same drought treatment ($P < 0.05$). $n = 3$. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. N0-N3 represent N addition levels at 0, 23, 46, and 69 kg N $\text{ha}^{-1} \text{yr}^{-1}$ respectively.

leaf starch and NSC concentrations (Figure 2). Under moderate drought, N addition significantly increased leaf starch and NSC concentrations, with the effect on starch concentrations reaching its maximum at medium N addition (N2). However, this positive effect diminished under severe drought (Figures 2B, C). Overall, the interaction effects of drought and N addition on starch and NSC concentrations were significant in needles (Figure 2; Supplementary Table S1).

Unlike the needles, there were significant differences in the effects of all drought and N addition treatments on carbon reserves in stems (Supplementary Figure S2, Supplementary Table S1). Single drought treatments had no effect on soluble sugar but significantly increased stem starch and NSC concentrations. Single N addition treatments significantly increased starch concentrations only at high N addition (N3) (Supplementary Figure S2B). Under moderate drought, N addition had opposite effects on soluble sugar (increase) and starch concentrations (decrease), resulting in non-significant changes in NSC concentrations. Under severe drought, N addition had no statistically significant effect on soluble sugar but significantly decreased starch and NSC concentrations (Supplementary Figure S2).

3.3 Responses of physicochemical traits

Drought, N addition treatments and their interaction had no significant effect on leaf C content (Figure 3A; Supplementary Table S1). Single drought treatments did not significantly affect leaf N content, but leaf N content was significantly higher in N1-N3 than in N0 under all three soil moisture conditions (Figure 3B). Both single drought and N addition treatments had no significant effect on leaf C/N ratio, while under moderate drought, higher N additions (N2 and N3) significantly decreased C/N ratio (Figure 3C). In addition, we found no statistically significant effects of single drought, N addition treatments, or their interaction on stem C and N content (Supplementary Figure S3, Supplementary Table S1).

The effects of single drought and N addition treatments and their interaction on LMA were not significant (Figure 3D; Supplementary Table S1). However, under moderate drought, low N addition (N1) and medium N addition (N2) significantly increased LMA and reached a maximum ($263.52 \pm 5.80 \text{ g m}^{-2}$) at low N (N1) addition.

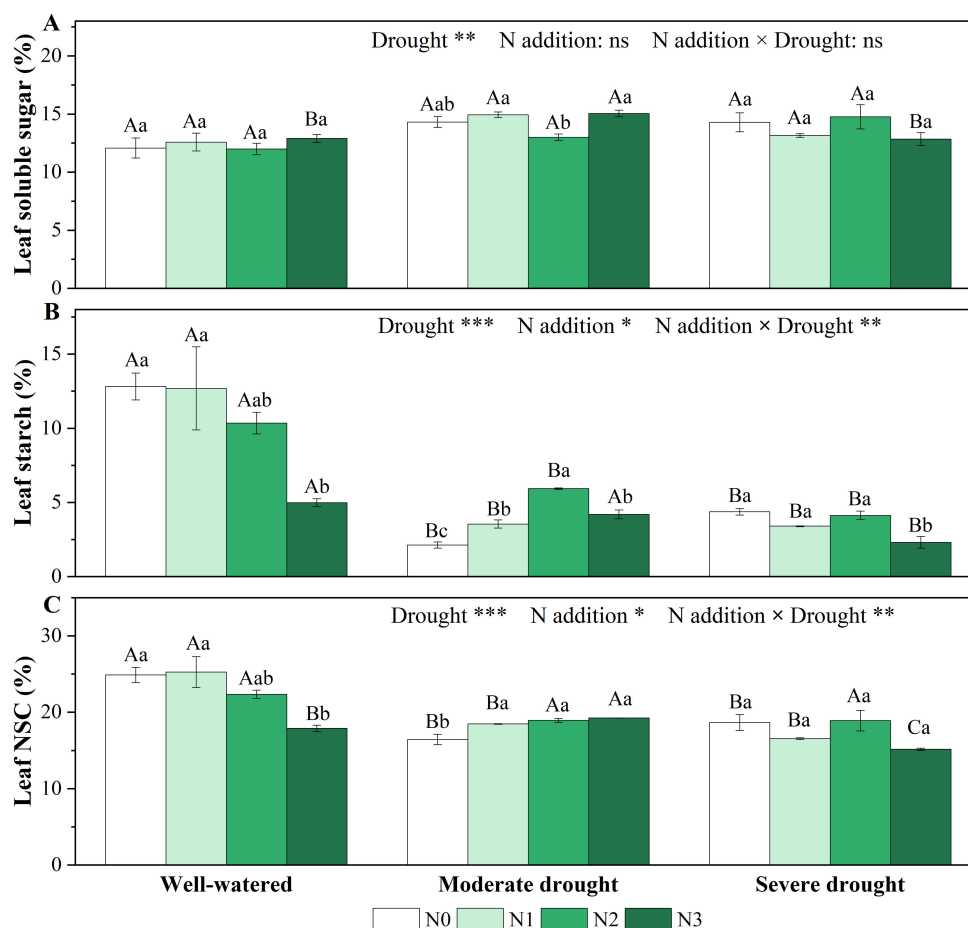


FIGURE 2

Responses of soluble sugar [(A), %], starch [(B), %], and non-structural carbohydrates [(C), NSC, %] in the needles of *P. koraiensis* to different treatments of soil water stress and N addition. Different uppercase letters indicated significant differences among different drought treatments at the same N addition level, and different lowercase letters indicated significant differences among different N addition levels in the same drought treatment ($P < 0.05$). $n = 3$. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. N0–N3 represent N addition levels at 0, 23, 46, and 69 kg N ha⁻¹ yr⁻¹ respectively.

3.4 Relationships in tree functional traits

Through regression analyses we found significant relationships between key functional traits (Supplementary Figure S4). Significant linear relationships were found among A_n , leaf N, leaf C/N, leaf starch, leaf soluble sugar, leaf NSC, WUE_i, and LMA, specifically reflecting the effects of drought, N addition, and their interactions on carbon assimilation and reserves (Figure 4). A_n ($R^2 = 0.46$, $P = 0.009$) and leaf C/N ratio ($R^2 = 0.99$, $P < 0.001$) were significantly reduced when leaf N content increased (Figures 4A, B). Leaf starch concentrations showed a significant positive correlation with A_n ($P = 0.017$, $R^2 = 0.39$) and a negative correlation with leaf soluble sugar concentrations ($R^2 = 0.39$, $P = 0.018$) (Figures 4C, D). NSC concentrations decreased with increasing N content ($P = 0.042$, $R^2 = 0.29$; Figures 4E). This indicated that the increase in leaf N content caused a reduction in carbon assimilation, resulting in changes in carbon reserves. Additionally, LMA is significantly negatively correlated with WUE_i ($R^2 = 0.30$, $P = 0.038$; Figures 4F).

4 Discussion

4.1 Responses of carbon assimilation to drought and nitrogen addition

In the study, the effects of single drought and N treatments on gas exchange traits (such as A_n and g_s) of Korean pine were obviously different. When soil water availability decreases, plants can reduce water loss by closing stomata, leading to the decrease in A_n . The reduction in g_s is the main cause of gas exchange decrease (stomatal limitation). Under severe water stress (severe drought), the epidermal cells surrounding the stomata lose water more rapidly than the guard cells. This imbalance in water loss can cause stomatal dysfunction, leading to the “passive opening” of stomata. This occurs because the guard cells, which are unable to maintain turgor, fail to close properly. As a result, the photosynthetic system, including key enzymes like Rubisco, becomes damaged, leading to a decrease in A_n due to non-stomatal limitations (Jones, 1985; Novick et al., 2015). Then A_n reaches

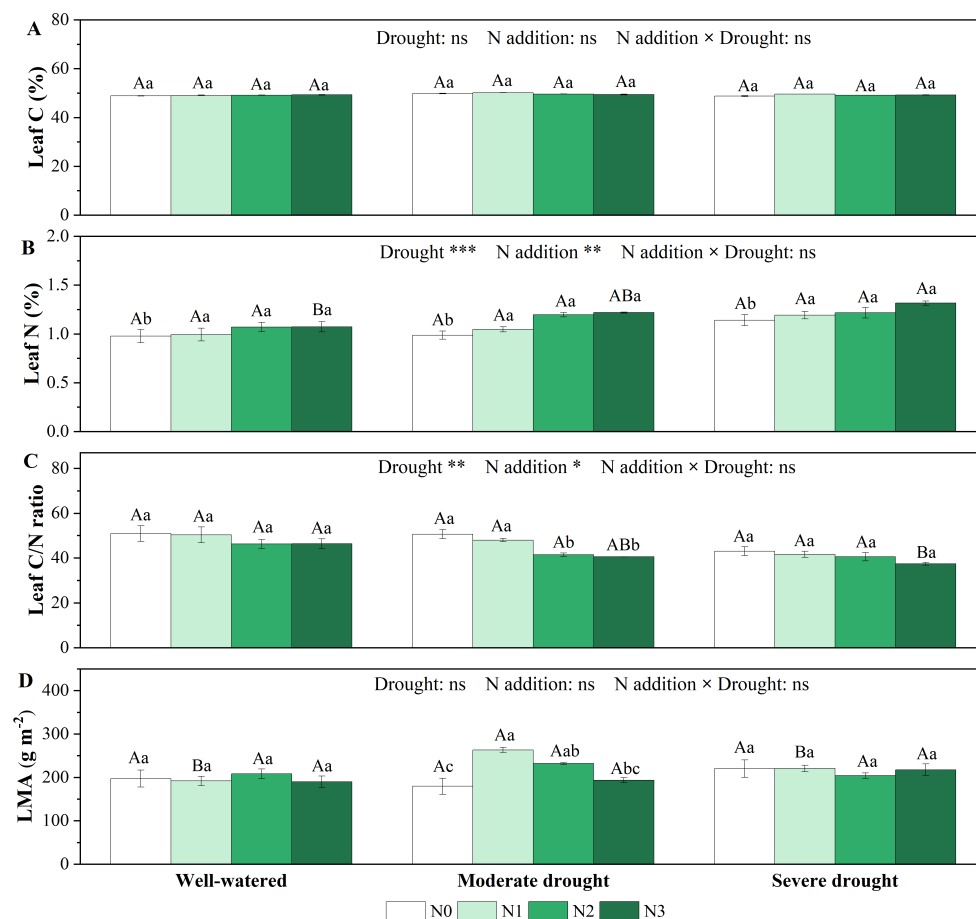


FIGURE 3

Responses of C content [(A), %], N content [(B), %], C/N ratio in the needles (C) and leaf mass per area [(D), LMA, g m⁻²] of *P. koraiensis* to different treatments of soil water stress and N addition. Different uppercase letters indicated significant differences among different drought treatments at the same N addition level, and different lowercase letters indicated significant differences among different N addition levels in the same drought treatment ($P < 0.05$). $n = 3$. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. N0–N3 represent N addition levels at 0, 23, 46, and 69 kg N ha⁻¹ yr⁻¹ respectively.

a minimum and g_s appears to increase (Figures 1A, B), which is why WUE_i reached a maximum under moderate drought in the study (Figure 1C). Similar response to single water stress was also observed with other coniferous species, such as *Pinus sylvestris* (Marozas et al., 2019) and *Pinus pinaster* seedlings (de Miguel et al., 2012).

Single N addition treatments, on the other hand, led to a significant increase in A_n of Korean pine but a decrease in its g_s , resulting in a significant increase in its WUE_i (Figure 1). A study on Chinese fir (*Cunninghamia lanceolata*) seedlings revealed a nonlinear photosynthetic response to N deposition, which was determined by alterations in photosynthetic capacity rather than stomatal conductance (Li et al., 2022). The promotion of leaf photosynthesis by N addition may benefit from changes in the content of enzymes closely related to photosynthesis (Cornwell et al., 2018).

However, with combined drought and N addition treatments, N addition failed to mitigate the negative effects of drought on carbon assimilation for Korean pine. Under drought stress (moderate and severe drought treatments), all N addition levels significantly reduced A_n and WUE_i , although N1 and N2 significantly increased g_s (Figures 1A–C). Similar results were reported for the coniferous

species of *Picea asperat* (Tang et al., 2017). Under drought, added N dissolves in available soil water and may cause additional water stress (van den Driessche et al., 2003). N addition can cause a shift in biomass allocation pattern (in favor of above-ground biomass) by increasing in biomass stem: root ratio, which further increases the evapotranspiration demand of plants, leading to higher drought sensitivity (Meyer-Grünefeldt et al., 2015). In contrast to coniferous species, N addition mitigates the negative effects of drought by enhancing carbon exchange in angiosperm species (Zhang et al., 2021a). Broadleaf angiosperm species have higher vein density than coniferous species, which will increase the area of leaf water exchange with the phylloclaytes (Sack and Holbrook, 2006). In addition, angiosperms have higher fine root density and volume than conifers and have a greater ability to access water in the soil (Wang C. et al., 2019). Furthermore, the tracheids of coniferous species are always less efficient at water transport than the vessels of broadleaf angiosperm species under sufficient water supply (Sperry et al., 2006).

Moreover, C/N represents the ability of plants to assimilate C when absorbing N, reflecting the efficiency of nutrient use. Under the combined stress, A_n and C/N decreased with the increase of leaf

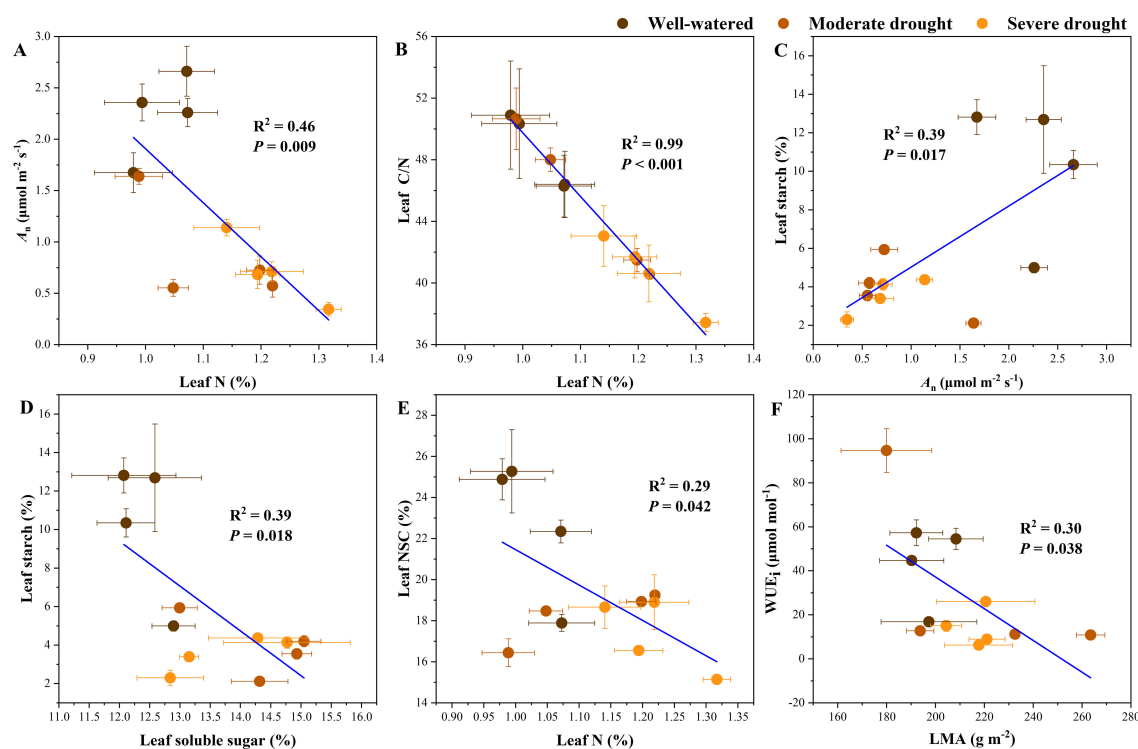


FIGURE 4

Relationships in key functional traits, including relationships between net photosynthetic rate (A_n) and leaf N content (A); between leaf N content and C/N (B); between leaf starch and A_n (C); between leaf starch and leaf soluble sugar (D); and between leaf N content and leaf NSC (E); between the leaf mass per area (LMA) and intrinsic water use efficiency (WUE_i) (F). The error bar represents SE of all measurements.

N content (Supplementary Figures S4, 4A, B), indicating that *P. koraiensis* saplings did not efficiently make use of the nutrients. We also observed a negative correlation between WUE_i and LMA (Supplementary Figures S4, 4F). At moderate drought, where WUE_i reached maximum values under N0 treatment, N addition (N1-N3) resulted in an increase in LMA (Figure 1C). Some studies stated that lower LMA indicates lower leaf construction costs associated with a rapid growth strategy (Wright et al., 2001, 2005). This infers that *P. koraiensis* saplings adopt a conservative strategy by increasing LMA to offset the decrease in water use efficiency (Figure 3D), thereby adapting better to the deterioration of water conditions.

4.2 Response of carbon reserves to drought and nitrogen addition

Although we found that all treatments of single drought and N addition reduced the leaf NSC, the effecting mechanisms of drought and N addition stress should be different. Generally, drought stress causes a reduction in carbon assimilation, and then stored NSC is mobilized, and starch stored in leaves undergoes hydrolysis to maintain cell expansion and sustain metabolic activity (McDowell et al., 2008; McDowell, 2011), which is also supported by our study (Figure 2). During single N addition treatments, N addition increased carbon assimilation by enhancing the net photosynthetic rate, but the

newly assimilated carbon is preferentially used for growth and respiration rather than carbon storage (Li et al., 2020). A recent meta-analysis demonstrated that the NSC in terrestrial plants respond differently to different environmental stress (Du et al., 2020). For example, the change of soluble sugars often occurs during N addition and drought, while starch changes with elevated CO_2 and warming (Du et al., 2020). However, we found similar soluble sugar contents with different treatments in the study. This may be a protective effect of its own (Figure 2A), maintaining a certain osmotic regulation ability to prevent leaves from excessively losing water (Liu et al., 2004). However, different from our results on coniferous species, leaf NSC and its component concentrations of two broadleaf species (*Quercus variabilis* and *Liquidambar formosana*) did not change significantly under single N and water treatment or their combination (Jiang et al., 2022).

We found that N addition significantly increased starch concentrations compared with N0 under moderate drought, indicating that sufficient N addition can slow down the hydrolysis of starch into soluble sugars (Figure 2B), which may be related to osmoregulation. Previous studies suggested that reduced N-supply under drought stress decreases the content of N-containing osmoprotectants such as proline, which positively affects enzyme and membrane integrity (Ashraf and Foolad, 2007; Gessler et al., 2017). N addition can improve plant water status through osmoregulatory mechanisms, by reducing the increase rate of malondialdehyde content (MDA) and alleviating damage to the

plant cell membrane (Liu et al., 2022). For example, it has been demonstrated that under drought stress, N addition significantly reduced the MDA content in three subtropical broadleaf plants (*Schima superba*, *Castanopsis fissa*, and *Michelia macclurei*) (Zhang et al., 2020) and conifer (*Pinus massoniana*) seedlings (Wang D. et al., 2019) to ameliorate the negative effects of drought. However, N addition cannot change the tendency of drought stress to inhibit plant physiological metabolism, but can only slow down the inhibition caused by water shortage. More serious excessive N addition is detrimental to the improvement in the enzymatic defense system of plant cells, leading to leakage of cellular electrolytes and a large increase in the membrane lipid peroxidation product MDA (Su et al., 2021).

Differing from coniferous species, studies on broadleaf species suggested no significant changes in leaf NSC with combined N addition and drought treatments (Zhang et al., 2021a). There may be several reasons to explain this. Firstly, the leaf structure and phloem anatomical features of coniferous species indicated that the outward flow of assimilates in vascular tissues and the rate of phloem transport are lower than in broadleaf species (Dannoura et al., 2011; Liesche and Schulz, 2018). Secondly, for coniferous trees, the imbalance between phloem loading (which may decrease with drought-induced reduction in net CO₂ assimilation) and unloading, as well as reduced transpiration due to stomatal closure, would reduce the hydrostatic pressure gradient along the phloem and thus reduce the transport rate (Dannoura et al., 2011). In this study, the reduction in A_n and g_s exacerbated the reduction in assimilate transport rate, leading to lower NSC reserves ultimately under the combination of drought stress and N addition (Figure 2B). The reduced photosynthetic rate required hydrolysis of NSC components to maintain metabolic processes of plants, which was reflected in the relationship between A_n and starch and the relationship between starch and soluble sugar (Supplementary Figures S4, 4C, D). It indicates that the interconversion between NSC components can regulate the carbon acquisition and expenditure in coniferous species.

4.3 Coordination mechanisms of carbon assimilation and reserves during drought and nitrogen addition

Drought had a negative effect on carbon assimilation, while the opposite was found for N addition. Combination treatments did not improve A_n reduction despite g_s increase; the WUE_i of *P. koraiensis* saplings was as well significantly reduced. Both drought and N addition significantly reduced the total NSC concentrations in leaves, which was caused by the decrease in starch concentrations, although the underlying mechanisms were different. Under the combined treatments, the starch concentrations were significantly increased, yet this only occurred under moderate drought conditions, indicating that different degrees of drought stress and N addition have distinct influences on gas exchange and carbon reserves. Hence, we summarize the physiological mechanisms by which *P. koraiensis* saplings respond to drought stress and N addition. Under drought stress, closure of stomata will lead to

reductions in photosynthesis, hydrolysis of starch and conversion to soluble sugars to maintain plant osmotic pressure and metabolism. N addition can increase photosynthetic rate, and newly assimilated carbon will be invested in growth and respiration preferentially over NSC storage. Under drought with N addition, *P. koraiensis* will maintain carbon and water fluxes by increasing stomatal conductance, but will fail to prevent A_n reduction, leading to a decrease in carbon assimilation. As a result of the decrease in carbon assimilation, stored starch underwent hydrolysis and stored NSC will be mobilized.

4.4 Future work

To better understand the physiological adaptation mechanisms underlying interactive stresses of drought and N deposition, further work should take into account: (1) In this study, we used N per unit mass but not N per unit area to analyze the leaf C and N contents, which may to some extent ignore the effects of leaf thickness and density (Rosati et al., 2000). (2) Integrate intrinsic regulatory mechanisms in different plant parts for more detailed comprehensive analysis, including migration between different aboveground and belowground organs, as well as responses of anatomical structures, hydraulic properties and eventually biomass; (3) More finely time scale measurements would be helpful to understand the diel and seasonal responses of conifer trees, encompassing different growth and development periods.

5 Conclusions

In this study, we investigated how drought and N addition stresses affect carbon assimilation and carbon reserves of *P. koraiensis* saplings. We found that N addition was not able to mitigate all the negative effects of drought stress on carbon assimilation. The interconversion between leaf NSC components can slow down the reduction of carbon assimilation, which was at the expense of carbon reserves. Our study indicated that *P. koraiensis* failed to benefit from N investment and adapted to reduced water use efficiency by increasing LMA, which suggests a conservative resource use strategy.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

JT: Investigation, Writing – original draft. HZ: Investigation, Writing – review & editing. AW: Conceptualization, Funding acquisition, Writing – review & editing. JW: Writing – review & editing. SR: Writing – review & editing. KZ: Investigation, Writing –

review & editing. RC: Methodology, Writing – review & editing. FY: Conceptualization, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fpls.2025.1574468/full#supplementary-material>

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High species diversity and biochar can mitigate drought effects in arid environments

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Introduction: Climate change, including drought, threatens ecosystems across the globe. The current study investigated the effects of species diversity and biochar application on the performance and productivity of five native Omani species under control and drought conditions.

Methods: A fully controlled greenhouse experiment was conducted in which five native species of three different diversities (one, two, and four species) were grown under four different treatments: biochar+drought, biochar, drought, and control. Productivity was measured through total biomass and root-to-shoot ratio), while performance was assessed in the form of plant functional traits (plant height, specific leaf area (SLA), and specific root length (SRL). Nutrient availability in the soil was measured using soil organic carbon (SOC) and soil total nitrogen (STN). Soil microbial content was determined using soil microbial biomass “Cmic” and soil microbial basal respiration. Biodiversity effects were analyzed using the complementarity effect (CE), selection effect (SE), and net biodiversity effect (NBE).

Results and discussion: The study indicated that high diversity and biochar resulted in: 1. species with 66.6% greater total biomass and a 3% reduction in RSR, 2. enhanced species performance, with plants growing 25% taller, 50% higher SLA, and 25% higher SRL, 3. more fertile soil, with SOC and STN increasing by 40% and 33.3%, respectively, and 4. improved microbial content, with Cmic rising by 15% and basal respiration increasing by one-third under drought conditions compared to monoculture. These results highlight the intricate interactions between climate change and biodiversity, which are crucial for predicting the impact of changes in functional composition on ecosystem processes and, subsequently, for restoring arid ecosystems in Oman.

KEYWORDS

arid lands, drought, plant species diversity, microbial content, oman

1 Introduction

Arid and semi-arid ecosystems comprise approximately 40% of the Earth's surface (Tariq et al., 2024) and are significantly influenced by climate change, particularly through drought, changes in land-use, and various human activities (Sala et al., 2000; Jung et al., 2020). Drought has complex effects on these ecosystems, impacting community composition and species diversity, and consequently, the functions and productivity of the ecosystem (Jung et al., 2020; Wei et al., 2022).

One of the important driver of community composition, ecosystem function, and climate change mitigation is the net biodiversity effect (Xu et al., 2024), which is mediated by complementarity and selection effects (Hu et al., 2021). The net biodiversity effect refers to the overall impact of species diversity on ecosystem functioning, particularly primary productivity (Chen et al., 2025). Studies have consistently shown a positive relationship between biodiversity and ecosystem productivity across various ecosystems (Bruno et al., 2005; Maron et al., 2021). Complementarity effects occur when species in diverse communities use resources more efficiently through niche differentiation or facilitation, leading to increased ecosystem productivity and stability (Wang et al., 2021). Selection effects occur when dominant species with particular traits affect ecosystem processes, which can be positive, negative, or neutral (Chen et al., 2025). A positive selection effect occurs when species with particular traits dominate communities and enhance ecosystem processes (Loreau and Hector, 2001), whereas a negative selection effect occurs when no dominant or high-performing species are found within the community (Jiang et al., 2008). Several studies have reported that plant diversity promotes ecosystem functioning through biomass production (Huang et al., 2020; Hu et al., 2021; Xi et al., 2023), however a robust conclusion regarding such role is still missing. Studies have shown that the biodiversity effects “net biodiversity, complementarity and selection effects” are mediated by the plant functional traits (e.g., plant height, specific leaf area (SLA), specific root length (SRL), and root to shoot ratio (RSR)) of the plant species that make these communities (Roscher et al., 2012). Plant height measures plant competitiveness in capturing resources, such as light (Pérez-Harguindeguy et al., 2013), SLA reflect growth rates (Violle et al., 2012), whereas SRL show the economic aspects of root systems as it measures the length to mass ration of the root system (Ostonen et al., 2007), and RSR which show the ability of plants to mitigate drought conditions, especially in arid ecosystem (Cambui et al., 2011).

In addition to plant diversity and functional traits, soil properties and microbial content are important for determining ecosystem functionality and resilience (Martinez-Almoyna et al.,

2020). Soil organic carbon (SOC) and soil total nitrogen (STN) are important indicators of soil fertility, which are affected by various biotic and abiotic factors (Crowther et al., 2016; Gibbons et al., 2017). Additionally, SOC and STN affect multiple functional processes in the soil, including its ability to retain water and maintain stable aggregates (Murphy, 2015). On the other hand, soil microbial communities (microbial carbon “Cmic” and soil basal respiration) considered as important drivers of ecosystem functions, particularly for nutrient cycling and decomposition processes, especially in arid ecosystems (Wang et al., 2020b).

It has been shown that higher plant diversity increases soil microbial biomass, respiration, and fungal abundance, which consequently improve nitrogen mineralization rates (Schnitzer et al., 2011). This relationship between plant diversity and soil microbial content is complex, as plant diversity influences soil microbial community structure and function, while soil microbes reciprocally affect plant performance and productivity, and in turn, ecosystem processes (Saleem et al., 2019; Jayaramaiah et al., 2025). Several previous studies have reported a relationship between plant diversity and soil microbial properties, which is not always straightforward. For instance, in temperate deserts, soil bacterial alpha and beta diversities are primarily determined by abiotic and spatial factors, followed by plant factors (Wang et al., 2020b). Additionally, the temporal effects of plant diversity on soil microbial content can change over time, suggesting that the recovery of soil microbial communities from land-use changes may take more than a decade (Strecker et al., 2016). Such properties can be significantly enhanced by soil management practices, such as biochar amendments, in areas that suffer from low diversity and drought, especially arid and semi-arid ecosystems (Ali et al., 2023). Biochar amendment can improve soil properties and soil microbial activities, which can consequently improve ecosystem structure and functions (Joseph and Lehmann, 2015; Mandal et al., 2016). It is considered an eco-friendly method to mitigate the effects of climate change (Griscom et al., 2017), especially adapting soil to extreme weather events, such as prolonged drought (Chausson et al., 2020) and as a result, benefits biodiversity (Morecroft et al., 2019; Seddon et al., 2021). Biochar is a carbon-rich material produced by biomass pyrolysis in an oxygen-limited environment (Lehmann et al., 2015). It enhances soil fertility directly by providing essential soil nutrients and soil carbon (Coomes and Miltner, 2017; Igalavithana et al., 2017) or indirectly by neutralizing soil acidity (Zhang et al., 2017) and increasing water holding capacity and soil aeration.

In the current study, a fully controlled greenhouse experiment was conducted to study the interactive effects of plant species diversity and biochar amendment, on plant performance, plant productivity, soil properties, soil microbial content and biodiversity effects under drought conditions using five native species to Oman (*Ranunculus muricatus* L., *Ipomoea obscura* (L.) Ker Gawl., *Pulicaria glutinosa* (Boiss.) Jaub. & Spach, *Dicoma schimperii* (DC.) Baill. ex O.Hoffm., *Paronychia arabica* (L.) DC.). Artificial plant communities were established using these five species with three levels of diversity (one, two, and four species). These communities were subjected to four treatments: control, drought,

Abbreviations: CE, Complementarity Effect; Cmic, Soil Microbial Biomass; NBE, Net Biodiversity Effect; RSR, Root to Shoot Ratio; SE, selection effect; SLA, Specific Leaf Area; SOC, Soil Organic Carbon; SRL, Specific Root Length; STN, Soil Total Nitrogen.

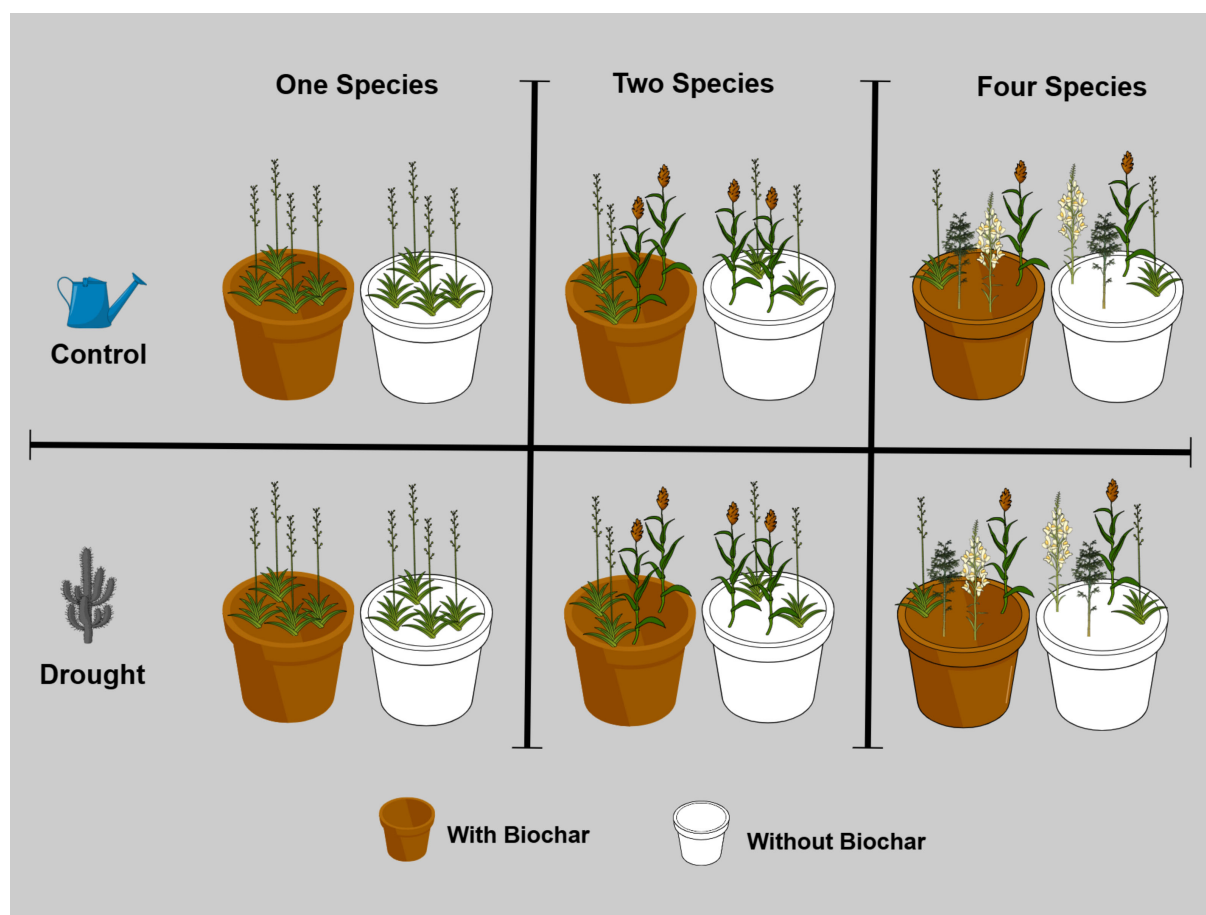


FIGURE 1

Experimental design to investigate the effects of drought (drought and control), biochar (with and without biochar), and species diversity (one, two, and four species), with five replicates per treatment ($n = 60$).

biochar, and biochar+drought. Specifically, the following questions were addressed:

1. Do species diversity and biochar amendment affect plant performance and productivity under drought conditions? How are these effects mediated by plant functional traits (plant height, SLA, and SRL)?
2. Does the relative importance of net biodiversity, complementarity, and selection effects change with species diversity and biochar amendment under drought conditions?
3. Are these effects controlled by soil properties (SOC and STN) and microbial content (Cmic and basal respiration)?

By integrating biodiversity, plant functional traits, soil properties, soil microbial content, and the use of biochar as an eco-friendly soil amendment, this study provides solutions for mitigating drought impacts in arid ecosystems that suffer from low species diversity. These findings shed light on the mechanisms driving ecosystem resilience, with practical implications for the restoration and conservation of arid environments under drought conditions.

2 Materials and methods

2.1 Plant species and experimental setup

A full factorial experiment was conducted, including four treatments (Control, Drought, Biochar, and Biochar + Drought) with three levels of species diversity (one, two, and four species) and five replicates per treatment in the greenhouse of Sultan Qaboos University, Muscat, Oman (23°36'0.95" N, 58°10'5.29" E) (Figure 1). Five native species were chosen to construct the experimental plant communities, *Ranunculus muricatus* L., *Ipomoea obscura* (L.) Ker Gawl., *Pulicaria glutinosa* (Boiss.) Jaub. & Spach, *Dicoma schimperi* (DC.) Baill. ex O.Hoffm., *Paronychia arabica* (L.) DC. (Supplementary Table S1 in the Supplementary Materials) based on their occurrence in the natural habitats of Oman (Pickering and Patzelt, 2008; Ghazanfar, 2015). For the treatments of the different species diversities, five monocultures (i.e., one for each species) were established for the 1-species treatment and five species mixtures for both the 2-species and 4-species treatments. Species mixtures were randomly selected from the original species pool, which consisted of five species, all of which had equal representation at each level of diversity (Supplementary Table S2 in the Supplementary Materials).

Each monoculture or species mixture was considered as one replicate of the diversity level, which resulted in five replicates for each of the three species diversity levels. In total the experiment had 60 pots (3 species diversity (1, 2 and 4 species) $\times$ 4 treatments “Control, Drought, Biochar, and Biochar + Drought” $\times$ 5 replicates).

On February 3rd, 2024, seeds of the five species were sown in separate trays (60 cm $\times$ 30 cm $\times$ 3 cm) filled with universal potting soil (Potgrond, Van Egmond Potgrond B.v, Rijnsburg, Holland) in the greenhouse under temperature controlled at 25°C during the daytime and 16°C during nighttime and watered twice a week. On March 5th, 2024, four seedlings of different species mixtures of the same size were transplanted into 60 pots (length = 50 cm, width = 21.5 cm, and height = 16 cm) (Figure 1; Supplementary Tables S1, S2) filled with pre-sieved soil collected by digging from the Sultan Qaboos University Botanic Garden. For the biochar treatment, 30 pots were amended with 1.25 kg of biochar to the topsoil before seedling transplantation; the other 30 pots did not receive any biochar, following the recommendation of Ali et al. (2023). All pots were randomly placed in the greenhouse and watered twice a week for three weeks, after which dead seedlings and seedlings of other species growing within the study pots were continuously removed throughout the experiment. To emulate the drought treatments, the pots were split into two treatments: the control pots ($n = 30$) which were watered normally with 660 ml twice a week, and the drought pots ($n = 30$) that were watered twice a week with just 220 ml, which represents 20% of soil saturation following previous studies (Ali and Bucher, 2022; Ali et al., 2023).

2.2 Plant harvest and measurements

On September 10, 2024, aboveground and belowground plant functional traits (plant height, SLA, SRL, and RSR) were measured along with total biomass following standardized protocols (Pérez-Harguindeguy et al., 2013). To account for intraspecific trait variability, traits were measured for every individual within each pot (Albert et al., 2012; Ali et al., 2017a). Plant height (cm) was measured as the distance between the lowest and highest photosynthetic parts of the plant using a meter. On three healthy and fully developed leaves for every individual in each pot, SLA was measured as the ratio between leaf area (LA, mm²) and dry mass (mg), expressed as (mm² mg⁻¹). LA was measured digitally by analyzing scanned digital images using Easy Leaf Area software (Easlon and Bloom, 2014). The leaves were weighed to record the fresh mass, oven-dried at 70°C for 48 h, and then weighed again to assess the leaf dry mass (mg). Finally, LA was divided by the leaf dry weight to calculate SLA. The biomass and root-to-shoot ratio (RSR) of the plants were calculated after cutting the plants at the soil surface, drying them at 70°C for 48 h, and weighing them as aboveground biomass (g). Additionally, the RSR for each individual was measured as the ratio of root dry weight to shoot dry weight, as described by Mašková and Herben (2018). Finally, the SRL (cm/g) was measured as the root length divided by the root dry mass after scanning the whole root using a flat-bed scanner at a resolution of 800 dpi, and measured root length (cm) for each

individual using the images scanned by RhizoVision Explorer (Seethepalli et al., 2021).

After harvesting the aboveground and belowground plant materials from all pots, the soil was mixed within each treatment and air-dried to measure the soil organic carbon (SOC) and soil total nitrogen (STN), which reflect soil fertility, soil quality, and consequently plant growth (Crowther et al., 2016). SOC was determined using a modified Walkley and Black wet oxidation method (Nelson et al., 1996) and STN was determined using the modified macro Kjeldahl digestion method (Bremner and Mulvaney, 1983); both were expressed as g/kg soil.

To understand how drought, biochar, and species diversity may affect plant performance and production by affecting soil microbial activity, soil microbial biomass and soil microbial basal respiration were measured using 3 g of fresh soil with an O₂-microcompensation apparatus following Scheu (1992). Soil microbial basal respiration (μl O₂ h⁻¹ g⁻¹ dry soil) was measured hourly for 24 h at 20°C. Additionally, soil microbial biomass (Cmic; μg C g⁻¹ dry soil) was calculated from the maximum initial respiratory response after the addition of glucose, as described by Eisenhauer et al. (2007).

Finally, the complementarity effect (CE), selection effect (SE), and net biodiversity effect (NBE) were measured to understand the effect of biodiversity under different diversity levels and treatments, following Loreau and Hector (2001). NBE was measured as the difference between the observed biomass of the species when grown in a mixed community and the expected biomass of the species in monoculture, based on the relative abundance of the species in the mixture, using the following equations:

$$NBE = \text{Observed Biomass} - \text{Expected Biomass}$$

$$\text{Expected Biomass} = \sum_{i=1}^N p_i \times M_i$$

Where N is the number of species in the mixture, p_i is the relative abundance of species i in the mixture, and M_i is the biomass of species i in monoculture. CE was measured using the following equation:

$$CE = N \times \overline{\Delta RY_i} \times \overline{M_i}$$

Where N is the number of species in the mixture, $\overline{\Delta RY_i}$ is the mean deviation of the relative yield of species i from its expected relative yield ($RY_i - \frac{1}{N}$), and $\overline{M_i}$ is the mean monoculture yield of species i . Finally, the SE was calculated as the following formula as covariance between the relative yield (RY_i) of species i and its monoculture yield (M_i) multiplied by the number of species in the mixture (s).

$$SE = N \times \text{cov}(RY_i, M_i)$$

2.3 Statistical analysis

R software version 4.4.3 were used to run all statistical analyses and produce all figures (R Development Core Team, 2025). The

effects of diversity (i.e., 1, 2, and 4 species) and the four combinations of biochar and drought treatments (control, drought, Biochar and Biochar + drought) were tested as fixed variables alone and in interaction on community productivity (i.e., biomass and RSR), plant functional traits (plant height, SLA, and SRL), soil abiotic properties (i.e., soil organic carbon (SOC) and soil total nitrogen (STN) contents), soil microbial activity (i.e., microbial biomass (Cmic) and basal respiration), and biodiversity effects (CE, SE, and NBE) as response variables. In addition, the plot ID was used as a random intercept using linear mixed effect models of the package “lme4” (Bates et al., 2015). For *post hoc* evaluation, Tukey’s multiple comparison test was applied between all the levels of the two fixed variables using the “emmeans” and “multcomp” packages (Hothorn et al., 2008; Lenth, 2022).

3 Results

Overall, the results of the current study showed significant effects of species diversity (two and four species), biochar and drought treatments (drought, Biochar and Biochar + drought), and their interactions on plant performance (plant height, SLA, and SRL), productivity (biomass and RSR), soil properties (SOC and STN), microbial content (Cmic and basal respiration), and biodiversity (NBE and CE) (Supplementary Table S3).

3.1 Effects of species diversity, biochar, and drought on species performance

Significant differences were found in the three plant functional traits that reflected plant performance (plant height, SLA, and SRL) in response to diversity, biochar, and drought (Figures 2A–C). Biochar significantly improved plant height and SLA compared to the control treatments, even under drought conditions. Such improvements were positively correlated with species diversity for plant height, SLA, and SRL, and significantly increased with increasing species diversity. Although drought negatively affected SRL, 4-species diversity had a significant positive effect on SRL. Biochar alone did not have any significant effect on SRL, but it improved significantly under drought conditions and when interacting with 2- and 4-species diversities. These results were confirmed by the LMMs, which explained 76%, 86%, and 71% of the variance by plant height, SLA, and SRL, respectively (Supplementary Table S3 in the Supplementary Materials). Although the interaction between species diversity, biochar, and drought did not significantly affect plant height and SLA, it significantly affected SRL (Figures 2A–C; Supplementary Table S3).

3.2 Effects of species diversity, biochar and drought on species productivity

The current results revealed that plants that grew under biochar treatment had higher total biomass than the control; furthermore, drought significantly reduced the total biomass, but this reduced

biomass improved in response to biochar even under drought treatment. Likewise, total biomass increased with increasing species diversity (Figure 3A; Supplementary Table S3 in the Supplementary Materials). The LMM results showed that 78% of the variance was explained by total biomass, and there was a significant interaction between species diversity, biochar, and drought on their effects on total biomass (Supplementary Table S3). The RSR showed the opposite trend to the total biomass, as species that grew under drought conditions had a higher RSR than the other treatments at the three species diversities (Figure 3B; Supplementary Table S3 in the Supplementary Materials), with 64% of the variance explained by LMMs for RSR (Supplementary Table S3). Drought significantly affected RSR compared to the control, but no other treatments or interactions significantly affected it (Figure 3B; Supplementary Table S3).

3.3 Effects of species diversity, biochar and drought on soil properties

Diversity, biochar, and drought had significant effects on soil properties (SOC and STN) (Figures 4A, B; Supplementary Table S3 in Supplementary Materials). The LMMs explained 84% and 69% of the variance in SOC and STN, respectively. Although diversity and drought significantly affected soil properties, biochar did not show any significant effect on soil properties (Figures 4A, B). Finally, the interaction between diversity, biochar, and drought significantly affected STN, but this was not the case for the interaction between 2-species diversity, biochar, and drought on their effects on SOC (Figures 4A, B; Supplementary Table S3 in Supplementary Materials).

3.4 Effects of species diversity, biochar, and drought on microbial content

The soil microbial biomass showed a significant positive response to the diversity of 4-species, a significant negative response to drought, and a significant negative interaction between 4-species and drought in comparison to the other treatments, and 59% of the variance was explained by LMMs (Figure 5A; Supplementary Table S3 in the Supplementary Materials). Soil basal respiration was positively affected by the two species diversity (2 and 4 species) and negatively by drought in comparison to the other treatments, where 73% of the variance was explained by LMMs (Figure 5B; Supplementary Table S3 in the Supplementary Materials). Biochar did not significantly affect soil microbial biomass or soil basal respiration, but it improved the soil basal respiration significantly when interacted with the 4-species diversity (Figures 5A, B; Supplementary Table S3 in the Supplementary Materials).

3.5 Effects of species diversity, biochar and drought on biodiversity effects

The complementarity effect values were consistently positive and were significantly affected by species diversity, biochar, and

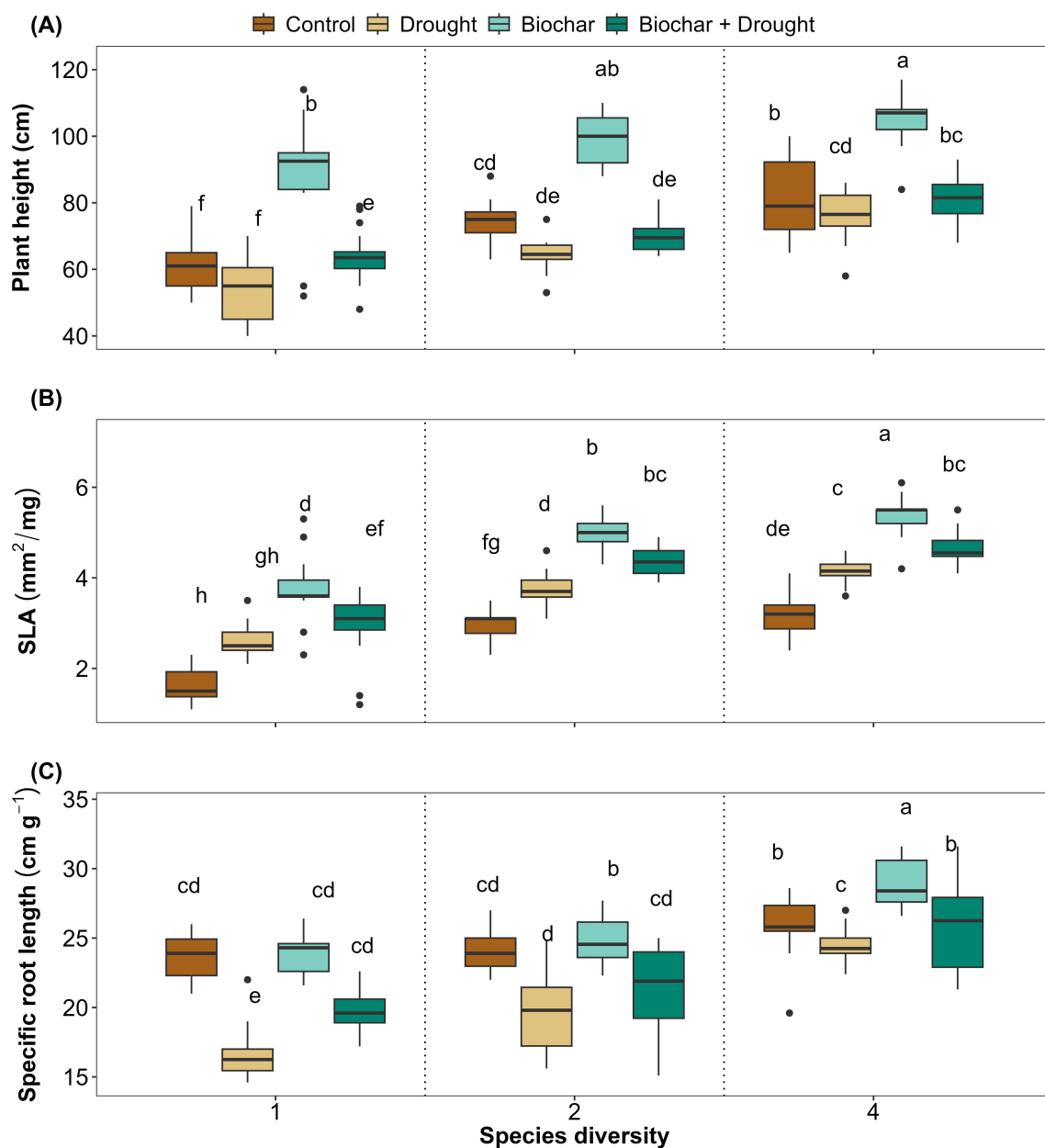


FIGURE 2

Effect of diversity and biochar application on (A) Plant height, (B) Specific leaf area (SLA), and (C) Specific root length (SRL) under control and drought conditions. Letters indicate significant differences among treatments based on Tukey's multiple comparison test.

biochar+drought. However, the effects of drought alone and the interactions between diversity, biochar, and drought were not significant compared to the other treatments, with 96% of the variance explained by the LMMs (Figure 6A; Supplementary Table S3 in the Supplementary Materials). In contrast, there were no significant effects of any of the treatments on the selection effect; their values were always negative, and only 23% of the variance was explained by the LMMs for the selection effect (Figure 6B; Supplementary Table S3 in the Supplementary Materials).

In contrast, the net biodiversity effect was significantly affected by species diversity, drought, biochar, and biochar+drought when compared to the control; however, there were no significant effects

of the different interactions on the net biodiversity effect (Figure 6C; Supplementary Table S3 in the Supplementary Materials), and 51% of the variance was explained by LMMs for the net biodiversity effect (Supplementary Table S3).

4 Discussion

The current study is one of the few to explore the combined effects of species diversity and biochar in mitigating drought effects in arid environments by measuring species performance, productivity, soil properties, microbial content, and biodiversity

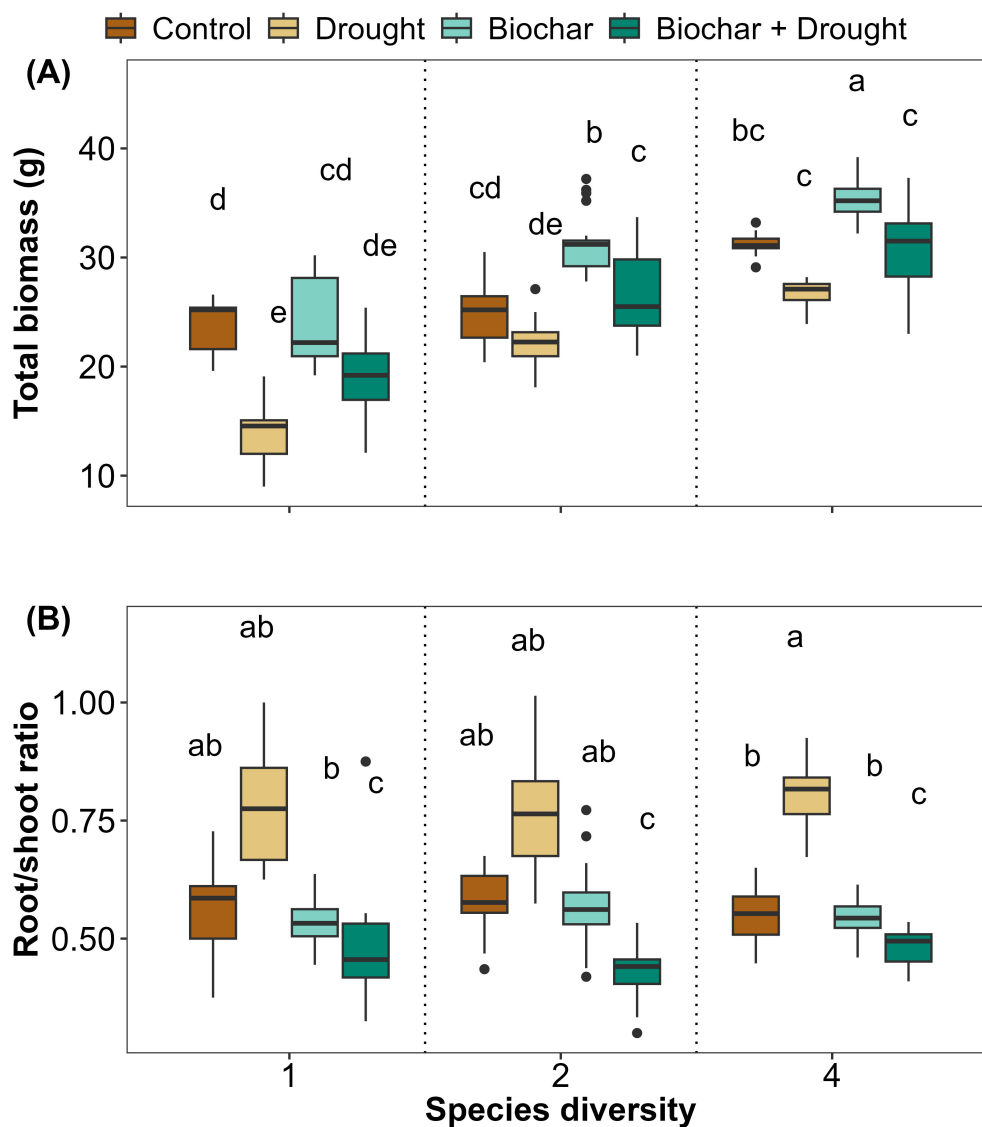


FIGURE 3

Effects of diversity and biochar application on (A) total biomass and (B) root/shoot ratio (RSR) under control and drought conditions. Letters indicate significant differences among treatments based on Tukey's multiple comparison test.

effects. It has been showed that both species diversity and biochar as soil amendments can mitigate drought effects under greenhouse conditions by enhancing species performance (higher plant height, SLA, and SRL), species productivity (high total biomass), soil properties (high SOC and STN), soil microbial content (higher Cmic and basal respiration), and biodiversity effects (complementarity and net biodiversity) of the plant communities.

4.1 Effect of species diversity and biochar amendment on species performance and productivity under drought

The present study found that high species diversity buffered the adverse impacts of drought on both species productivity (biomass) and performance (plant functional traits), especially when biochar

was added to the soil, confirming that in diverse communities, drought-sensitive species are less affected by dry conditions compared to their performance in monocultures (Wright et al., 2021), which suggest that biodiversity can mitigate harsh environmental conditions and can potentially be used as a tool to protect plant species against several environmental changes such as drought (Chen et al., 2022; Dietrich et al., 2022; Li et al., 2023; Liu et al., 2024; Wang et al., 2024). Biochar amendment has also demonstrated positive effects on plant productivity and performance under drought conditions, as it can improve the biochemical and physiological traits, root architecture, and cellular homeostasis of plants (Bisht et al., 2024).

Regarding biomass production, species produced more biomass as species diversity increased, even under drought conditions, confirming the previous findings of Kreyling et al. (2017) who found that while drought reduced aboveground biomass by 30%,

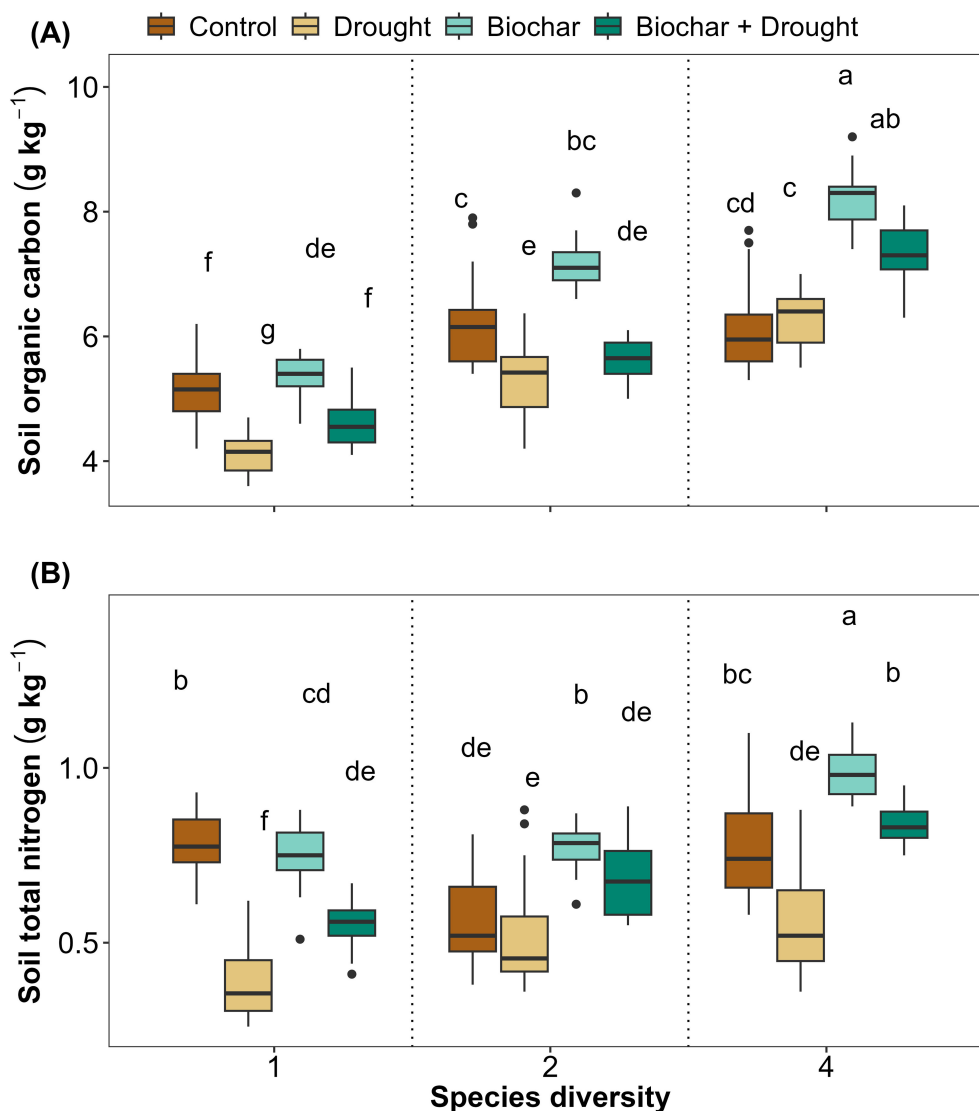


FIGURE 4

Effects of diversity and biochar application on (A) soil organic carbon (SOC) and (B) soil total nitrogen (STN) under control and drought conditions. Letters indicate significant differences among treatments based on Tukey's multiple comparison test.

species richness promoted recovery, particularly in low-productivity communities. In another study by [van Rooijen et al. \(2015\)](#) higher plant diversity showed a lower negative response to drought in terms of biomass production. These findings demonstrate that biodiversity can increase ecosystem resistance to drought, with the negative effects being less pronounced in high-diversity plant communities ([Wagg et al., 2017](#); [Chen et al., 2022](#)). The results also showed improved biomass in response to biochar amendment, even under drought conditions, confirming the role of biochar in enhancing nutrient supply rather than increasing water uptake by improving soil microbial communities ([Hardy et al., 2019](#)). Specifically, biochar application increased nitrogen acquisition through biological nitrogen fixation and enhanced potassium uptake, which may have increased stress tolerance ([Mannan et al., 2021](#)).

RSR, which is a measure of plant productivity, was only significantly affected by drought. The highest RSR was obtained under drought and 4-species diversity, suggesting that under drought conditions, species tend to reduce their aboveground biomass rather than reducing their root biomass to adapt to water deficiency and absorb as much water as possible ([Lemoine et al., 2013](#)). These findings are consistent with previous studies suggesting that increased species richness enhances multifunctionality and stability of ecosystem functions under drought conditions ([Grossiord et al., 2014](#); [Grange et al., 2024](#)).

Plant height, SLA, and SRL, which are considered good measures to detect the effects of diversity and climate change on an ecosystem scale, a significant effect of species diversity on these parameters was detected, as plant height and SLA increased in response to species diversity under both drought and biochar

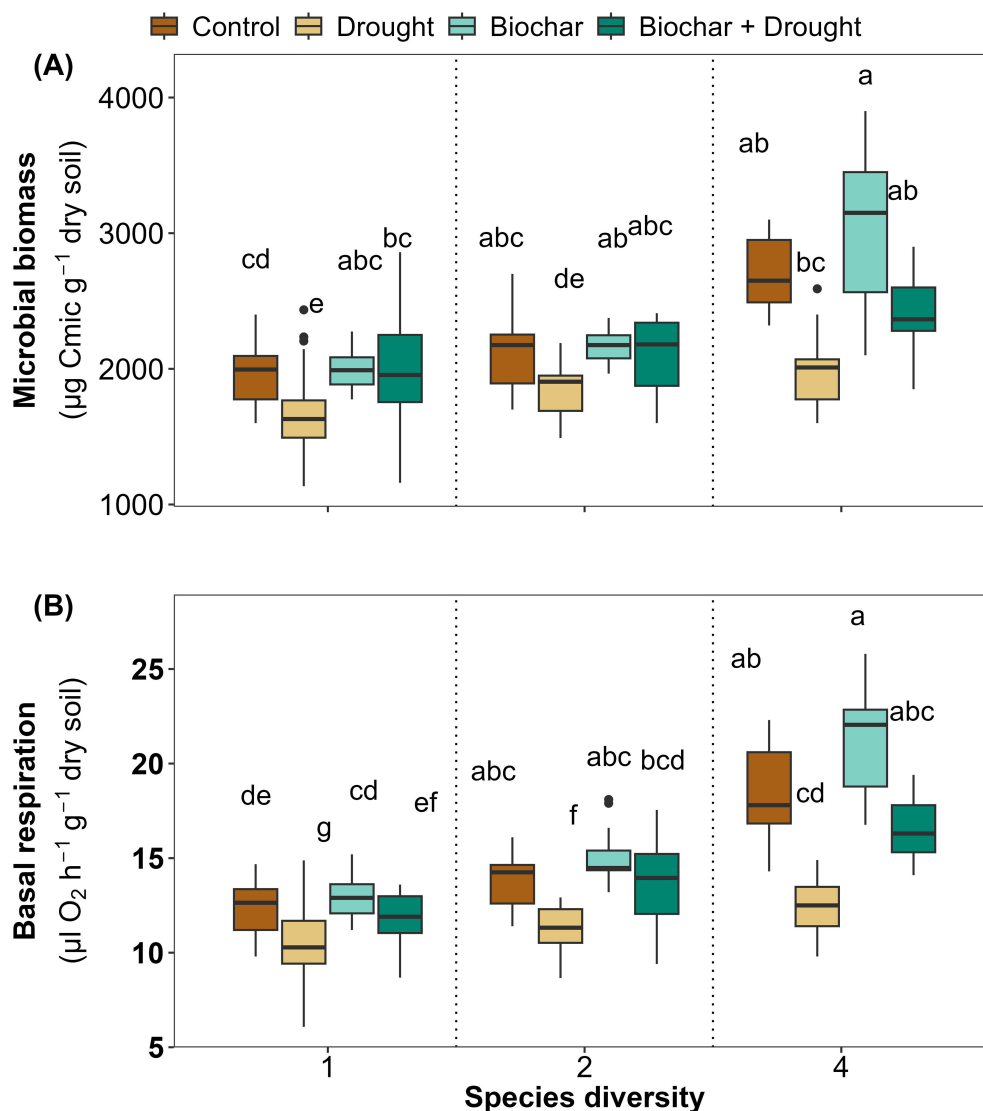


FIGURE 5

Effects of diversity and biochar application on (A) microbial biomass (Cmic) and (B) soil basal respiration under control and drought conditions. Letters indicate significant differences among treatments based on Tukey's multiple comparison test.

treatments. These results suggest that in communities with high species diversity, species can better utilize light and nutrients owing to the greater variation in plant height, SLA, and SRL (Freschet et al., 2021; Hou et al., 2024). As previously discussed, drought can affect the allocation strategies of plants owing to its effect on soil nutrient availability as a result of water shortage (Knapp et al., 2017), which can be mitigated by improving plant species diversity (Hou et al., 2024). Biochar also improved plant height and SLA under drought conditions, especially in species-rich communities, confirming previous findings that biochar application improves plant performance under drought conditions (Ali et al., 2017b) by increasing the water-holding capacity and physical and biological properties of soils, which can indirectly affect leaf and root characteristics and consequently improve nutrient acquisition (Moles et al., 2009). The current results showed also positive effects of 4-species diversity and its interaction with drought on

SRL, which suggest that under high species diversity and drought plants adopt a drought tolerant strategy to allow efficient water absorption capacity (Bristiel et al., 2019), such responses of SRL to drought were not obvious under low species diversity as plants under drought treatment showed lower SRL in comparison to the other treatments, which suggest previous findings that drought reduce SRL in species poor communities (Larson and Funk, 2016; Lozano et al., 2020).

4.2 Role of soil properties and microbial content in mitigating drought

In the current study, species diversity and biochar application had significant effects on SOC and STN under drought conditions, which can be discussed as species diversity enhancing SOC and STN

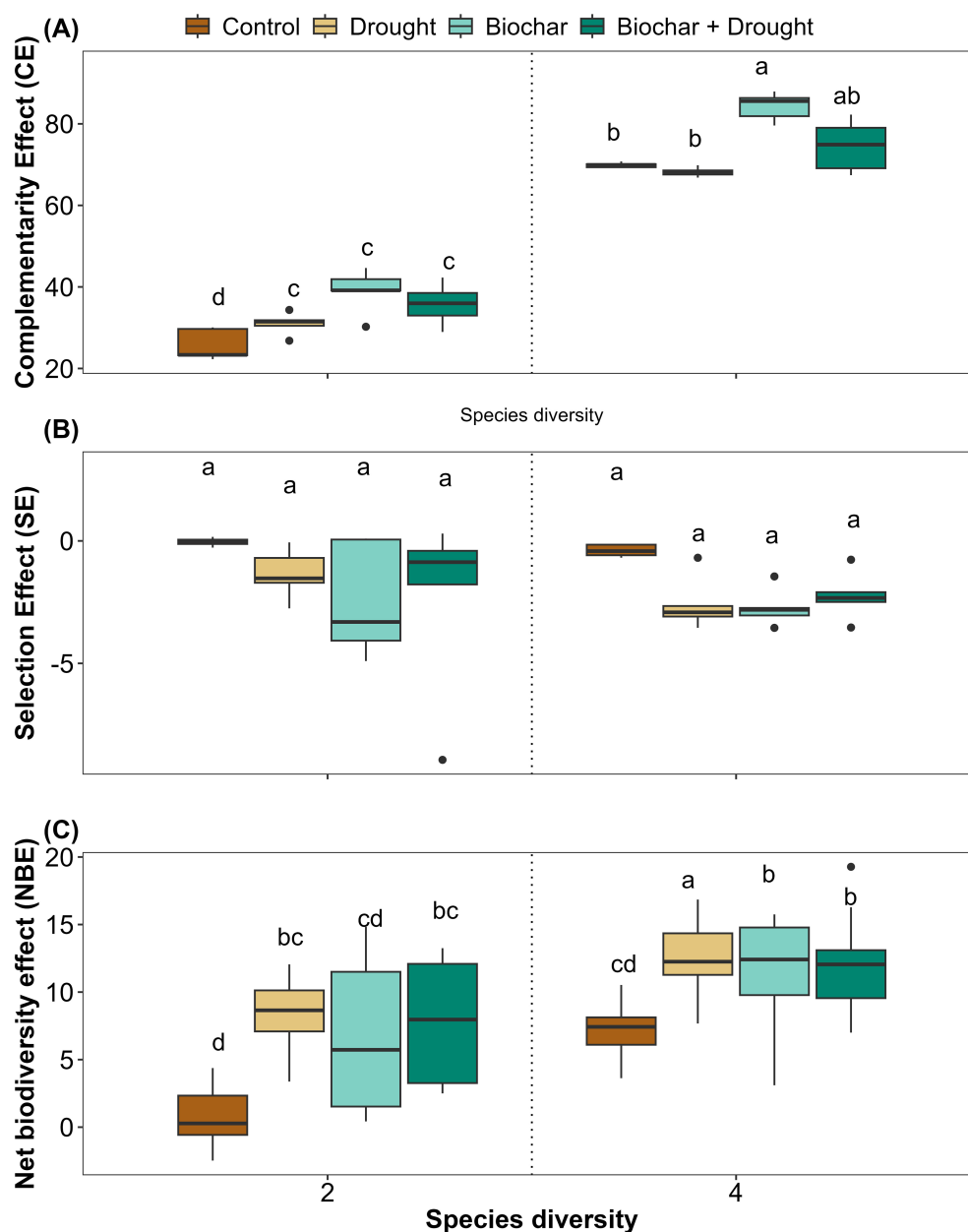


FIGURE 6

Effects of diversity and biochar application on (A) complementarity effect (CE), (B) selection effect (SE), and (C) net biodiversity effect (NBE) under control and drought conditions. Letters indicate significant differences among treatments based on Tukey's multiple comparison test.

storage through increased community productivity and plant-soil feedback mechanisms (Liu et al., 2019), which is important in water-limited environments, as diverse plant communities can better utilize limited soil moisture (Dietrich et al., 2022; Li et al., 2023). Likewise, biochar amendments consistently increase SOC and STN across different soil types and environmental conditions (Han et al., 2016; Dong et al., 2022; Zhang et al., 2022) because the recalcitrant nature of biochar makes it highly stable in soil, contributing directly to the carbon and nitrogen pools in soil

(Kimetu and Lehmann, 2010). Under drought conditions, biochar can help retain soil moisture and nutrients by improving soil structure and providing habitat for microorganisms (Wang et al., 2016; Li et al., 2020).

The soil microbial content, species diversity, and biochar application significantly improved Cmic and basal respiration in soil, particularly under drought conditions, which is consistent with several previous studies that showed that higher plant species diversity generally increases microbial content even

under drought conditions (Li et al., 2022; Xi et al., 2023; Liu et al., 2024), suggesting that high species diversity can reduce the drought effects by improving soil bacterial and fungal diversity, soil glomalin, and soil enzymes which consequently will increase plant access to nutrients and will improve soil microbial community resistance to several environmental stressors such as drought (Bennett et al., 2020; Li et al., 2022), as soil with a high microbial content can contain taxa that adapt to drought conditions (Wardle et al., 2004).

Biochar amendment also tends to increase Cmic and basal respiration across different ecosystems (Paetsch et al., 2018; Ge et al., 2019). Under drought conditions, biochar amendment can be particularly beneficial as it can enhance microbial biomass and soil enzyme activities under limited water availability (Jaborova et al., 2022).

4.3 Net biodiversity, complementarity, and selection effects under different species diversity, biochar amendment, and drought

The current study also demonstrated how species diversity and biochar amendment under drought conditions affect the overall community productivity through NBE, CE, and SE. The results showed significantly higher NBE and CE under the 4-species diversity mixture, which has been observed in several previous studies (Wang et al., 2020a; Hou et al., 2024). Such an increase in CE under high diversity, even under drought, confirms that diversity can mitigate the negative impacts of drought on ecosystem productivity (Fichtner et al., 2020; Chen et al., 2022). Additionally, the current results showed positive NBE and CE and negative SE, which was previously discussed that the increase in biomass is associated with positive CE and negative SE (Craven et al., 2016). Positive values of NBE indicate that species in the 4-species diversity perform better than expected based on their biomass in the 1-species diversity, suggesting complementarity or facilitation effect (Chen et al., 2025). Based on these results, CE can be considered a good measure for understanding how biodiversity influences ecosystem functions and reflects species interactions. Moreover, there were no differences in SE, confirming that the current experimental plots did not have any dominant or high-performing species. These results confirm that strong complementarity is more resilient to climate change and can maintain ecosystem functions under drought conditions (Hou et al., 2024; Chen et al., 2025).

5 Conclusions

The current study clearly demonstrated that higher species diversity can mitigate the negative effects of drought, especially when the soil is amended with biochar. These effects were evident

as high diversity and biochar produced more productive species (higher total biomass and lower RSR), better species performance (taller plants, higher SLA, and SRL), more fertile soil (higher SOC and STN), better microbial content (higher Cmic and basal respiration), and higher net biodiversity and complementarity effects under drought conditions than monoculture and control. These results provide a deeper understanding of drought-biodiversity interactions, which is crucial for predicting how changes in functional composition affect ecosystem functions and the restoration of arid environments in Oman. One of the limitations of the current study is that it was performed under greenhouse conditions, necessitating future studies that may focus on the long-term effects of diversity and different types of biochar under field conditions.

Data availability statement

The original contributions presented in the study are included in the article/[Supplementary Material](#). Further inquiries can be directed to the corresponding author/s.

Author contributions

HA: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. AA-W: Methodology, Project administration, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as potential conflicts of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fpls.2025.1563585/full#supplementary-material>

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Spatiotemporal evolution and driving factors of soil erosion function in a typical basin of the alpine region in the upper Yellow River

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In recent years, soil erosion has become increasingly severe in the Tibet Plateau, especially in the upper Yellow River Basin. Although numerous studies have been conducted on soil erosion in this region, most of them are limited to short time spans and fail to reflect the temporal variations of soil erosion at long-term scales. In this study, the spatiotemporal changes in soil erosion intensity and soil conservation function were evaluated using the InVEST model, and driving factors were identified using Geodetector in the Shagou River watershed from 1980 to 2020. The results showed that over the past 40 years, the Shagou River watershed mainly suffered mild erosion, the soil erosion intensity increased by 81.40% from 1980 to 2000, reaching a peak of approximately 1292.49 t/(km²·a). From 2000 to 2020, it decreased by 40.45% with 769.63 t/km²·a, indicating a clear improvement trend. From 1980 to 1990, the growth rate of soil conservation function was most significant, reaching 25.89%, while the growth rate from 2010 to 2020 was relatively small, only 6.23%. Over the past 40 years, the total soil conservation function increased by 1.12×10⁷ t, with a growth rate of 88.24%, reflecting the effectiveness of soil conservation measures. In addition altitudes, slopes, and land use types had significantly affected both on actual soil erosion intensity and soil conservation function. Geodetector analysis revealed that the primary factors influencing soil erosion intensity were vegetation cover and elevation, along with their two - factor interaction. Regarding the soil conservation function, the main influencing factors were elevation and precipitation, with the interaction dominated by elevation. This study should provide a theoretical basis and scientific reference for ecological protection and sustainable development in the alpine region of the upper Yellow River Basin.

KEYWORDS

InVEST model, soil erosion intensity, soil conservation function, Geodetector, upper Yellow River

1 Introduction

In recent years, climate warming and human activities have exacerbated soil erosion across the Tibetan Plateau in China, resulting in an increasingly sedimentation problem, particularly in the upper reaches of the Yellow River (Wang et al., 2024; Yu et al., 2024). This region, characterized by temperate semi-arid grasslands and arid desert grasslands (Mao et al., 2023), is subject to complex erosion processes driven by frequent fluctuations in wet and dry climatic conditions, resulting in severe soil erosion (Guo et al., 2024) and increased sediment transport to the Yellow River (Man et al., 2024). Annually, as much as $3 \times 10^7 \text{ m}^3$ of sediment from river tributaries, bank collapses, and quicksand was deposited in the Longyangxia Reservoir. These rivers are the primary sediment contributors to the upper reaches of the Yellow River (Zhao, 2019; Li et al., 2024). Given this context, research into soil erosion and its ecological implications on the Tibetan Plateau is critical for mitigating sediment loads and supporting the sustainable development of this region.

Soil is the foundation of ecosystem service and functionality (Li et al., 2022a). Its ecosystem conservation capacity plays a pivotal role in its service functions (Liu et al., 2019). Models are usually an important tool to assess soil conservation function. Among the models, the InVEST (Integrated Valuation of Ecosystem Services and Tradeoffs) model has superior accuracy and applicability in quantifying soil conservation function (Yang et al., 2022) that helps allow for intuitive and rational evaluations of soil conservation function (Guo et al., 2022). Additionally, the Geodetector provide a powerful tool that is widely used to investigate the attribution of spatial divergence and influence mechanisms (Wang and Xu, 2017; Gong et al., 2023; Liu et al., 2023; Chen et al., 2023).

In the middle and upper reaches of the Yellow River, many studies have been conducted to characterize soil erosion distribution, evaluate soil sensitivity (Wu and Wang, 2021; Xiao et al., 2021), and quantify ecological services (Yang et al., 2020, Yang et al., 2021a, Yang et al., 2021b, Yang et al., 2021c; Wei et al., 2022; Zhao et al., 2023; Xu et al., 2023; Liu et al., 2024; Qiao et al., 2024). However, most studies mainly focused on short-term time scales (Li et al., 2022b, Li et al., 2024). The long-term trends and driving mechanisms of soil erosion and soil conservation function, particularly in the upper alpine zones of the Yellow River Basin, remain insufficiently explored. It is difficult to capture both the long-term cumulative impacts and spatial heterogeneity of soil erosion processes. Additionally, existing research often fails to effectively represent the nonlinear relationships between dynamic factors such as climate variability and vegetation dynamics and the intensity of erosion.

Therefore, this study focuses on the Shagou River watershed, a first-order tributary located in the alpine region of the upper of Yellow River. The research utilizes the InVEST model combined with the Geodetector to analyze the spatiotemporal characteristics of soil erosion and soil conservation function in the Shagou River watershed over the past 40 years. The study investigates the differentiation under different land use types, slope gradients, and

elevation gradients. Specially, the objectives are to identify the spatiotemporal changes of soil erosion intensity and soil conservation function, explore the driving factors, and provide scientific recommendations for the high-quality development of the upper Yellow River basin, as well as the ecological protection and sustainable development of the Tibetan Plateau.

2 Materials and methods

2.1 Study area

The Shagou River watershed is in Guinan County, Qinghai Province, China (Figure 1). The river runs from southeast to northwest, and goes to the Longyangxia Reservoir. The river is a first-order tributary of the Yellow River, with a watershed area of 1,531 km² and an elevation range of 2,501–4,312 m. This watershed exhibits a distinct topography, with higher elevations in the southeast and lower elevations in the northwest. Alpine meadows dominate the upper reaches, and transition to desertification in the central region. The primary soil type is sandy loam, while calcareous chestnut soils are prevalent in the Yellow River valley, particularly in its lower reaches.

This region features a typical plateau continental climate, characterized by a long Winter and short Summer. Precipitation and heat coincide seasonally, with a multi-year average annual rainfall of approximately 143 mm (Liu, 2017). The land use is primarily composed of grasslands, bare lands, and croplands.

2.2 Data sources

The datasets primarily include soil, land use types, DEM, meteorological, and vegetation cover. Specifically, the monthly precipitation data from 1980 to 2020 with a resolution of 1 km was obtained from the National Earth System Science Data Center (<http://www.geodata.cn>). Land use data from 1980 to 2020 was sourced from GlobelLand30 (<http://globallandcover.com>). The 30-m resolution DEM data was obtained from the Geospatial Data Cloud (<https://www.gscloud.cn>). Soil properties (i.e., HWSO soil properties data) and Normalized Difference Vegetation Index (NDVI) data were both acquired from the National Tibetan Plateau Science Data Center (<https://data.tpdc.ac.cn>).

2.3 InVEST model

The Sediment Delivery Ratio module within the InVEST model was utilized to establish a generalized methodology for quantifying soil erosion and sediment yield across diverse landscapes. The input data includes the soil erodibility factor (K), slope length factor (L) and slope gradient factor (S), rainfall erosive factor (R), vegetation cover and management factor (C), and soil conservation measure factor (P).

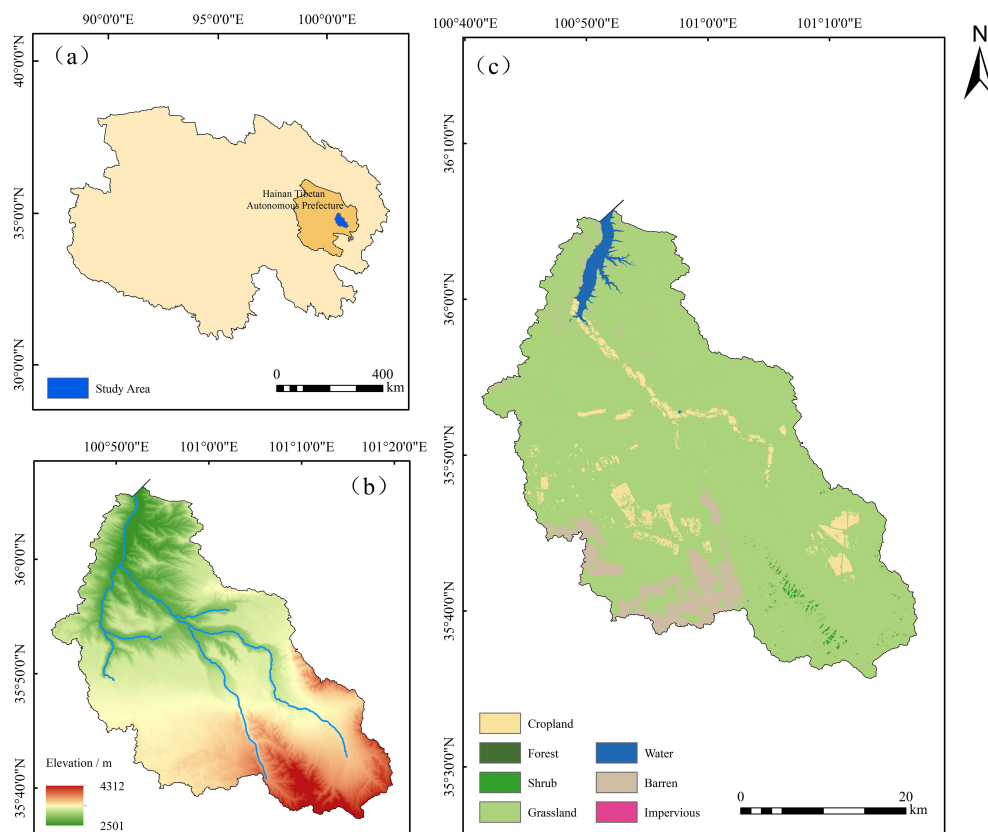


FIGURE 1
Location of the study area (a), digital elevation model (DEM, (b)), and land use types of the Shagou River watershed (c).

2.3.1 K factor

The K factor was calculated using the Equation 1 proposed by Williams (1990) (Figure 2a):

$$K = \left\{ 0.2 + 0.3 \exp \left[-0.256 \text{SAN} \left(\frac{1 - \text{SIL}}{100} \right) \right] \right\} \left[\frac{\text{SIL}}{\text{CLA} + \text{SIL}} \right]^{0.3} \times \left\{ 1 - \frac{0.25C}{C + \exp(3.72 - 2.95C)} \right\} \times \left[1 - \frac{0.7(1 - \frac{\text{SAN}}{100})}{(1 - \frac{\text{SAN}}{100}) + \exp(-5.51 + 22.9(1 - \frac{\text{SAN}}{100}))} \right] \quad (1)$$

Where K is the soil erodibility factor [$\text{t} \cdot \text{km}^2 \cdot \text{h} / (\text{km}^2 \cdot \text{MJ} \cdot \text{mm})$], SAN, SIL, and CLA denote the percentages of sand, silt, and clay in the soil, respectively; C is the soil organic carbon content. The calculation result K in US customary units should be multiplied by the conversion factor 0.1317 to obtain SI units.

2.3.2 L and S factor

The DEM data was used to calculate the L and S factor. Considering that most areas in the Shagou River watershed feature slopes of less than 10° , the targeted topographic factor Equations 2, 3 proposed by Fu et al. (2015) was used to calculate L and S (Figures 2b, c):

$$L = \left(\frac{\lambda}{22.13} \right)^m; m = \begin{cases} 0.2 & \theta < 0.5^\circ \\ 0.3 & 0.5^\circ \leq \theta < 1.5^\circ \\ 0.4 & 1.5^\circ \leq \theta < 3^\circ \\ 0.5 & \theta \geq 3^\circ \end{cases} \quad (2)$$

$$S = \begin{cases} 10.8 \sin \theta + 0.03 & \theta < 5^\circ \\ 16.8 \sin \theta + 0.5 & 5^\circ \leq \theta \leq 10^\circ \\ 21.9 \sin \theta + 0.96 & \theta \geq 10^\circ \end{cases} \quad (3)$$

Where L and S is the slope length and slope factor, respectively (dimensionless); λ denotes the horizontal projected slope length; m is the slope length index (also dimensionless); θ is the ground slope.

2.3.3 C factor

The C factor was calculated using the following Equations 4, 5 suggested by Cai et al. (2000):

$$f = \frac{\text{NDVI} - \text{NDVI}_{\min}}{\text{NDVI}_{\max} - \text{NDVI}_{\min}} \quad (4)$$

$$C = \begin{cases} 1, & f = 0 \\ 0.6508 - 0.3436 \lg(f \times 100), & 0 < f \leq 78.3\% \\ 0, & f > 78.3\% \end{cases} \quad (5)$$

Where f is the vegetation cover (%), NDVI is the normalized vegetation index, whereas $\text{NDVI}_{\min}$ and $\text{NDVI}_{\max}$ refer to the minimum and maximum NDVI values, respectively.

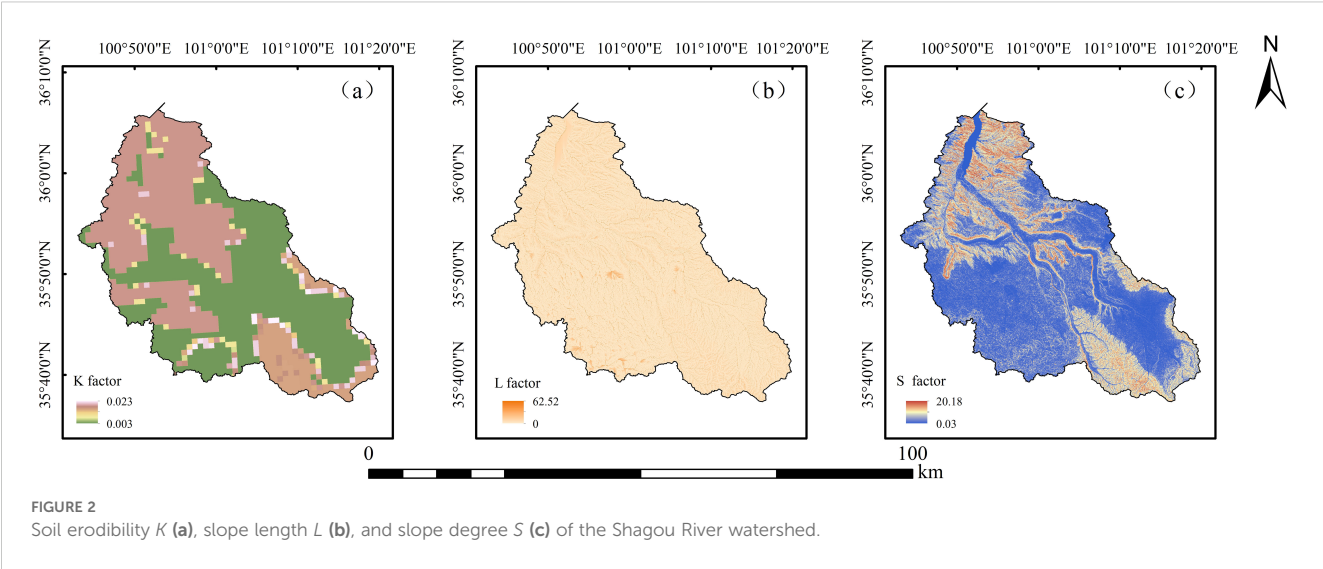


TABLE 1 Values *P* factor for various land use types in the Shagou River watershed.

Land use	Cropland	Forest	Grassland	Water	Barren	Impervious	Shrub
<i>P</i> value	0.35	1	1	0	1	0	1

2.3.4 *R* factor

In this study, the Wischmeier’s monthly scale Equation 6 was utilized to obtain the *R* factor (Wischmeier and Mannering, 1969), as follows:

$$R = \sum_{i=1}^{12} \left(1.734 \times 10^{1.5lg \frac{P_i}{P} - 0.8188} \right) \tag{6}$$

Where *P* is the annual precipitation (mm), *P_i* refers to the precipitation in the month *i* (mm);*R* is the rainfall erosivity factor (MJ·mm)/(km²·h·a).

2.3.5 *P* factor

This factor refers to the ratio of soil loss after implementing soil conservation measures to soil loss from planting downslope. In the study, the values of *P* in Table 1 were sourced from the research of Li et al. (2022a).

2.4 Actual soil erosion intensity

The Revised Universal Soil Loss Equation, which serves as the erosion module of the InVEST model, was employed to compute the actual soil erosion intensity. When soil and water conservation measures were not in place, the potential soil erosion was designated as *SL₀*. In the context of this study, considering the implementation of soil conservation measures, the actual soil erosion intensity was denoted as *SL_t*. (Equations 7–9) were utilized to determine the quantity of soil conservation:

$$SL_0 = R \times K \times L \times S \tag{7}$$

$$SL_t = R \times K \times L \times S \times C \times P \tag{8}$$

$$SD = SL_0 - SL_t \tag{9}$$

Where *SL₀* is the potential soil erosion intensity (t/(km²·a)), *SL_t* refers to the actual soil erosion intensity (t/(km²·a)), and *SD* (t/(km²·a)) is the soil conservation amount.

2.5 Geodetector

Soil erosion intensity and soil conservation function were influenced by various factors and their interactions, and the Geodetector was used to detect their contribution to soil erosion intensity and soil conservation function. The *q* value can be obtained based on the following Equation 10 (Wang and Xu, 2017):

$$q = 1 - \frac{\sum_{h=1}^L N_h \sigma_h^2}{N \sigma^2} \tag{10}$$

Where *q* is the explanatory ability of the independent variable *X* regarding the spatiotemporal variation of the dependent variable *Y*, with a range of 0-1. The closer of *Y* is to 1, the more significant its spatial variability. Moreover, *L* refers to the variance of *Y* values in stratum *h* and the whole region, respectively. Furthermore, interaction detection analyzes the combined effects of factors on *Y* by examining their interactions.

In addition, interaction detection analyzes the *q* values (*q* (*X*₁) and *q* (*X*₂)) to the interaction *q* value (*q* (*X*₁∩*X*₂)) effects to identify their interaction. The types of interactions include nonlinear weakness (*q* (*X*₁∩*X*₂)) < Min(*q* (*X*₁), *q* (*X*₂)), single-factor

nonlinear weakness ($\text{Min}(q(X1), q(X2)) < q(X1 \cap X2) < \text{Max}(q(X1), q(X2))$), two-factor enhancement ($q(X1 \cap X2) > \text{Max}(q(X1), q(X2))$), independent ($q(X1 \cap X2) = q(X1) + q(X2)$), and nonlinear enhancement ($q(X1 \cap X2) > q(X1) + q(X2)$).

3 Results

3.1 Spatiotemporal changes in actual soil erosion intensity

Based on the “Soil Erosion Intensity Classification Standards” (SL190-2008), the calculated actual soil erosion intensity were classified into six levels, including slight erosion (0–200 t/(km²·a)), mild erosion (200–2500 t/(km²·a)), moderate erosion (2500–5000 t/(km²·a)), severe erosion (5000–8000 t/(km²·a)), very severe erosion (8000–15000 t/(km²·a)), and extreme erosion (>15000 t/(km²·a)).

During the study period from 1980 to 2020, the actual soil erosion intensity in the Shagou River watershed was predominantly characterized by slight erosion intensity (Figure 3). In 1980, slight erosion was mainly concentrated in the middle and lower reaches of the watershed, often distributed in a strip-like pattern along the river channels (Figure 3a). Moderate erosion was observed at the river confluence areas, while slight erosion near the river inlet displayed a distinct block-like aggregation. The upper reaches of the

watershed were predominantly affected by mild erosion, with moderate erosion following a strip-like pattern along the river channels, and sporadic slight erosion distributed at the watershed’s boundaries and at the uppermost parts of the main river channels.

In 1990, the extent of actual soil erosion intensity showed little change (Figure 3b). The slight erosion in the upper reaches, along the main river channels and the watershed boundary, degraded into mild erosion over a very small area, while the extent of slight erosion in the middle and lower reaches expanded.

By 2000 (Figure 3c), compared to 1990, the range of slight erosion intensity along the main river channels in the upper, middle, and lower reaches, as well as along the eastern bank near the river inlet, had significantly expanded, with a predominant block-like aggregation. Some areas also exhibited a trend of transitioning from strip-like aggregation to block-like aggregation.

In 2010 and 2020 (Figures 3d, e), the actual soil erosion intensity extent showed marked improvement. In 2010, the range of slight erosion intensity decreased substantially, with block-like slight erosion intensity in the middle and lower reaches along the river channels degrading into sparse strip-like patterns. Most of the slight erosion intensity in the upper reaches, along both the eastern and western banks, also degraded into mild erosion intensity. By 2020, all the strip-like aggregated slight erosion intensity in the middle and lower reaches along the river channels had transformed into mild erosion intensity, further reducing the extent of slight

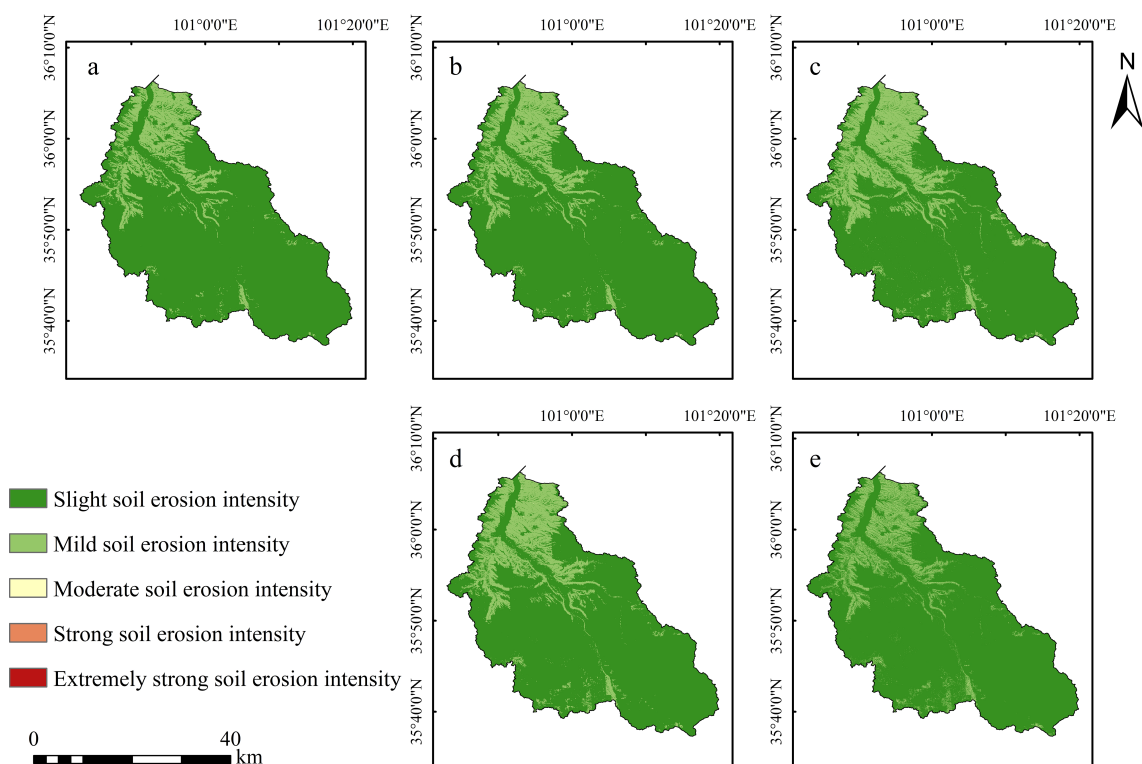


FIGURE 3

Spatial distributions of actual soil erosion intensity in the Shagou River watershed from 1980 to 2020. (a:1980, b: 1990, c: 2000, d: 2010, e: 2020).

erosion intensity. In the upper reaches, only scattered slight erosion intensity remained along the watershed boundary and the main river channels.

Temporally, the actual soil erosion intensity status in the Shagou River watershed showed an evolution trend of first increasing and then decreasing (Figure 4). The year 2000 marked the peak of this evolution process, with the total actual soil erosion intensity reaching 0.20×10^7 t and an erosion intensity of 1292.21 t/(km²·a). In contrast, in 1980, the actual soil erosion intensity level was at its lowest, with a total erosion amount of 0.11×10^7 t and an intensity of 712.35 t/(km²·a). From 1980 to 2000, the total actual soil loss in the watershed increased from 0.11×10^7 t to 0.20×10^7 t, with a net increase of 887,939.47 t, corresponding to a growth rate of approximately 81.40%. From 2000 to 2020, however, the actual soil loss showed a significant decline, with a total reduction of 800,507.51 t, representing a decrease of 40.45%.

In conclusion, the year 2000 served as a critical turning point for the actual soil erosion intensity trend in the Shagou River watershed. Since then, the soil erosion status in the watershed has been continuously improving in a positive direction, reflecting a trend of ecological restoration and environmental optimization.

3.1.1 Effect of altitude on actual soil erosion intensity

Based on the actual elevation conditions in the watershed, geographic information system spatial analysis techniques were applied to reclassify the elevation data into three gradients: low altitude (<3000m), medium altitude (3000-3500m), and high altitude (>3500m) (Figure 5a).

The results indicate significant differences in actual soil erosion intensity across different elevation regions within this watershed. The greatest soil erosion intensity occurred in the low-altitude areas, followed by the high-altitude areas, with the weakest erosion intensity in the medium-altitude areas. Over the nearly 40-year study period, the actual soil erosion intensity from high to low was as follows: low-

altitude areas (2750.85 t/(km²·a)), high-altitude areas (269.12 t/(km²·a)), and medium-altitude areas (252.80 t/(km²·a)).

During the period from 1980 to 2020, the actual soil erosion intensity in different elevation regions exhibited different temporal trends. In the low- and medium-altitude areas, soil erosion intensity initially increased and then decreased, while in the high-altitude areas, the soil erosion intensity exhibited a complex pattern of first decreasing, then increasing, and subsequently decreasing again. Notably, the change in erosion intensity in the medium-altitude areas was the most significant, with the actual soil erosion intensity in 2000 increasing by 92.34% compared to 1980, and decreasing by 53.83% compared to 2020.

3.1.2 Effects of slope on actual soil erosion intensity

Based on the technical specifications in the “Technical Regulations for Slope Classification Map of Land Survey: TD/T1072-2022”, the slope of the watershed was classified into six categories, including flatland (<2°), gentle slope (2°-8°), slight slope (8°-15°), moderate slope (15°-25°), steep slope (25°-35°), and very steep slope (>35°).

The results indicate a significant positive correlation between actual soil erosion intensity and slope. As the slope gradually increases, soil erosion intensity increased, with the most notable changes observed in the steep and very steep slope regions (Figure 5b). Precise measurements revealed the following soil erosion intensities for each slope category: very steep slope (6228.73 t/(km²·a)), steep slope (3634.20 t/(km²·a)), moderate slope (1839.09 t/(km²·a)), slight slope (720.42 t/(km²·a)), gentle slope (119.06 t/(km²·a)), and flatland (46.49 t/(km²·a)).

Throughout the study period, actual soil erosion intensity in different slope categories exhibited an initial increase followed by a decrease. From 1980 to 2000, the most significant increase in soil erosion intensity was observed in the gentle slope region, which rose by 123.00% over the 20-year period. Significant increases were also observed in the slight slope, flatland, and moderate slope regions,

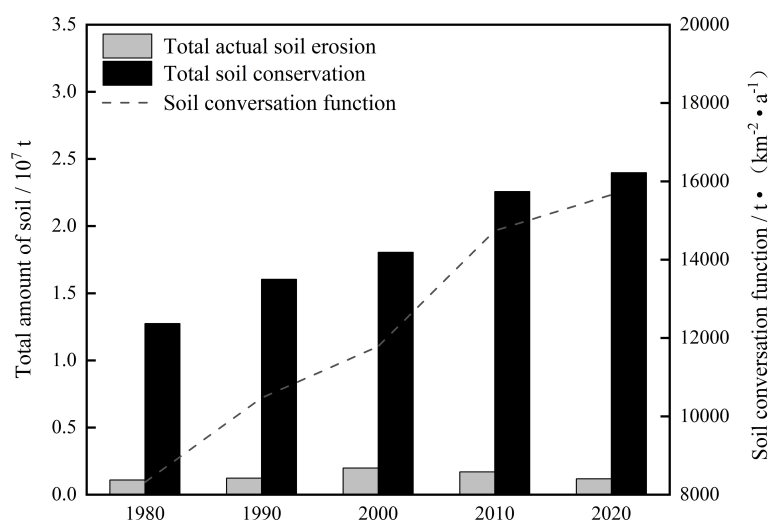


FIGURE 4

Total actual soil erosion and soil conservation function in the Shagou River watershed from 1980 to 2020.

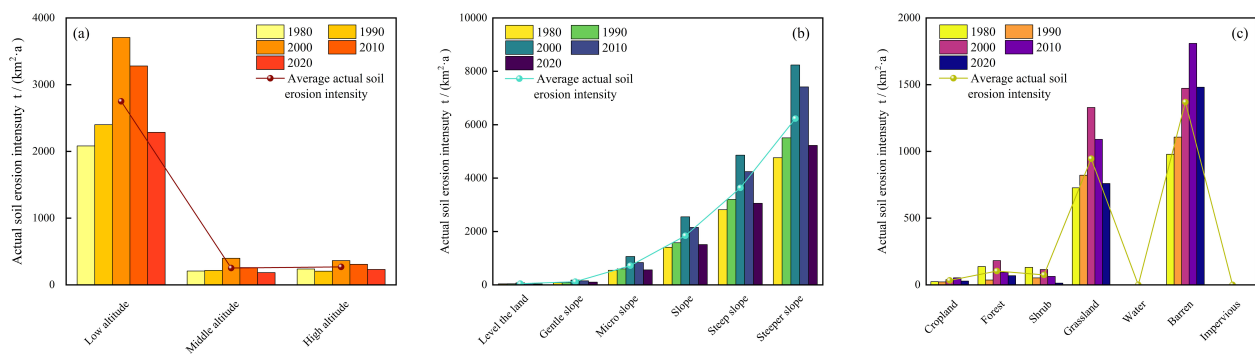


FIGURE 5

Actual soil erosion intensity at different elevations (a), slopes (b), and land use types (c) from 1980 to 2020.

with increases of 94.02%, 93.29%, and 81.12%, respectively. In contrast, the increases in the very steep slope (72.88%) and steep slope (72.74%) regions were relatively smaller. From 2000 to 2020, the decline in soil erosion across different slope types was as follows, from lowest to highest: very steep slope (36.56%) < steep slope (37.11%) < moderate slope (40.80%) < gentle slope (43.31%) < slight slope (47.03%) < flatland (53.12%).

3.1.3 Effects of land use types on actual soil erosion intensity

As shown in Figure 5c, there were significant differences in the actual soil erosion intensity across different land use types. The erosion intensities followed the sequence, i.e., bare land suffered the biggest value of 1369.49 t/(km²·a), followed by grassland (945.40 t/(km²·a)), forestland (103.55 t/(km²·a)), shrubland (74.80 t/(km²·a)), and cropland (33.29 t/(km²·a)).

From 1980 to 2000, dynamic monitoring revealed that actual soil erosion intensity in cropland, forestland, and shrubland followed a similar trend, initially decreasing and then gradually increasing. In contrast, the soil erosion intensity in grassland and bare land showed a continuous intensification. Between 2000 and 2020, the soil erosion intensity in forestland, shrubland, and grassland exhibited a continuous decline, while the soil erosion intensity in cropland and bare land initially increased and then decreased.

Over the 20-year period, despite considerable differences in actual soil erosion intensity across land use types, the overall trend for all land use types showed a reduction in soil erosion. This finding is of significant scientific value for further understanding the dynamic relationship between land use and soil erosion intensity within this watershed.

3.2 Characteristics of spatiotemporal changes in soil conservation function

A steady increase in the soil conservation function occurred in the Shagou River watershed (Figure 4). The corresponding soil conservation functions increased from 8317.72 t/(km²·a) in 1980, 10470.86 t/(km²·a) in 1990, 11786.62 t/(km²·a) in 2000, 14739.62 t/

(km²·a) in 2010, and to 15657.49 t/(km²·a) in 2020. In contrast to the actual ones, the total amount of soil conservation reached its maximum value of 2.40×10^7 t in 2020, while the minimum value of 1.27×10^7 t was recorded in 1980. A further analysis of the change rates of soil conservation across various periods showed that the most significant growth took place between 1980 and 1990, with a growth rate of 25.89%. In contrast, the period from 2010 to 2020 witnessed the lowest growth rate, which was merely 6.23%.

Spatially, the pattern of soil conservation function in the middle reaches of the watershed remained relatively stable over the 40 years (Figure 6). However, significant changes were observed in the upper reaches along the main river channels, this watershed boundaries, and the lower reaches along the river course. Specifically, the areas of high soil conservation function (>5000 t/(km²·a)) along the eastern bank near the river inlet and in the upper reaches expanded significantly. The originally sparse linear aggregation areas gradually evolved into continuous block-like regions. In summary, over the past 40 years, the total soil conservation in the Shagou River watershed increased by 1.12×10^7 t, with a growth rate of 88.24%.

3.2.1 Effects of altitudes on soil conservation function

In the study area, significant differences were observed across different periods and elevation conditions (Figure 7a). The soil conservation function was more prominent in high-altitude areas, and the soil conservation function was ranked from the highest to the lowest as follows: high altitude (29218.29 t/(km²·a)), low altitude (20606.33 t/(km²·a)), and medium altitude (4646.25 t/(km²·a)).

From the internally perspective, the soil conservation function in the low, medium, and high-altitude regions all exhibited an increasing trend. Notably, the growth trend in the high-altitude areas was particularly significant, with a growth rate of 88.81% compared to 1980. The growth rate in low-altitude areas was 88.23%, and in medium-altitude areas, it was 86.61%.

3.2.2 Effects of slopes on soil conservation function

In the study area, there was a significant positive correlation between soil conservation function and slope (Figure 7b).

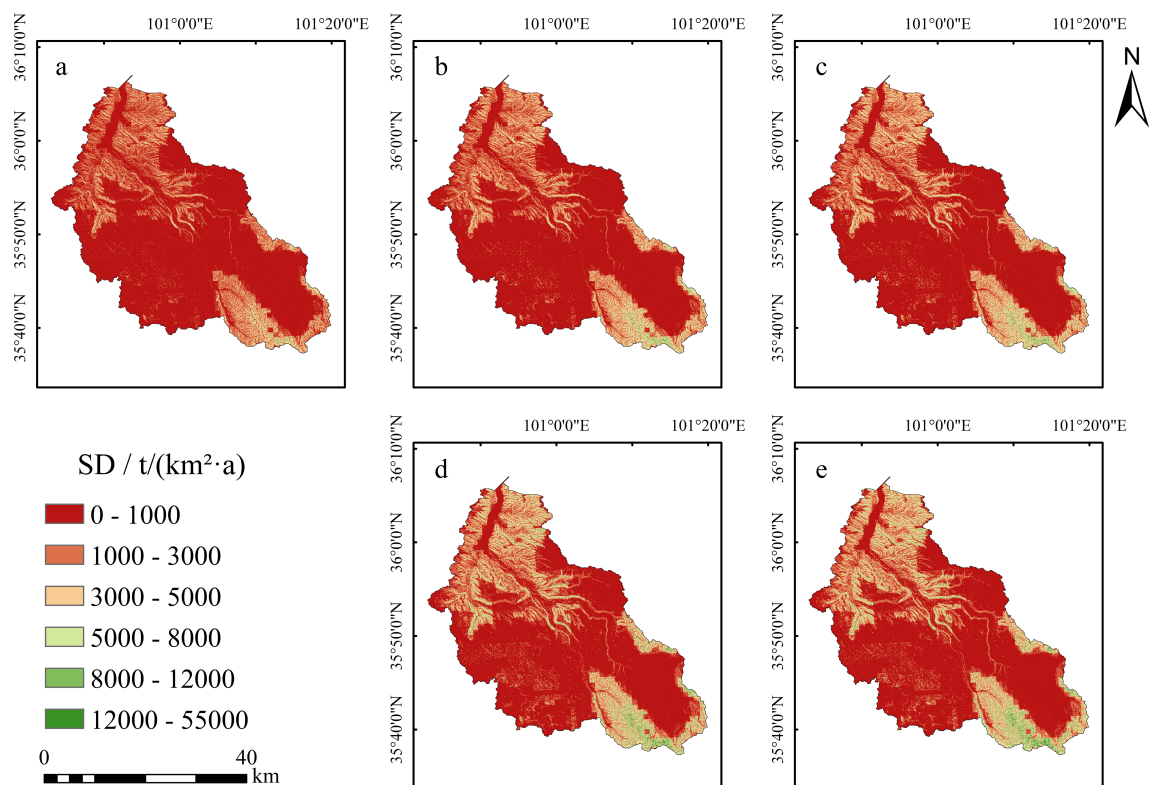


FIGURE 6

Maps of the spatial distributions of soil conservation function in the Shagou River watershed over the past 40 years (a:1980, b: 1990, c: 2000, d: 2010, e: 2020) and (SD: the soil conservation amount).

Specifically, the growth rate of soil conservation function was exceptionally rapid in several slope intervals, including from gentle slope to slight slope, slight slope to moderate slope, and gentle slope to flatland, with growth rates exceeding 100%. The soil conservation function was the highest on very steep slopes [48712.19 $t/(km^2 \cdot a)$], followed by steep slopes [43159.99 $t/(km^2 \cdot a)$], moderate slopes [26700.38 $t/(km^2 \cdot a)$], slight slopes

[10587.03 $t/(km^2 \cdot a)$], gentle slopes [2431.13 $t/(km^2 \cdot a)$], and flatland exhibited the lowest value [1042.71 $t/(km^2 \cdot a)$].

During the study period, the moderate slope region exhibited the most significant increase in soil conservation function, with a growth rate of 88.39%. In other regions, the growth rates decreased from steep slope (87.81%), very steep slope, (87.35%), slight slope (87.15%), gentle slope (87.08%), and the flatland (85.97%).

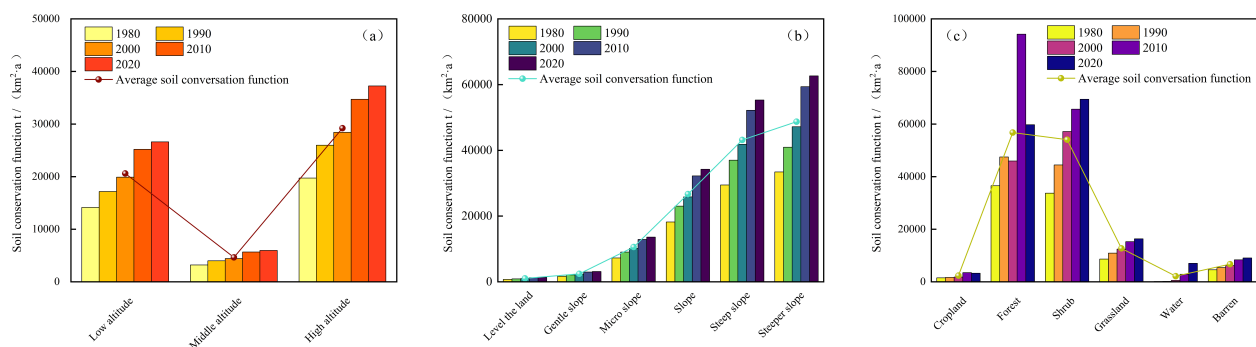


FIGURE 7

Soil conservation function on different elevations (a), slopes (b), and land use types (c) from 1980 to 2020.

3.2.3 Effects of land use types on soil conservation function

There were significant differences in soil conservation function across various land types within the study area (Figure 7c). Forestland had the highest value [56776.72 t/(km²·a)], followed by shrubland [54089.59 t/(km²·a)], grassland [12716.32 t/(km²·a)], bare land [6721.37 t/(km²·a)], and cropland had the lowest value [2348.12 t/(km²·a)].

Between 1980 and 2020, the soil conservation function in all land types exhibited an upward trend. Notably, the changes in cropland and shrubland were the most significant. Over nearly 40 years, soil conservation function in cropland increased by 116.49%, and in shrubland, it increased by 105.94%. Following these, the increases in bare land, grassland, and forestland were also notable, with bare land increasing by 98.68%, grassland by 89.23%, and forestland by 63.43%. This upward trend highlights the evolving role of different land use types in soil conservation function and provides valuable insights for ecological restoration and soil conservation planning.

3.3 Analyses of driving factors

3.3.1 Driving factors of actual soil erosion intensity

Based on the average q -values across the five time periods (Figure 8), the elevation ranked the first ($q = 0.24$), followed by vegetation coverage ($q = 0.24$) and annual rainfall ($q = 0.19$). Slope ($q = 0.02$) and land use type ($q = 0.01$) had relatively weaker effects. Notably, all the five factors passed the significance test, indicating their indispensable roles in the soil erosion process.

From 1980 to 2020, the elevation consistently served as the dominant factor explaining the spatial distribution of actual soil erosion intensity, while land use type exhibited relatively limited explanatory power. A detailed analysis revealed that the influence of

elevation and slope gradually diminished over time. In contrast, the explanatory power of vegetation coverage, annual rainfall, and land use type steadily increased, highlighting their growing importance in shaping the patterns of soil erosion.

Further examination of interactions among the factors revealed significant bivariate enhancement effects across the combined factors (Figure 9). The synergistic effect of “elevation $\cap$ vegetation coverage” was the most influential, with its q -value peaking at 0.38 in 2020. This made it the key driver of the spatial distribution of soil erosion intensity, followed by the combinations of “vegetation coverage $\cap$ annual rainfall” and “elevation $\cap$ land use type”, which collectively regulated the occurrence and development of soil erosion intensity to varying degrees. At the watershed scale, interactions dominated by elevation and vegetation coverage exhibited the strongest explanatory power when combined with other factors (Figure 9).

3.3.2 Driving factors of soil conservation function

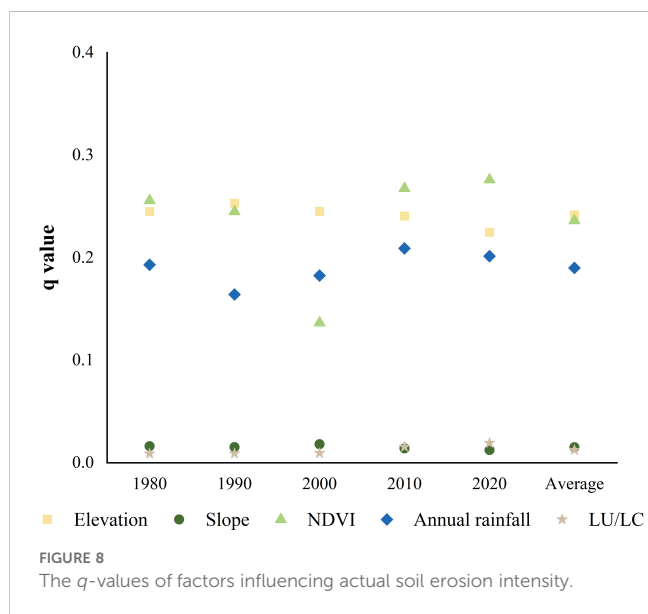
In this study, the driving factors of soil conservation function were thoroughly analyzed using the Geodetector. Figure 10 demonstrated that the average q -values of the factors were the lowest for the slope (0.013), followed by land use type (0.027), vegetation coverage (0.059), and annual rainfall (0.175). The elevation played a more prominent role in soil conservation function with the highest value of 0.237.

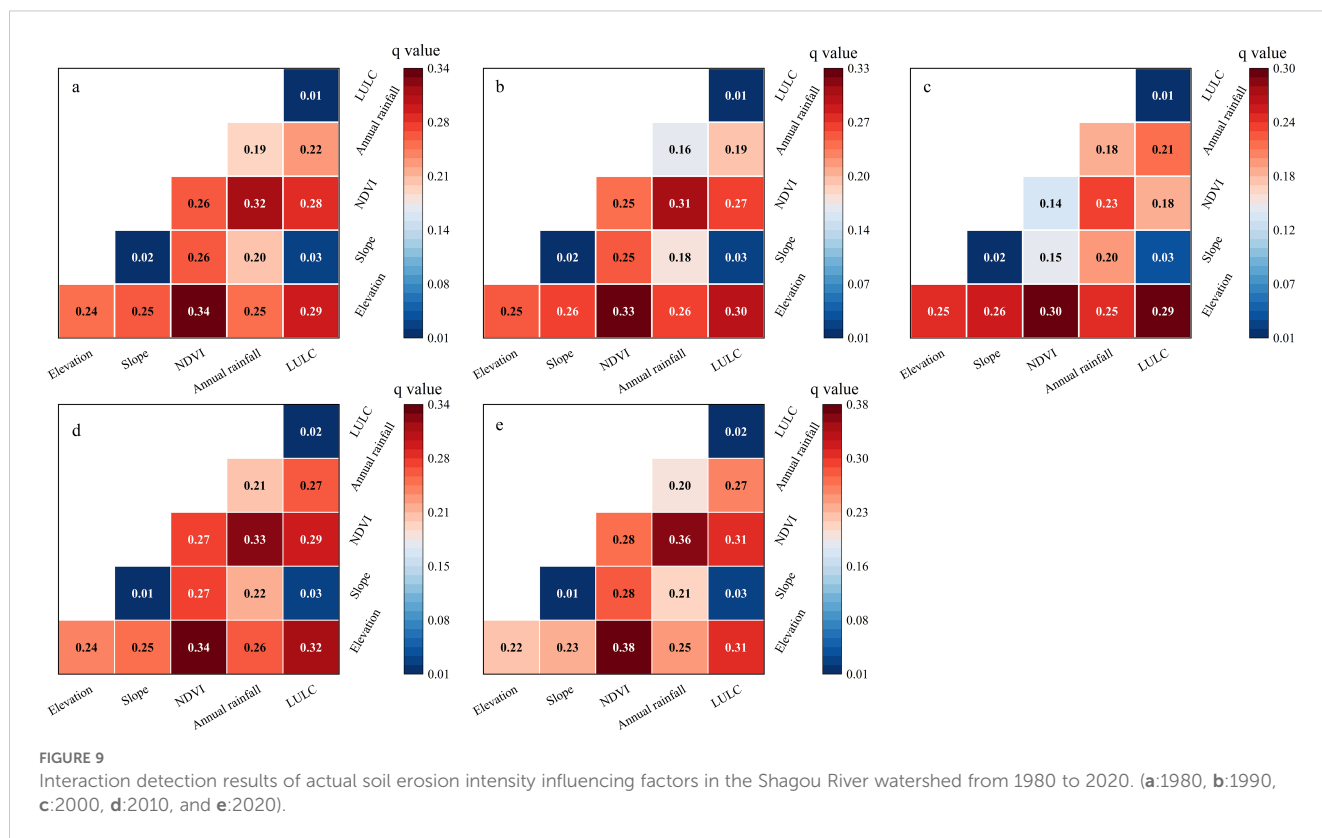
All the five factors exhibited significant bivariate enhancement relationships (Figure 11). Specifically, the combined effect of these factors on soil conservation function was not a simple linear sum but generated synergistic enhancement effects. Among the combinations, the combinations of the elevation factor with other factors exhibited the most significant explanatory power. This provides crucial insights and theoretical support for accurately interpreting the complex causes and dynamic changes in soil conservation function. The findings offer significant guidance and practical value for maintaining soil ecosystems and for scientifically soil protection and management strategies.

4 Discussion

Soil erosion intensity and soil conservation function serve as two crucial indicators for assessing ecosystems and guiding the prevention and control of land degradation. In this study, InVEST model was employed to evaluate the soil erosion intensity and soil conservation function in the Shagou River watershed from 1980 to 2020. The average soil erosion intensity was found to be 936 t/(km²·a), while the average soil conservation function reached 12194 t/(km²·a). These results are in line with the findings of previous studies (Chen et al., 2020; Kang et al., 2018), which effectively validates the reliability of the outcomes of this study.

From 1980 to 2020, the soil erosion intensity steadily increased that is consistent with previous conclusions (Cen et al., 2023; Hou et al., 2024; Li et al., 2023; Yan et al., 2023; Yang et al., 2024). However, certain areas still exhibit weak soil conservation function. This suggests that the potential risk of soil erosion in this watershed





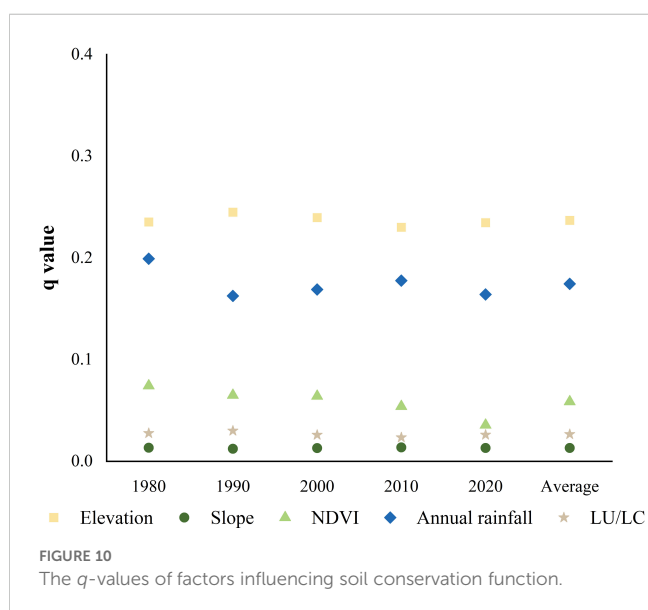
is still high, likely due to intensified soil erosion resulting from high frequency of precipitation and low vegetation cover.

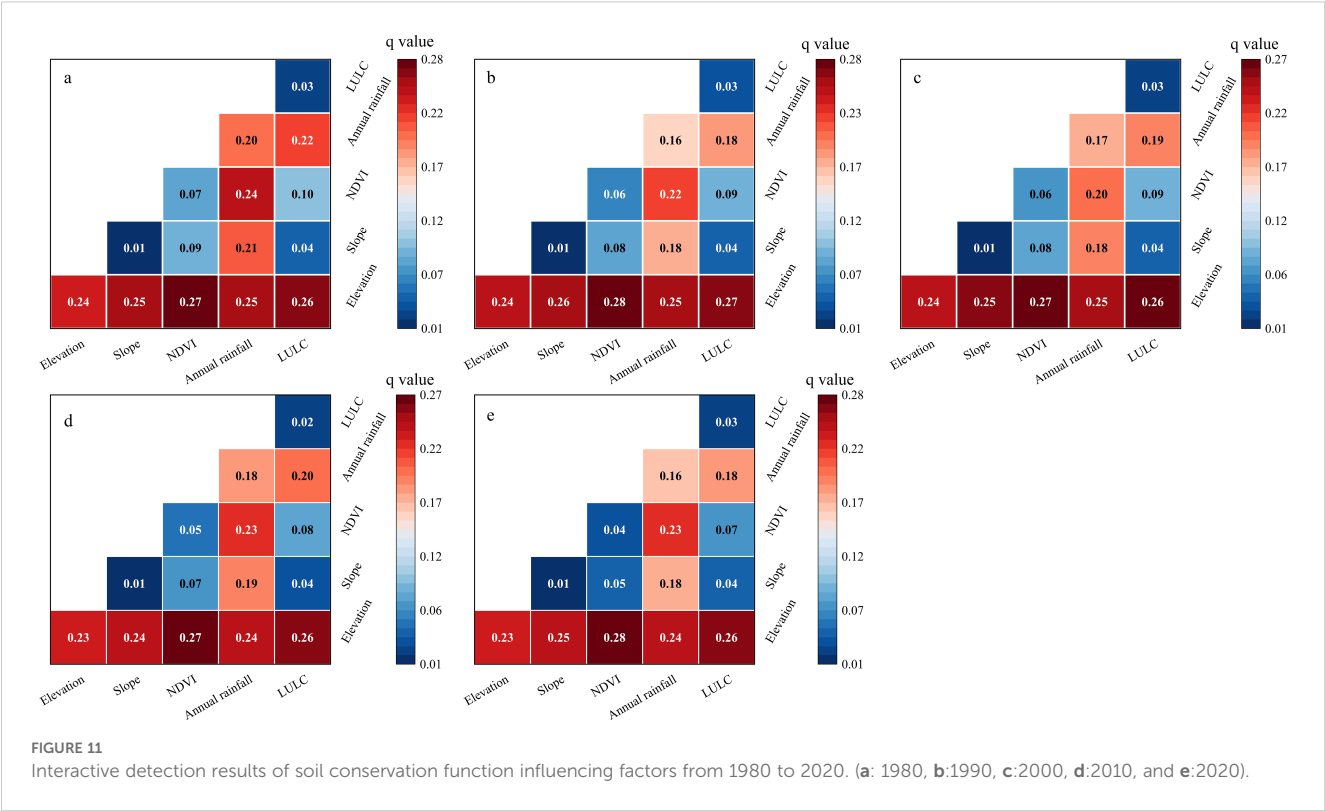
In this study, higher soil conservation function occurred in woodland, shrubland, and grassland types that was consistent with assertions by previous studies (Kumar et al., 2023). This may be attributed to high vegetation cover in the low-elevation areas. Additionally, the root systems of forest land are more developed compared to those of grasslands, resulting a greater soil conservation function in the forest land. Conversely, the highest

intensity of soil erosion in bare land areas with loose sediment texture impedes moisture conservation and renders high erosion (Shen et al., 2024).

Soil erosion intensity is influenced by both natural factors and human activities. The over-exploited natural resources and unregulated urbanization, as well as rising temperatures and precipitation had contributed to a significant increase in soil erosion intensity within the Shagou River watershed. Fortunately, emphasis on ecological protection and public awareness of environmental conservation has increased in recent years. A series of ecological protection projects have been carried out to reduce soil erosion. These include converting farmland into forests and grasslands, as well as sand prevention and control initiatives. The significance of sustainable development has also been emphasized. Consequently, the total amount of soil erosion in the study had reduced by 40.45% from 2000 to 2020, resulting in improved soil conservation function across the study period.

The upper reaches of the Yellow River Basin are situated on the ecologically fragile Tibetan Plateau, where they confront substantial environmental challenges. Accelerated global warming, rising atmospheric humidity, and expansive human activities have collectively driven elevated surface runoff volumes. This hydrological transformation has triggered a worrying shift in land cover dynamics, where vegetated zones are progressively being converted into human settlements and barren landscapes (Figure 12). Such land-use changes have intensified soil erosion processes, significantly diminishing the region's natural soil retention capacity. To address these soil degradation issues in the Shagou River watershed and comparable areas, stakeholders should prioritize enhanced monitoring systems for

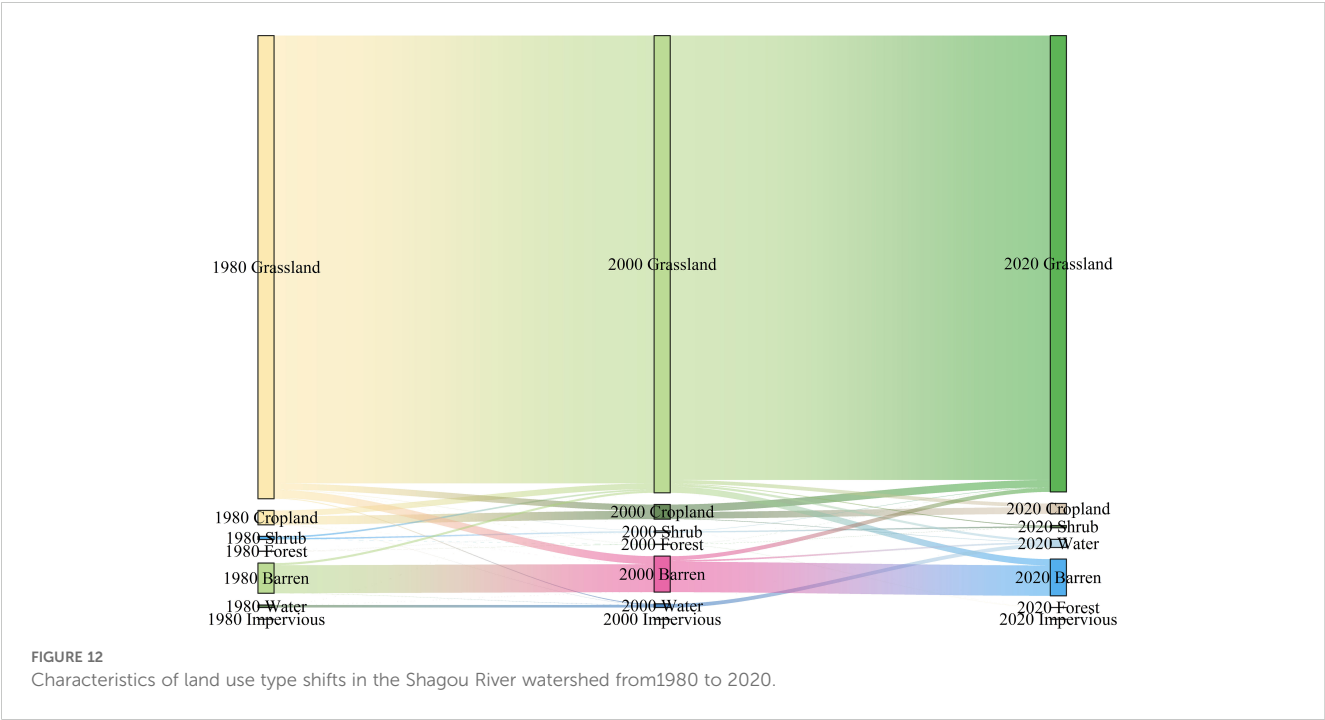




land cover transformations and land-use typologies. Targeted interventions should include the establishment of designated soil erosion control zones in vulnerable areas. Concurrently, regulatory frameworks must enforce strict controls over new land-use applications, including rigorous evaluations of project types and scale. Equally critical is the enforcement of prohibitions against

environmentally disruptive activities that exacerbate erosion risks. These combined measures aim to balance developmental needs with ecological preservation through proactive land management and sustainable resource utilization strategies.

It should be noted that this study may involve certain limitations. Specifically, the simulation employed default parameters for the study



period and maintained constant K values throughout. Furthermore, the P values were adopted from prior research, which could potentially lead to computational inaccuracies. Nevertheless, it is crucial to underscore that the yield outcomes derived from this study remain plausible and offer meaningful contributions. These findings can serve as a valuable reference for both academic exploration and practical implementations within the upper alpine region of the Yellow River basin.

5 Conclusions

In this study, the InVEST model was employed to analyze the soil erosion and soil conservation function, and the driving factors were identified using Geodetector for the typical alpine watershed in the upper Yellow River during 1980–2020. The results showed that soil erosion intensity in the Shagou River watershed steadily increased from 721.48 t/(km²·a) to a 2000 peak of 1292.49 t/(km²·a), an 81.40% rise from 1980 to 2000. After 2000, it declined, reaching 769.63 t/(km²·a) in 2020, a 40.45% drop, due to ecological restoration. Furthermore, the most severe erosion occurred in low - altitude areas (below 3000 m) and on steep slopes (greater than 35°). Bare land exhibited the highest soil erosion intensity, measuring 1369.49 t/(km²·a), whereas cultivated land had the lowest, at just 33.29 t/(km²·a).

Between 1980 - 1990, soil conservation function grew most, at 25.89%, while 2010–2020 had the lowest rate, 6.23%. Over the past 40 years, the Shagou River watershed's soil conservation function improved substantially, with a 1.12×10^7 t increase. The upper and middle reaches, especially upstream mountains, saw the biggest rises. Soil conservation function varied by period, altitude, and slope. High - altitude [29,218.29 t/(km²·a)] and steep [48,712.19 t/(km²·a)] areas were most effective, while middle - altitude [4646.25 t/(km²·a)] and flat [1042.71 t/(km²·a)] areas were less so. Forest land was key for soil conservation, and cultivated land had the weakest capacity.

In this watershed, elevation and vegetation cover were the main drivers of soil erosion intensity, with land use type having less impact. The influence of elevation declined, while that of vegetation cover and annual precipitation grew. Elevation and vegetation cover, especially in interaction with other factors, were dominant, with elevation being the core factor for soil conservation function. Slope had the weakest explanatory power for soil conservation function, and the interaction of elevation with other factors had the most significant effects.

This study shows that ecological restoration and soil - water conservation measures in the watershed have had long - term positive impacts, particularly in the upper - reach key ecological protection areas. Through enhanced vegetation restoration and slope - related conservation efforts, soil erosion intensity has been notably reduced, and soil conservation function has improved. These measures not only boost total soil conservation function in the watershed but also foster the restoration and stability of its ecosystem.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material. Further inquiries can be directed to the corresponding author.

Author contributions

XK: Resources, Writing – original draft. QL: Methodology, Resources, Validation, Writing – review & editing. ZS: Software, Visualization, Writing – review & editing. QY: Investigation, Software, Writing – review & editing. BN: Resources, Supervision, Writing – review & editing. SW: Investigation, Writing – review & editing. KM: Investigation, Writing – review & editing. WD: Investigation, Writing – review & editing.

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Conflict of interest

Authors XK and QL were employed by the company Power China Northwest Engineering Corporation Limited. Author WD was employed by the company Qinghai Yellow River Upstream Hydropower Development Co., Ltd.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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The response of the stem sap flow dynamics of *Tamarix ramosissima* to rainfall variability in the desert-oasis transition zone of Northwest China

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Plant transpiration is a fundamental process for maintaining the water cycle, regulating temperature and facilitating nutrient uptake, while also playing a critical role in climate regulation and ecosystem services. However, a significant knowledge gap remains in the understanding of how plant transpiration responds to changes in precipitation patterns within dryland ecosystems. In the present study, the stem sap flow of the phreatophyte xerophytic shrub *Tamarix ramosissima*, meteorological factors, soil moisture content, and bare soil evaporation were examined to assess the effects of two different rainfall categories (category I: lower mean rainfall amount and duration; category II: higher mean rainfall amount and duration) on stem sap flow dynamics. Our results reveal that the rainfall reduced the stem sap flow by 46.5% and 29.5% compared to the previous days across rainfall category I and II, respectively. The daily and diurnal variation of stem sap flow during the three days following rainfall showed non-significant variation compared to pre-rainfall, regardless of rainfall category. The soil moisture content at depth of 0–40 cm (SMC_{0-40cm}) exhibits a pronounced increase to rainfall events, irrespective of rainfall category, although these events did not significantly increase the soil available moisture content within this depth. Concurrently, the weighing micro-lysimeters utilized in this study revealed that approximately 91.5% of the total precipitation during the experimental period evaporated into the atmosphere. In addition, the daily stem sap flow on the rainfall day and the following three days post rainfall was strongly positively correlated with photosynthetically active radiation, air temperature, and vapor pressure deficit within the two rainfall categories rather than with SMC_{0-40cm} . Together, our findings indicate that the effects of rainfall variability on stem sap flow of *T. ramosissima* are primarily

driven by meteorological factors, independent of the rainfall category. The results of this study provide a valuable insight for assessing species-specific water-use strategies and implementing effective reforestation practices in the future.

KEYWORDS

sap flow, phreatophyte xerophytic shrub, desert-oasis transition zone, soil water variability, meteorological factors

1 Introduction

Climate change impacts water vapor transport and precipitation patterns at global and regional scales, such as rainfall intensity, duration, and intermittency, by altering the thermodynamic distribution characteristics and energy balance of the Earth's surface and atmosphere (Greve et al., 2014; Novick et al., 2016). Long-term historical observations and modeled scenarios indicate that variability in rainfall patterns will increase (IPCC, 2021). Alterations in precipitation patterns will adversely affect regional hydrological processes, energy balance, and the stability of ecosystems (Donat et al., 2017; Yao et al., 2024). Evapotranspiration, as a key component of regional hydrological processes, couples the water and carbon cycles (Good et al., 2015; Kropp et al., 2017). Arid regions constitute approximately 41% of the total Earth's land surface, with evaporation accounting for 90-95% of total precipitation, of which vegetation transpiration contributes 40-90% (Ouyang et al., 2021; Smith et al., 2024). Accurately quantifying vegetation transpiration is crucial for understanding the carbon and water cycle in water-limited areas. Rainfall is major driver of biological processes in water limited ecosystem (Sponseller, 2010). And episodic precipitation events of variable timing and frequency can trigger rapid pulses of plant activity (Zhao and Liu, 2010; Chen et al., 2014), thereby enhancing the sensitivity of vegetation to rainfall variability. Thus, elucidating the relationship between transpiration and rainfall variability is essential for understanding the response of plants to climate change in the desert regions.

The stem sap flow is an important indicator of water movement in plants (Wang et al., 2015). Compared to other transpiration monitoring methods (e.g., eddy covariance and lysimeters), sap flow gauges could continuously measure the transpiration and help to mitigate the errors from the allocation of transpiration and evaporation (Hirschi et al., 2017; Perez-Priego et al., 2017; Moorhead et al., 2019). Sap flow responses offer a more precise elucidation of water consumption rates and the tradeoffs in the balance between water supply and demand (Liu et al., 2022; Wang et al., 2022; Liu et al., 2024). The relationship between sap flow and meteorological factors (e.g., photosynthetically active radiation (PAR), water vapor pressure deficit (VPD), air temperature (T_a)) and soil moisture content (SMC) has been analyzed across multiple temporal scales, ranging from diurnal and seasonal dynamics to

intra-annual and interannual scales (Zheng and Wang, 2015; Hayat et al., 2020; He et al., 2020; Iqbal et al., 2021; Liu et al., 2022; Su et al., 2022). However, elements of the water cycle in desert plants remain uncertain, particularly with regard to the quantitative understanding of the response to precipitation patterns in the context of climate change. And the response of sap flow dynamics to rainfall may vary on the plant's habitat and species, water consumption relationships, and functional types within a given area (Zhao and Liu, 2010; Chen et al., 2014; Wang et al., 2020). For example, the sap flow of *Robinia pseudoacacia* increased with precipitation, while non-significant relationship was found between *Quercus liaotungensis* Koidz and precipitation (Du et al., 2011). After 3.8 mm of precipitation, a rapid increase in sap flow was observed in *Nitraria sphaerocarpa*, while a more pronounced enhancement in sap flow occurred in *Elaeagnus angustifolia* following 5.2 mm of precipitation (Zhao and Liu, 2010).

Tamarix ramosissima is a dominant native phreatophyte xerophytic shrub in the terminal area of the Shiyang River in northwest China. The distribution of lateral fine roots (<2 mm) of *T. ramosissima*, which play a crucial role in water and nutrient uptake, has been found to be primarily concentrated within the top 40 cm of soil (Liu et al., 2022), a layer where SMC are strongly impacted by rainfall. Previous studies have primarily focused on quantifying the transpiration of *T. ramosissima* and examining its controlling factors (Qu et al., 2007; Yu et al., 2017; Liu et al., 2022; Sun et al., 2022). However, the effect of rainfall variability on the sap flow dynamics of phreatophyte xerophytic shrubs is largely unknown. Therefore, it is urgent to explore the response of sap flow dynamics to different rainfall patterns in order to assess whether alterations in rainfall patterns exacerbate the threat to the survival of the *T. ramosissima*. Given this concern, the stem sap flow, meteorological factors, soil moisture content, and bare soil evaporation were measured in order to gain a comprehensive understanding of the response of the stem sap flow dynamics of *T. ramosissima* to precipitation characteristics during the growing season. The objectives of this study were to: (i) understand the response of stem sap flow of *T. ramosissima* to two contrasting rainfall events and associated soil moisture content; (ii) determine the driving factors of daily stem sap flow under two rainfall categories, and (iii) identify the hourly stem sap flow dynamics within different rainfall categories. The results of this study were expected to provide a scientific basis for understanding the mechanisms that underlie the response of desert plants to global climate change.

2 Materials and methods

2.1 Study site

The study area is located in the downstream of the Shiyang River, which is 60 km from Minqin county. The experiment site is surrounded by Tengger Desert and Badain Jaran Desert, and belong to desert-oasis transition zone. The mean annual air temperature of this region in the past 68 years (1953–2020) is 8.6°C (range from -8.1°C to 23.6°C), and the mean annual precipitation is about 110 mm. The rainfall is concentrated between June to September, accounting for approximately 80% of annual total precipitation. The annual potential evapotranspiration is approximately 1383.0 mm, with a dryness index (ET/P) as high as 12.2. This region has a typical continental desert climate. The groundwater table is approximately 10 m below the surface. And the soil texture is loam (Supplementary Table S1).

The experiment site was located in the artificial shelter forest-belt in the Desert Oasis transition zone of Minqin of China. The original shelter-belt has been almost completely destroyed as a result of

long-term human activities in this area. The existing shelter-belt, established in 2005, exhibits the average coverage of 25% and a stand density of 416 plants per hectare. The dominant shrub species of shelter-belt is *T. ramosissima*, with a height ranging from 1.5 to 2.5 m. *T. ramosissima* has an inverted cone-shaped canopy with no trunk and multiple branches spread obliquely from the base (Figure 1). *T. ramosissima* exhibits a vertical roots system that can penetrate up to 4 m below ground (Liu et al., 2022). The understory vegetation of *T. ramosissima* primarily consist of perennial herbaceous and shrubs, including *Nitraria tangutorum*, *reaumuria songarica*, and *kalidium foliatum*.

2.2 The stem sap flow measurements

We measured the stem sap flow of *T. ramosissima* during the growing seasons from May to mid-October of 2020. The stem sap flow gauges (Flow 32, Dynamic Inc., Houston, TX, USA), based on the energy balance method, were used to measure the stem sap flow. Considering

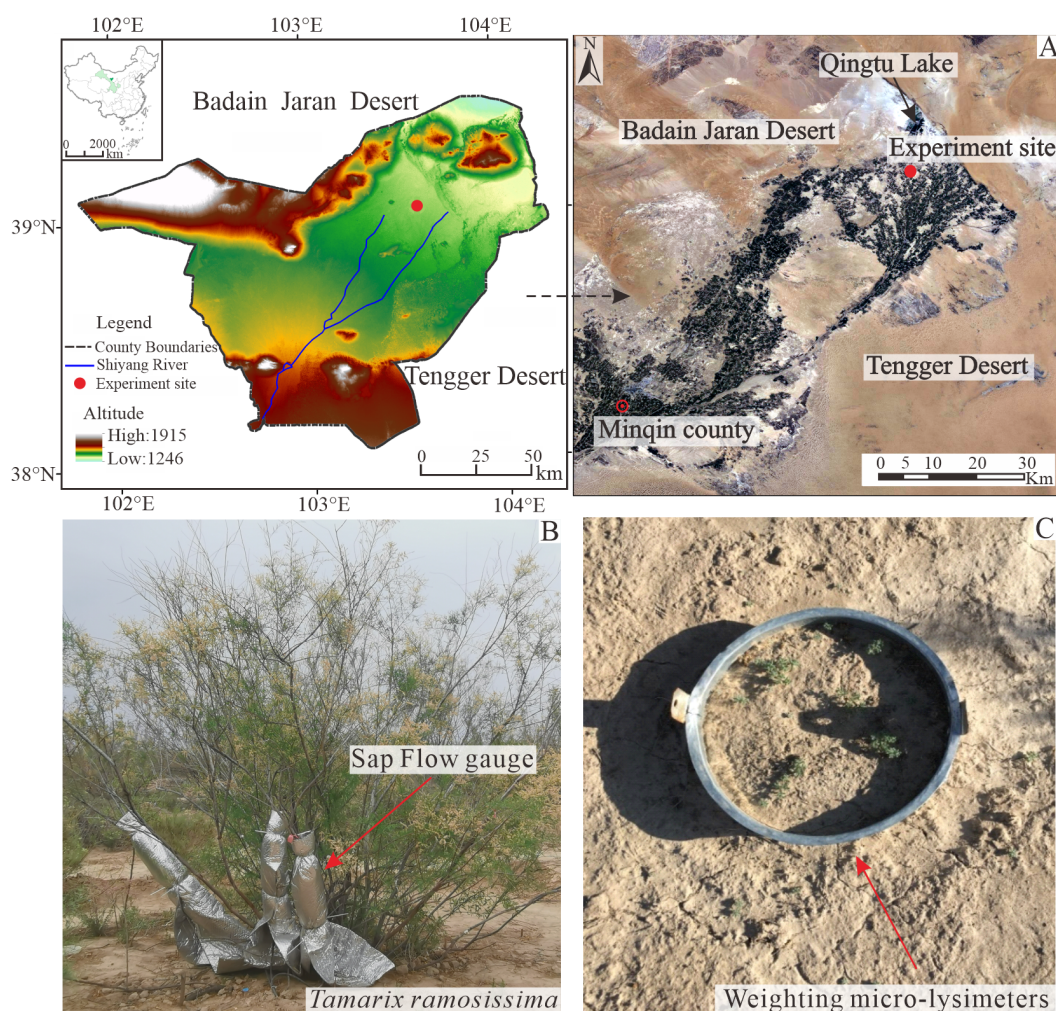


FIGURE 1

(A) Location of the experiment site in the Desert Oasis transition zone of Minqin of China, (B) the representative *T. ramosissima* shrubs and the equipment for stem sap flow measurements, and (C) the picture of weighting micro-lysimeter for bare soil evaporation measurement.

the potential positive correlation between stem sap flow and stem cross-sectional area (Wang et al., 2022), and stem diameter was taken as the criteria to measure the stem sap flow. The diameter of 216 stems of *T. ramosissima* with 15-years old were investigated before stem sap flow gauges equipment. The results showed that the stem with diameter of 10–20 mm and 20–25 mm accounted for 60.2% and 17.6% of the total investigated diameter of the 15-years old *T. ramosissima*, respectively (Table 1). In order to accurately capture the response of stem sap flow dynamics to rainfall variability, six stems with different diameters were selected. The selected stems exhibiting optimal growth conditions and free from visible pest or disease infestations were selected for measurement of stem sap flow. The canopy area, height, and basal diameter of six selected stems were obtained using a steel tape measure with 1 mm resolution. And the diameters of these selected stems were 10.2 mm, 14.3 mm, 11.8 mm, 18.8 mm, 22.0 mm and 31.2 mm (Table 2). Six gauges with five models were deployed to measure stem sap flow, including two gauges of model for 11 mm (SGEX9), one gauge of each model for 14 mm (SGEX13), 18 mm (SGEX13), 22 mm (SGEX19), and 31 mm (SGEX25). Therefore, the sap flow of selected stems could represent the stem sap flow characteristics of the 15-years old *T. ramosissima*.

All selected branches were in good condition and able to support the weight of the stem sap flow gauge throughout the experimental periods. Gauges were carefully installed following the manufacturer's recommendations, and more detailed information on the installation can be found in (Liu et al., 2022). After the installation of the stem sap flow gauges, the heater input voltage was monitored and adjusted according to the sensor voltage requirements. To minimize the risk of overwriting previously recorded data arising from the large volume of incoming signals, the output from the gauges was sampled at 10-second intervals and stored as 30-minute mean values using a

CR1000 datalogger (Campbell Scientific, Logan, USA). The methodology for calculating stem sap flow of *T. ramosissima* is detailed in (Wang et al., 2020; Liu et al., 2022).

2.3 Meteorology and soil moisture content measurements

In the experiment site, a TE525 bucket rainfall gauge (Campbell Scientific, Inc, USA) (0.1 mm per tip) was installed to record the precipitation amount and duration, and rainfall intensity ($\text{mm}\cdot\text{h}^{-1}$) could be obtained accordingly. During the experimental period, rainfall events were recorded on 24 days, of which 6 rainfall events with precipitation less than 1 mm. The accumulation precipitation in the experimental period was 63.8 mm, the longest rainfall duration and highest rainfall intensity were 10.5 h and $2.2 \text{ mm}\cdot\text{h}^{-1}$, respectively.

Considering the effects of gully micro-geomorphology, an automatic weather station was established to monitor micrometeorological factors. Air temperature (Ta), relative humidity (RH) (HMP155A, Campbell Scientific, Logan, USA), wind speed and wind direction (WS and SD) (WindSonic75, Gill Instruments Limited, UK) were observed at 2.5 m above the soil surface, respectively. The photosynthetically active radiation (PAR) at the height of 2.5 m from the soil surface were monitored by PQS1 (PQS1, Kipp & Zonen, Inc). All the data signals were recorded at 10 s intervals and stored as 30 min averages using a CR3000 datalogger (Campbell Scientific, Logan, USA). The daily Ta, daily RH, daily WS and mean daily PAR in this study are the average values from 00:00 to 24:00 (local time), respectively. The vapor pressure deficit (VPD) was calculated with RH and Ta using the method described in (Cambell and Norman, 1998).

TABLE 1 The characteristics of investigated 216 stems of *T. ramosissima* with 15-years old of age.

Diameter classification (mm)	Ranges	Average diameter (mm)	Frequency	Relative frequency (%)
0<D<10mm	7-9.75	8.5	16	7.4
10≤D<15mm	10-14.97	12.6	65	30.1
15≤D<20mm	15-19.75	17.3	65	30.1
20≤D<25mm	20-24.8	22.3	38	17.6
25≤D<30mm	25.2-29.6	26.5	16	7.4
30≤D<35mm	30.5-33.9	32.2	10	4.6
35≤D<40mm	35.4-37.6	36.2	5	2.31
40≤D<45mm	–	–	0	0
45≤D ≤ 50mm	50	50	1	0.5

“–” indicate that no stems with a diameter between 40 mm and 45 mm were observed in this investigation.

TABLE 2 The summary morphological characteristics of selected stems of *T. ramosissima*.

Stem number	1	2	3	4	5	6
Height (cm)	124	145	152	157	165	178
Stem diameter (mm)	10.2	14.3	11.8	18.8	22.0	31.2

In the experiment site, the volumetric soil moisture (SMC, $\text{cm}^3 \cdot \text{cm}^{-3}$) was monitored along with five replicates located outside the canopy of selected *T. ramosissima*, where stem sap flow measurements were also conducted. The 5TM soil probes (Campbell Scientific, Inc, USA) were buried at six depths below the soil surface (5 cm, 10 cm, 20 cm, 40 cm, 80 cm, and 160 cm). The data were recorded at 10 s intervals and stored as 30 min average values with a CR3000 datalogger (Campbell Scientific, Logan, USA). The monitored soil moisture content data was calibrated and corrected with the gravimetric method every month. Soil relative extractable water (REW) was calculated as follows (Equation 1) (Granier, 1987):

$$REW = \frac{\theta - \theta_{wp}}{\theta_{fc} - \theta_{wp}} \quad (1)$$

where θ is the monitored volumetric soil moisture content, θ_{fc} ($\text{cm}^3 \cdot \text{cm}^{-3}$) and θ_{wp} ($\text{cm}^3 \cdot \text{cm}^{-3}$) are soil water content at field capacity and wilting point. The θ_{fc} and θ_{wp} were derived from the soil-water characteristic curve. The wilting point was considered to be $0.12 \text{ cm}^3 \cdot \text{cm}^{-3}$, based on the method described in (Wiecheteck et al., 2020).

2.4 Bare soil evaporation measurements

Soil evaporation was measured using 14 sets of weighting micro-lysimeters (Figure 1C). We selected seven typical *T. ramosissima* within the experimental stand and two weighting micro-lysimeters adjacent to each selected shrub, one below the canopy and the other in the gap between shrub. The weighting micro-lysimeters consist of a weighting system and lysimeter vessel comprising a stainless steel cylinder with a diameter of 25 cm and a height of 50 cm. The weight of micro-lysimeters weighted at 08:00 AM and 20:00 PM daily during the experimental period using the SP30001 electronic scales with an accuracy and range of 0.5 g and 100 kg, respectively. The evaporation of bare soil was calculated according the water balance method, as follow (Equation 2) (Lyles et al., 2024):

$$E = \frac{(G_1 - G_2)}{A} \times 10 + P - D \quad (2)$$

where E is the bare soil evaporation (mm), when it is negative, it indicates the presence of condensate water, G_1 And G_2 are the mass measured at t_1 and t_2 , A is the cross-sectional are of weighting micro-lysimeters (cm^2), 10 is the conversion, P is the rainfall amount from t_1 to t_2 (mm), D is the drainage of same period (mm).

2.5 Classification of rainfall category

The 18 rainfall events during the experimental period in 2020 were classified into two rainfall categories based on rainfall amount and rainfall duration using the K-means clustering (Table 3). Starting from these cluster centres, the rainfall events are selected into two cluster in the way that keep the overall within-group variance at a minimum. Attempts were made until the most suitable clusters appeared and normally, and the classification must meet the t-test criterion of significant level ($P < 0.05$) (Wang et al., 2020).

As presented in Table 3, rainfall category I has the lower mean value of rainfall amount and rainfall duration (1.59 ± 0.22 mm and 2.02 ± 0.29 h, respectively). In contrast, rainfall category II is associated with higher mean values for rainfall amount and duration (7.2 ± 0.46 mm and 4.75 ± 1.48 h, respectively). And there is non-significant difference in rainfall intensity between rainfall category I and rainfall category II. During the experimental period, rainfall events occurred with a frequency of 72.2% for category I and 27.8% for rainfall category II. The accumulated rainfall amount of rainfall category I and rainfall category II were 27.8 mm and 36.0 mm, respectively.

2.6 Data processing and analysis

To eliminate the effect of the large variations in stem sap flow, the half-hourly stem sap flow data presented in this study is the average values for all six selected stems. Daily stem sap flow was the sum of half-hourly stem sap flow in a day. Given that this study focuses on only two rainfall categories, t-test was employed to assess the differences in meteorological factors, SMC and REW at different soil layers during the two rainfall categories. ANOVA was performed to evaluate the statistical differences in daily stem sap

TABLE 3 Statistics information of different rainfall categories during the experimental period in 2020.

Rainfall category	Rainfall characteristics	Ranges	Mean $\pm$ standard deviation	Accumulated rainfall (mm)	Times
I	Rainfall amount (mm)	0.1-3.9	$1.59 \pm 0.22a$	27.8	13
	Rainfall duration (h)	0.5-5	$2.02 \pm 0.29a$		
	Rainfall intensity ($\text{mm} \cdot \text{h}^{-1}$)	0.2-3.9	$0.75 \pm 0.48a$		
II	Rainfall amount (mm)	5.3-11.3	$7.2 \pm 0.46b$	36.0	5
	Rainfall duration (h)	3-10.5	$4.75 \pm 1.48b$		
	Rainfall intensity ($\text{mm} \cdot \text{h}^{-1}$)	0.9-1.8	$1.33 \pm 0.58a$		

The different letters indicate significant difference of rainfall amount and rainfall duration (t-test, $P < 0.05$). The average values mentioned above are expressed as the means $\pm$ standard error.

flow and meteorological factors across pre-rainfall, rainfall, and post-rainfall periods within the same category. The correlation test and linear regression fitting were employed to explore the relationship between environmental factors and stem sap flow in rainfall day and post-rainfall for two rainfall categories. The level of significance was set at 95% confidence interval ($P=0.05$). All statistics analyses were performed with SPSS 22 (SPSS Inc., USA).

Structural equation modeling (SEM) was employed to quantify both the direct and indirect relationships between environmental factors affecting the stem sap flow of *T. ramosissima* on the rainfall day and the subsequent three days. A conceptual model was developed based on the correlation analysis between the forcing variables and the response variable. All variables significantly correlated with stem sap flow were incorporated into the base model. Non-significant relationships were removed during model refinement using modification indices. Model coefficients were estimated via the maximum-likelihood method. When lower value of chi-square (χ^2 , ≤ 2) and root mean square error of approximation (RMSEA, ≤ 0.05), and higher P -value ($P < 0.05$) suggest that the overall goodness of model fit (Schermelleh-Engel et al., 2003). SEM analysis was performed using AMOS 26.0 (SPSS Inc., USA).

3 Results

3.1 Variation in environmental factors and bare soil evaporation

The temporal variations in mean daily PAR, Ta, $T_{a_{\text{Max}}}$, $T_{a_{\text{Min}}}$, RH, and VPD during the study period in 2020 are presented in Figure 2 and Supplementary Figure S1. These variables exhibited distinct seasonal patterns throughout the experimental period. Specifically, mean daily PAR, Ta, RH, and VPD showed pronounced seasonal fluctuations. The ranges of these variables during the study period were as follows: mean daily PAR ranged from 137.2 to 765.7 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Supplementary Figure S2), Ta ranged from 20.0 to 29.6°C, $T_{a_{\text{Max}}}$ ranged from 11.84 to 37.07°C, $T_{a_{\text{Min}}}$ ranged from -7.85 to 23.21°C, RH ranged from 13.2% to 76.5%, WS ranged from 0.4 to 2.5 $\text{m}\cdot\text{s}^{-1}$, and VPD ranged from 0.5 to 3.5 kPa. The highest monthly mean values for PAR and VPD were observed in June; in comparison, the peak monthly mean values for Ta and RH occurred in July (24.79°C) and September (49.36%), respectively.

The SMC in 0–40 cm of the soil profile was more responsive to rainfall, with a delayed response to heavy rainfall and generally remains stable at 40–160 cm (Figure 3A). Therefore, the depths of 0–40 cm and 40–160 cm were classified as shallow ($\text{SMC}_{0-40\text{cm}}$) and middle ($\text{SMC}_{40-160\text{cm}}$) soil layers, respectively. Daily $\text{SMC}_{0-40\text{cm}}$ and daily available $\text{SMC}_{0-40\text{cm}}$ ranged from 0.10 to 0.12 $\text{cm}^3\cdot\text{cm}^{-3}$ and from -0.01 to 0.01 $\text{cm}^3\cdot\text{cm}^{-3}$ during the experimental period, respectively. In comparison, daily $\text{SMC}_{40-160\text{cm}}$ and daily available $\text{SMC}_{40-160\text{cm}}$ remained constant, recorded at 0.07 $\text{cm}^3\cdot\text{cm}^{-3}$ and -0.13 $\text{cm}^3\cdot\text{cm}^{-3}$ during the study period (Figure 3B). Daily REW at 0–40 cm and 40–160 cm soil layers ranged from -0.08 to 0.13, and -1.01 to -0.99, respectively (Figure 3C).

The statistical information of average daily meteorological factors and daily maximum meteorological factors among two rainfall categories is shown in Table 4 and Supplementary Table S2. And mean daily PAR, Ta, RH, and VPD ranged from 137.2 to 765.7 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, from 4.2 to 28.6 °C, from 14.1 to 77.3%, and from 0.5 to 2.5 kPa, respectively, across the two different rainfall categories. On rainfall days, the mean daily RH and VPD were significantly higher in rainfall category II than in category I ($P < 0.05$), with non-significant differences observed for mean daily PAR and Ta between the two rainfall categories ($P > 0.05$). A significant difference in mean daily RH and PAR was observed between the rainfall day and the subsequent three days ($P < 0.05$). However, daily Ta did not exhibit significant variation within this category ($P > 0.05$). Relative to rainfall days, RH showed a significant decline, whereas VPD exhibited a significant increase during the three days following rainfall events ($P < 0.05$). Conversely, non-significant differences in mean daily PAR and Ta were detected among the two rainfall categories ($P > 0.05$).

Compared to the pre-rainfall day, there was non-significant increase in SMC, available SMC, or REW values at 0–40 cm and 40–160 cm soil layers on the rainfall day or the subsequent three days across both categories ($P > 0.05$). Throughout the rainfall day and the following three days in rainfall category I, the average daily SMC at depths of 0–40 cm and 40–160 cm remained unchanged relative to pre-precipitation levels.

Furthermore, the results revealed that the available SMC at 0–40 cm and 40–160 cm soil layers was 0.00 $\text{cm}^3\cdot\text{cm}^{-3}$ and -0.13 $\text{cm}^3\cdot\text{cm}^{-3}$, respectively, indicating that the soil may unable to provide adequate moisture for plant uptake during this period. In rainfall category II, the daily mean SMC at 0–40 cm and 40–160 cm soil layers increased from 0.11 $\text{cm}^3\cdot\text{cm}^{-3}$ and 0.07 $\text{cm}^3\cdot\text{cm}^{-3}$ on pre-rainfall day to 1.65 $\text{cm}^3\cdot\text{cm}^{-3}$ and 0.11 $\text{cm}^3\cdot\text{cm}^{-3}$ on the first day following rainfall events. Nevertheless, the available SMC in these layers remained at 0.00 $\text{cm}^3\cdot\text{cm}^{-3}$ and -0.13 $\text{cm}^3\cdot\text{cm}^{-3}$, respectively. These findings suggest that the average daily SMC remained in a state of deficiency irrespective of the soil layer or rainfall category.

Concurrently, the weighing micro-lysimeters showed that the evaporation of bare soil was 58.4 ± 1.2 mm, accounting for around 91.5% of the total precipitation during the experimental period.

3.2 Dynamics of daily stem sap flow within two rainfall categories

Daily stem sap flow of *T. ramosissima* was classified based on the rainfall classification during the study period of 2020. There were 13 and 8 daily stem sap flow data samples in rainfall category I and rainfall category II, respectively. The daily stem sap flow of *T. ramosissima* ranged from 265.9 to 535.1 $\text{g}\cdot\text{d}^{-1}$ in rainfall day of category I, and from 167.9 to 636.9 $\text{g}\cdot\text{d}^{-1}$ in rainfall day of category II. Moreover, the mean daily stem sap flow of *T. ramosissima* was 329.2 ± 46.1 $\text{g}\cdot\text{d}^{-1}$ and 411.8 ± 68.1 $\text{g}\cdot\text{d}^{-1}$ on the rainfall day in category I and rainfall category II, respectively (Figure 4). Non-significant difference in the mean daily stem sap flow was observed between the two rainfall categories ($P > 0.05$).

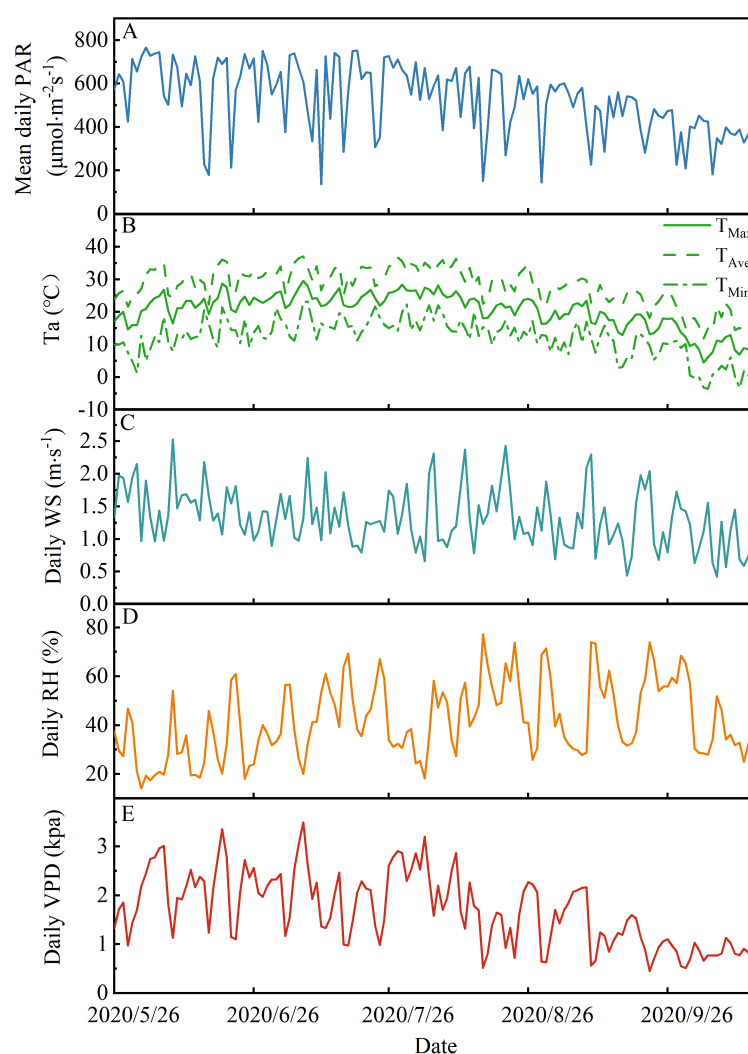


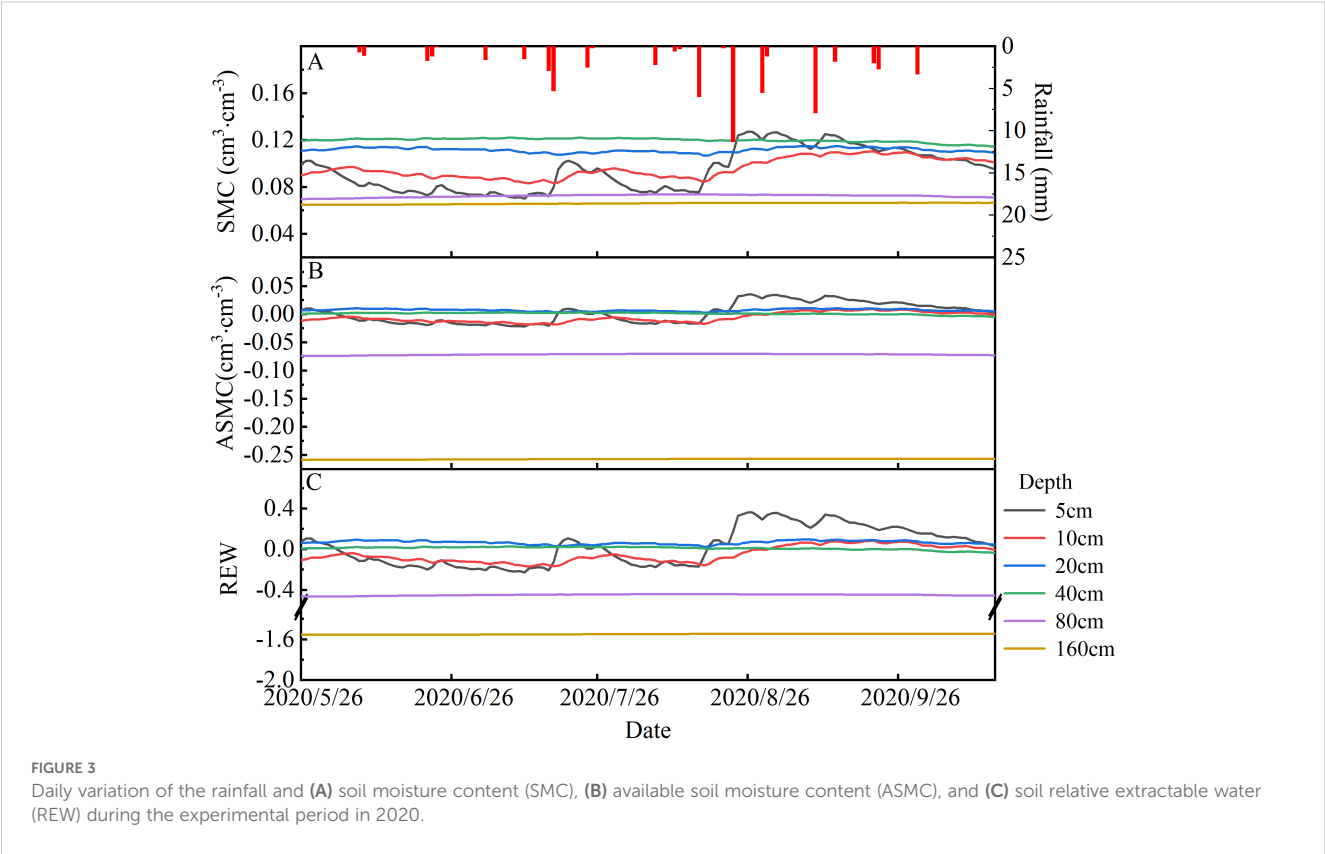
FIGURE 2

Changes in meteorological factors during the experimental period in 2020. (A) Mean daily (average value from 00:00 to 24:00, local time) photosynthetically active radiation (PAR), (B) maximum temperature, average air temperature, and minimum temperature (T_{Max} , $T_{Average}$ and T_{Min}), (C) daily wind speed (WS), (D) daily relative humidity (RH), and (E) daily vapor pressure deficit (VPD) during the experimental period in 2020.

Non-significant difference was observed in mean daily sap flow on pre-rainfall day between the two rainfall categories ($P>0.05$). The average daily stem sap flow of *T. ramosissima* on pre-rainfall day was $605.0 \pm 94.8 \text{ g}\cdot\text{d}^{-1}$ for rainfall category I and $584.0 \pm 105.0 \text{ g}\cdot\text{d}^{-1}$ for rainfall category II. The occurrence of rainfall events significantly decreased daily stem sap flow in both rainfall categories ($P<0.05$). Specifically, compared with the daily stem sap flow on pre-rainfall day, the average daily stem sap flow of *T. ramosissima* decreased by 45.6% in rainfall category I and by 29.5% in rainfall category II. Furthermore, non-significant difference was found in mean daily stem sap flow on pre-rainfall day between the two rainfall categories ($P>0.05$).

Compared to the daily stem sap flow of the pre-rainfall day, non-significant increase was observed in the following three days after rainfall in both rainfall category I and rainfall category II ($P>0.05$). On the first, second, and third days post-rainfall, the

ranges of average daily stem sap flow for rainfall category I and rainfall category II were $319.5\text{--}846.4 \text{ g}\cdot\text{d}^{-1}$ and $223.4\text{--}970.9 \text{ g}\cdot\text{d}^{-1}$, $327.9\text{--}897.9 \text{ g}\cdot\text{d}^{-1}$ and $232.5\text{--}1018.6 \text{ g}\cdot\text{d}^{-1}$, and $365.0\text{--}979.7 \text{ g}\cdot\text{d}^{-1}$ and $242.2\text{--}1098.2 \text{ g}\cdot\text{d}^{-1}$, respectively. The mean daily stem sap flow of *T. ramosissima* on the first, second, and third day after rainfall were $519.2 \pm 77.6 \text{ g}\cdot\text{d}^{-1}$, $594.3 \pm 80.0 \text{ g}\cdot\text{d}^{-1}$, and $639.41 \pm 86.5 \text{ g}\cdot\text{d}^{-1}$ in rainfall category I, respectively. In rainfall category II, the corresponding values were $615.0 \pm 110.7 \text{ g}\cdot\text{d}^{-1}$, $650.4 \pm 118.5 \text{ g}\cdot\text{d}^{-1}$, and $695.3 \pm 129.7 \text{ g}\cdot\text{d}^{-1}$. Compared to the daily stem sap flow of rainfall day, the daily stem sap flow of *T. ramosissima* in the subsequent three days of rainfall have significant increase in both category I and category II ($P<0.05$). However, non-significant differences were detected in daily stem sap flow of *T. ramosissima* between the two rainfall categories on the same day after rainfall ($P>0.05$). Meanwhile, the daily maximum sap flow has been compared among the pre-rainfall, rainfall, and post-rainfall



periods among different rainfall categories (Supplementary Figure S3). Compared to the daily maximum sap flow of the pre-rainfall day, non-significant increase was observed in the following three days after rainfall in both rainfall category I and rainfall category II ($P>0.05$). Moreover, non-significant differences in maximum sap flow of *T. ramosissima* between the two rainfall categories on the same day post-rainfall was observed($P>0.05$).

3.3 Response of daily stem sap flow to environmental factors within different rainfall categories

The daily stem sap flow of rainfall day and the following three days after rainfall are affected by different factors in two rainfall categories (Table 5). The daily stem sap flow on rainfall day and the

TABLE 4 Statistical information of mean daily meteorological factors among two rainfall categories during the experimental period in 2020.

Rainfall category	Time	PAR ($\mu\text{mol}\cdot\text{m}^{-2}\text{s}^{-1}$)	Ta ($^{\circ}\text{C}$)	RH (%)	VPD (kPa)
Category I	PR	519.2 $\pm$ 51.7abA	23.3 $\pm$ 1.2aA	45.4 $\pm$ 3.9abA	1.9 $\pm$ 0.2bA
	RD	401.8 $\pm$ 39.5aA	19.9 $\pm$ 1.7aA	59.2 $\pm$ 3.8bA	1.1 $\pm$ 0.2aA
	FDAR	600.4 $\pm$ 67.9bA	20.5 $\pm$ 2.3aA	50.0 $\pm$ 7.5abA	1.6 $\pm$ 0.2bA
	SDAR	556.4 $\pm$ 33.2abA	20.5 $\pm$ 1.3aA	41.5 $\pm$ 3.6aA	1.7 $\pm$ 0.2bA
	TDAR	623.9 $\pm$ 29.3bA	21.4 $\pm$ 1.5aA	38.4 $\pm$ 3.0aA	2.0 $\pm$ 0.2bA
Category II	PR	464.3 $\pm$ 56.2abA	22.3 $\pm$ 0.4aA	45.9 $\pm$ 6.3abA	1.7 $\pm$ 0.2bA
	RD	315.5 $\pm$ 79.2aA	18.3 $\pm$ 1.4aA	72.7 $\pm$ 2.8cB	0.7 $\pm$ 0.1aB
	FDAR	556.1 $\pm$ 71.1abA	18.9 $\pm$ 1.8aA	63.1 $\pm$ 6.2bcA	1.0 $\pm$ 0.3abA
	SDAR	602.8 $\pm$ 43.9bA	20.8 $\pm$ 0.9aA	50.1 $\pm$ 3.8abA	1.6 $\pm$ 0.2bA
	TDAR	549.7 $\pm$ 60.6abA	22.1 $\pm$ 0.9aA	43.1 $\pm$ 2.6aA	1.8 $\pm$ 0.2bA

PR, RD, FDAR, SDAR, and TDAR are pre-rainfall, the rainfall day, the first day after rainfall, the second day after rainfall, and the third day after rainfall. The average values mentioned above are expressed as the means $\pm$ standard error. Different upper-case letters indicate significant differences in mean daily meteorological factors on the same day among the different rainfall categories (t-test, $P<0.05$). Different lower-case letters indicate significant differences in mean daily meteorological factors among pre-rainfall, rainfall and pos-rainfall day in the same rainfall category (ANOVA, $P<0.05$).

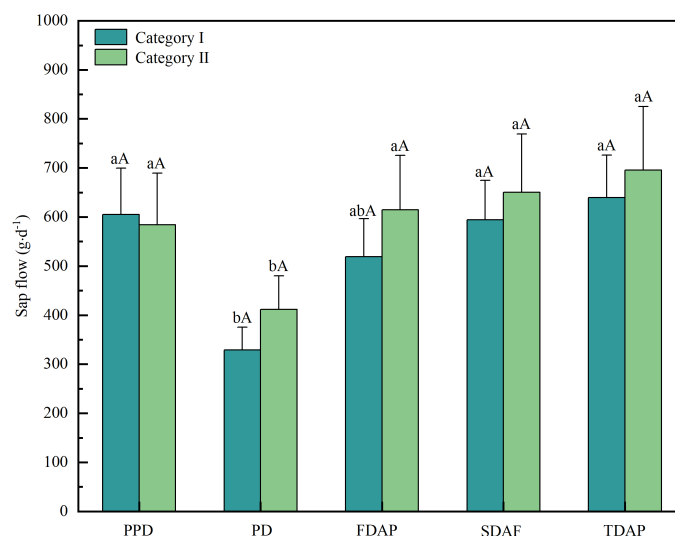


FIGURE 4

Comparison of the mean daily stem sap flow among the pre-rainfall, rainfall, and post-rainfall periods among different rainfall categories during the experimental period in 2020 for *T. ramosissima*. PR, RD, FDAR, SDAR, and TDAR refer to pre-rainfall, the rainfall day, the first day after rainfall, the second day after rainfall, and the third day after rainfall, respectively. Different uppercase letters denote significant differences in daily stem sap flow on the same day among category I and category II ($P < 0.05$). Different lowercase letters signify significant differences in daily stem sap flow among the pre-rainfall, rainfall, and post-rainfall periods within the same rainfall category ($P < 0.05$).

subsequent three days throughout the study period exhibited strong correlations with mean daily PAR, Ta, RH, and VPD in both rainfall categories ($P < 0.01$). In contrast, non-significant correlation was observed between daily stem sap flow and daily SMC in the 40–160 cm soil layer, regardless of the rainfall category ($P > 0.05$). Furthermore, the correlation analysis revealed a significant negative relationship between daily stem sap flow and SMC in the 0–40 cm soil layer on the rainfall day and subsequent three days in rainfall category I. However, no such correlation was observed in rainfall category II.

To assess the potential lag effects of rainfall on the stem sap flow of *T. ramosissima*, the relationship between daily stem sap flow and environmental factors was analyzed separately for the three days following rainfall. The linear relationships between daily stem sap flow and mean daily PAR, mean daily Ta, daily maximum air temperature (T_{Max}), daily minimum air temperature (T_{Min}), daily RH, daily VPD, daily SMC, and daily REW_{0–40cm} of the three days following rainfall within the two rainfall categories are shown in Figure 5. Daily stem sap flow of the three days following rainfall was positively correlated with increases in mean daily PAR, mean Ta, T_{Max} , T_{Min} , and VPD among the two rainfall categories. In contrast, daily stem sap flow decreased with increasing RH in both rainfall categories. Unexpectedly, with the increase in SMC_{0–40 cm}, the daily stem sap flow of the three days following rainfall showed a significantly decline in rainfall category I. Furthermore, the relationship between daily maximum stem sap flow and daily maximum PAR, mean daily Ta, daily maximum Ta, daily minimum Ta, daily minimum daily RH, daily maximum VPD, SMC_{5cm}, and SMC_{10cm} for *T. ramosissima* in the following three days of rainfall events of two rainfall categories during the experimental period in 2020 have been explored (Supplementary Figure S4). Daily maximum sap flow over the three days following

rainfall was positively correlated with daily maximum PAR, daily mean Ta, daily minimum Ta, and daily maximum VPD across two rainfall categories. The daily maximum sap flow over the three days following rainfall was negatively with daily minimum RH, SMC_{5cm} and SMC_{10cm}.

In our structural equation models, mean daily PAR, daily Ta, daily RH, and daily VPD explained 75% and 95% of the variance in daily stem sap flow for rainfall categories I and II, respectively (Figure 6). VPD had a significant direct impact on daily stem sap flow within category I ($P < 0.001$); however, there was non-significant direct impact on daily stem sap flow within category II ($P > 0.05$). PAR indirectly affects stem sap flow through Ta and VPD in rainfall category I. Additionally, PAR showed a significant direct positive association with stem sap flow ($P < 0.001$). And VPD exhibited the highest standardized total effect on stem sap flow in rainfall category I; in contrast, PAR demonstrated the highest standardized total effect on stem sap flow in rainfall category II. Notably, SMC had no direct or indirect impact on stem sap flow within the two rainfall categories during the study period.

3.4 Half-hour stem sap flow dynamics within two different rainfall categories

Diurnal variations in mean half-hourly stem sap flow for *T. ramosissima* on the pre-rainfall day, rainfall day, and the three days following rainfall across the different rainfall categories are presented in Figure 7. The half-hourly stem sap flow on pre-rainfall day was consistently higher than that observed on the rainfall day, regardless of the rainfall category. The mean half-hourly stem sap flow on pre-rainfall and the rainfall day exhibited distinct diurnal patterns in both rainfall categories, with peak values occurring at around 12:00 (local

TABLE 5 Correlation coefficients between daily rainfall stem sap flow of *T. ramosissima* and environmental factors under two rainfall categories among the experimental period in 2020.

Rainfall category	PAR	Ta	Ta _{Max}	Ta _{Min}	RH	VPD	SMC _{0-40cm}	SMC _{40-160cm}	REW _{0-40cm}	REW _{40-160cm}
Category I	0.77**	0.71**	0.82**	0.30**	-0.45**	0.78**	-0.39**	0.07	-0.39	0.56**
Category II	0.90**	0.79**	0.84**	-0.18	-0.87**	0.88**	-0.04	-0.39	-0.03	-0.02

PAR, Ta, Ta_{Max}, Ta_{Min}, RH, and VPD are photosynthetically active radiation, average daily air temperature, maximum daily air temperature, minimum daily air temperature, relative humidity and vapor pressure deficit. SMC and REW are short for soil moisture content and relative extractable water. **P<0.01.

time). Furthermore, the results shown that daytime stem sap flow (from 6:00 to 20:00, local time) on the pre-rainfall and rainfall day of *T. ramosissima* in the two rainfall categories accounted for 98.8% to 99.9% and 98.4% to 99.7% of the total whole-day pre-rainfall stem sap flow, respectively.

Compared to pre-rainfall conditions, there was non-significant variation in half-hourly stem sap flow during the three days following rainfall in rainfall category I and rainfall category II. Although the mean half-hourly stem sap flow increased after the rainfall events relative to the rainfall day, the proportion of daytime stem sap flow to total daily stem sap flow remained largely unchanged, regardless of rainfall category. After the rainfall events, the half-hourly stem sap flow rapidly recovered to its pre-rainfall status, with a peak at noon time within the two rainfall categories. The results showed that, in the

three days after rainfall events, 98.2%-98.7% and 99.8%-99.9% of the total daily stem sap flow occurred during the day time in rainfall categories I and II, respectively.

4 Discussion

4.1 Controlling factors of daily stem sap flow dynamics in two rainfall categories

In accordance with the principles of basic plant physiology, it can be hypothesized that precipitation will exert a considerable influence on the sap flow dynamics of *T. ramosissima*. Nevertheless, the results of this study demonstrate that there is no statistically significant positive

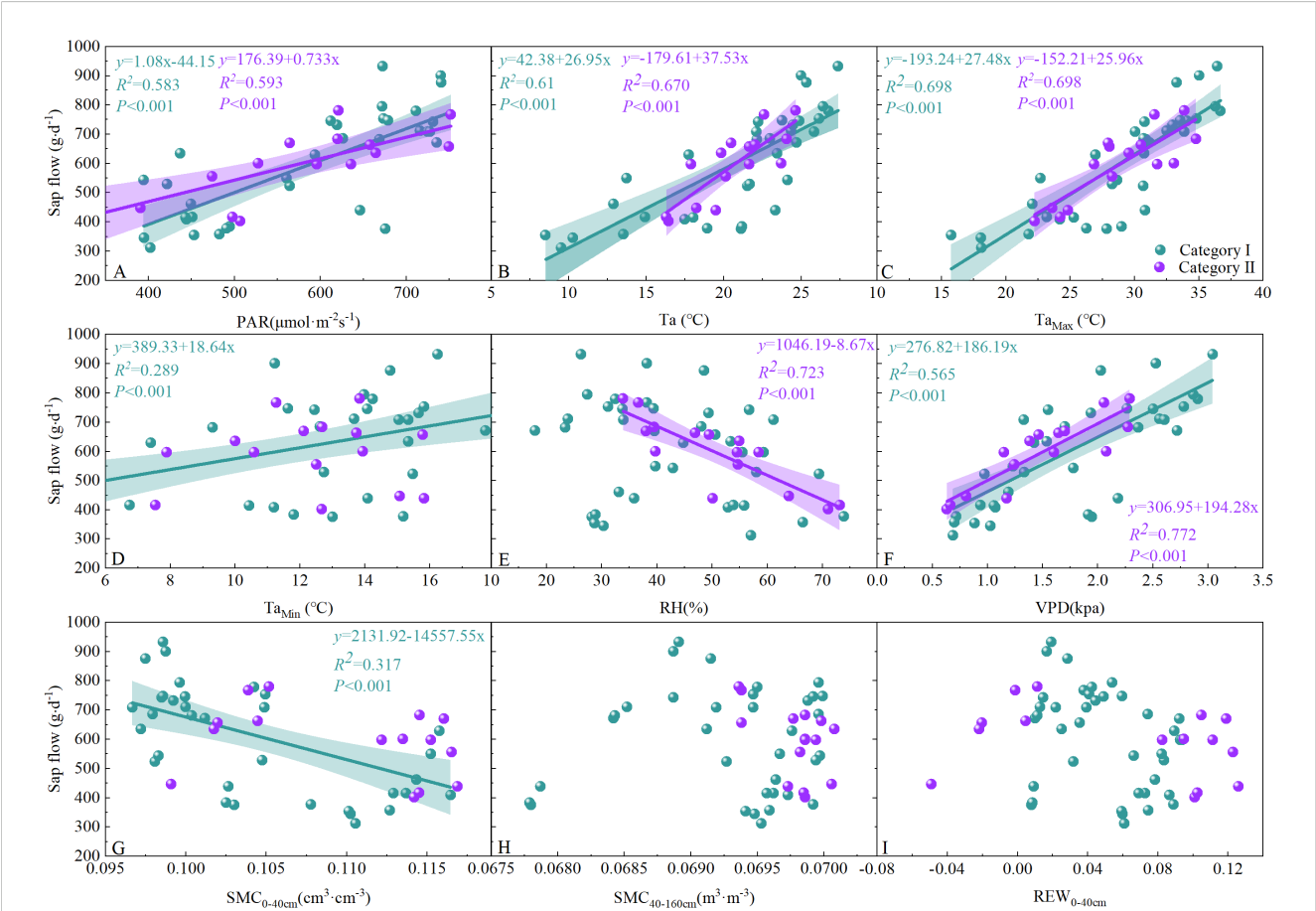


FIGURE 5 Relationship between daily stem sap flow of *T. ramosissima* and mean daily PAR, daily Ta, daily Ta_{max}, daily Ta_{min}, daily RH, daily VPD, SMC_{0-40cm}, SMC_{40-160cm} and REW_{0-40cm} within the different rainfall categories during the experimental period in 2020.

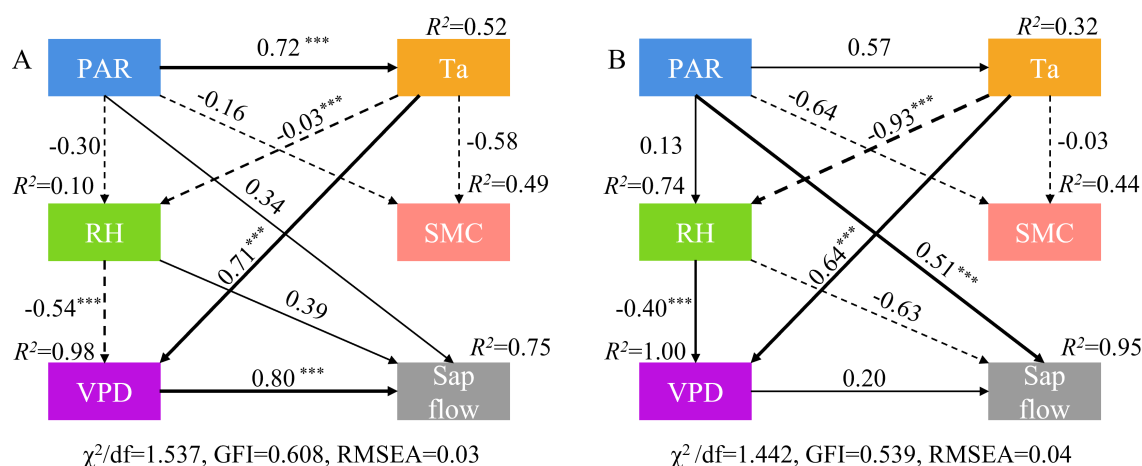


FIGURE 6

Structural equation models showing the relationships among PAR, Ta, RH, SMC and daily stem sap flow for *T. ramosissima* in the rainfall day and the following three days of the category I (A) and category II (B). The value beside each arrow represents the standardized path coefficient. The thickness of the arrow is proportional to the standardized path coefficient on the lines, where solid lines indicate positive values and dashed lines indicate negative values. *** $P < 0.001$.

correlation between daily stem sap flow and SMC_{0-40cm} after precipitation (Figures 5, 6) within the two rainfall categories, contrary to the initial hypothesis. This finding aligns with the “plus-reserve” hypothesis, which posits that smaller rainfalls only affects relatively minor ecological events (e.g., micro-fauna and mic-flora), whereas the larger rainfall affects the physiology and growth of plants (Schwinning and Sala, 2004). Plants do not usually respond directly to rainfall, but rather to the increase in SMC that it causes. The response thresholds of rainfall thresholds are often determined by the ability of plants to utilize soil moisture of different infiltration depth or duration (Schwinning and Sala, 2004). The result of previous studies has demonstrated that stem sap flow increases significantly with higher levels of rainfall (Zhao and Liu, 2010; Jian et al., 2016; Wang et al., 2020; Iqbal et al., 2021), as water is often the limiting factor in desert ecosystems, and positive feedback between SMC and stem sap flow is typically expected. Contrary to this finding, the result of our study indicate that the daily stem sap flow of *T. ramosissima* on pre-rainfall day was consistently higher than that on the rainfall day, irrespective of the rainfall category. Furthermore, there was a non-significant increase in daily stem sap flow in the three days following rainfall events, compared with the results observed in pre-rainfall and on the rainfall day. These results align with the conclusions of previous studies (Chen et al., 2014; Yan et al., 2018). And this uncertainty may be attributed to changes in atmospheric and soil conditions induced by rainfall events, which indirectly result in alterations to the unique physiological characteristics of vegetation. During the growing season, the SMC may be insufficient to meet atmospheric demand, particularly when Ta and VPD are highest, leading to suppressed stem sap flow. During the experimental period, a total of 63.8 mm of precipitation was recorded. Of this, 44% was of rainfall category I, while 56% was of rainfall category II. The results of this study show that the SMC at 0–40 cm depth exhibited a pronounced response to rainfall events; in comparison, the SMC at other depths remained largely unchanged. However, the finding of this study shown that rainfall category I does

not exert an appreciable influence on available SMC at 0–40 cm depth. Despite an increase SMC at 0–40 cm depth and 40–160 cm depth from $0.11 \text{ cm}^3 \cdot \text{cm}^{-3}$ and $0.07 \text{ cm}^3 \cdot \text{cm}^{-3}$, respectively, prior to precipitation, to $1.65 \text{ cm}^3 \cdot \text{cm}^{-3}$ and $0.11 \text{ cm}^3 \cdot \text{cm}^{-3}$ on the first post-precipitation day, there was no corresponding increase in available SMC ($0.00 \text{ cm}^3 \cdot \text{cm}^{-3}$ and $-0.13 \text{ cm}^3 \cdot \text{cm}^{-3}$, respectively) at the aforementioned depths in rainfall category II. Nevertheless, the recorded maximum rainfall was 11.3 mm (on 23 August) during the experimental period. More specifically, the SMC at depths of 5 cm, 10 cm, 20 cm and 40 cm have been re-analysed. Although the soil moisture content increased from $0.10 \text{ cm}^3 \cdot \text{cm}^{-3}$ to $0.13 \text{ cm}^3 \cdot \text{cm}^{-3}$ at a depth of 5 cm and from 0.09 to $0.10 \text{ cm}^3 \cdot \text{cm}^{-3}$ at a depth of 10 cm (Supplementary Table S3), the wilting point at these depths is $0.12 \text{ cm}^3 \cdot \text{cm}^{-3}$. These findings clearly demonstrate that the rainfall level during the experimental period was insufficient to significantly increase the available SMC at 0–40 cm depth.

The daily stem sap flow of *T. ramosissima* is strongly influenced by meteorological factors. When the VPD is high and accompanied with very low SMC, the stem sap flow of plants will decrease or even diminish, which leads to the die of plants. However, *T. ramosissima* is a phreatophyte xerophytic shrub that depends on deep soil moisture or groundwater (Liu et al., 2022). Even under conditions of extremely low SMC in both the 0–40 cm and 40–160 cm soil layers, it maintains normal physiological processes by accessing deep soil moisture or groundwater. Therefore, the sap flow of *T. ramosissima* is controlled by meteorological factors. On typically sunny days, stem sap flow increases as PAR and Ta rise, while RH decreases. This phenomenon may be attributed to the expansion of the potential gradient between leaf-to-air boundaries (Doyle et al., 2007; Huang et al., 2010). Nevertheless, it is anticipated that rainfall events will markedly escalate the RH and concurrently diminish Ta. It is expected that this change will result in a reduction in daily stem sap flow on the rainfall day and may be associated with the fact that stomata tend to close with the change in meteorological conditions and leaf water

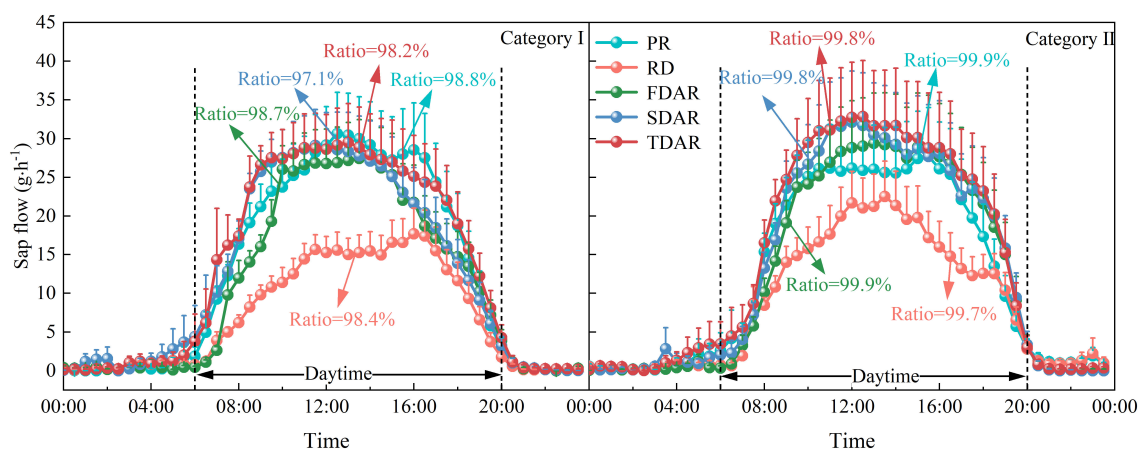


FIGURE 7

Diurnal variation in mean half-hourly stem sap flow in pre-rainfall, rainfall, and post-rainfall days within the two rainfall categories during the experimental period in 2020 for *T. ramosissima*. PR, RD, FDAR, SDAR, and TDAR refer to the pre-rainfall day, the rainfall day, the first day following rainfall, the second day following rainfall, and the third day following rainfall, respectively. Daytime is defined from 06:00 to 20:00 (local time), and the ratio indicates the percentage of total daytime sap flow to total day value in pre-rainfall, rainfall and post-rainfall days.

status (Granier, 1987; Irvine et al., 1998), which is in accordance with the results of previous studies (Zhao and Liu, 2010; Wang et al., 2020). Following the cessation of rainfall, an increase in PAR, T_a , and RH over the subsequent three days resulted in a marked increase in the daily stem sap flow of *T. ramosissima*. However, compared to pre-rainfall conditions, there was no notable change in SMC or available SMC following rainfall. Conversely, rainfall events result in a reduction in PAR and T_a , accompanied by an increase in RH, which contributes to the negative relationship between SMC_{0-40cm} and daily stem sap flow (Figure 5G).

4.2 The effects of rainfall on the daily stem sap flow dynamics of *T. ramosissima*

In general, native plants exhibit reduced responsiveness to environmental variation relative to invasive plants in resource-limited environments, particularly when plant functions are directly linked to resource conservation (Du et al., 2011; Funk, 2013; Ghimire et al., 2018). *T. ramosissima* is a native phreatophyte xerophytic shrub in the terminal area of the Shiyang River in northwest China, which may contribute to weakly response of sap flow dynamics to rainfall variability. The divergence between native and exotic plants may be attributed to differences in hydraulic root resistance, resource competition, and the competitive abilities of individual shrub (Ghimire et al., 2018; She et al., 2019). Under conditions of dry air, stomatal control over transpiration is intensified (Bernier et al., 2006). The prolonged exposure of plants to conditions of water scarcity results in a diminished responsiveness to alterations in the surrounding environment (Mcdowell et al., 2011; Xu and Zhou, 2011). Diminished sensitivity to environmental stress during drought reflects an adaptive regulation of transpiration that prioritizes water conservation (Zhang et al., 2019; Su et al., 2022). Meanwhile, Xu et al. (2009) employed the same method to measure the stem sap flow of irrigated *T. ramosissima* in the Tarim Desert Highway shelterbelt,

located in the Taklimakan Desert. Their results showed that the annual and average daily water consumption of *T. ramosissima* were 1253.39 kg and 6.27 kg·d⁻¹, respectively, which is extremely higher than the values obtained in our study (75.43 kg and 523.8 g·d⁻¹, respectively). Daily stem sap flow of *T. ramosissima* with deep groundwater table (<9 m) remained relatively low during the experimental period, indicating that *T. ramosissima* adopted a conservation water use strategy. This physiological response appears to be mediated through progressive stomatal regulation in response to elevated atmospheric VPD. Such stomatal control mechanisms enable the maintenance of favorable plant water status above critical thresholds, thereby preventing xylem dysfunction through hydraulic failure and cavitation.

The disparate responses of the plant to specific rainfall thresholds were predominantly associated with the source of water on which plant survival was contingent (e.g., topsoil or deep soil water), in addition to the plants' distinctive water-consumption patterns (Beatley, 1974; Ewers and Oren, 2003; Iqbal et al., 2021). For example, Yan et al. (2018) compared the stem sap flow dynamics of *Pinus tabulaeformis* and *Betula albosinensis* under varying moisture conditions. The results showed that with increasing soil moisture content, the stem sap flow of *P. tabulaeformis* increased significantly; in comparison, the stem sap flow of *B. albosinensis* remained predominantly stable. In addition, Jia et al. (2024) found that soil moisture is an important factor affecting stem sap flow. However, this study did not identify any rainfall thresholds that could significantly increase the stem sap flow of *T. ramosissima*. The daily sap flow of *T. ramosissima* on the pre-rainfall day (22 August), the rainfall day (with the largest rainfall of 11.3 mm on 23 August), the first day after rainfall (24 August), the second day after rainfall (25 August), and the third day after rainfall (26 August) were 544.8 ± 95.6 g·d⁻¹, 379.0 ± 95.7 g·d⁻¹, 597.1 ± 110.0 g·d⁻¹, 600.7 ± 108.8 g·d⁻¹ and 682.8 ± 121.0 g·d⁻¹ respectively. Although the daily stem sap flow on post-rainfall days appeared to increase visually compared to pre-rainfall levels, statistical analysis revealed no significant difference in sap flow after the precipitation (Supplementary Figure S5). Additionally, the diurnal

variations in half-hourly stem sap flow and meteorological factors revealed that the peak time for VPD lagged behind that for stem sap flow of *T. ramosissima*, both before and after the rainfall events on 23 August (Supplementary Figure S6). In general, as atmospheric evaporation demand (PAR, Ta, and VPD) increases, the stem sap flow will gradually increase. When PAR and VPD reach their peaks, *T. ramosissima* close some stomata to prevent excessive water extraction from the trunk from xylem vessel embolism and the collapse of the hydrological conductive system of the xylem. Therefore, we are more inclined to believe that the hysteresis between VPD and stem sap flow is a form of self-protection for plant, mitigating water stress in a waterless environment. Moreover, Liu et al. (2022) found that *T. ramosissima* take up water mainly from deep soil moisture and groundwater (>90%). These results indicate that the variation in rainfall pattern are unlikely to significantly affect the daily stem sap flow of *T. ramosissima* via alteration in topsoil moisture. It can therefore be concluded that the level of rainfall recorded during the experimental period was insufficient to trigger a significant increase in stem sap flow in *T. ramosissima*.

5 Conclusion

This study explored the response of stem sap flow dynamics to two different rainfall categories. The result showed that rainfall events led to a reduction in daily stem sap flow by 46.5% and 29.5% across rainfall category I and II, respectively. Nonetheless, non-significant differences in daily stem sap flow were observed during the three days following rainfall events in comparison to pre-rainfall conditions, irrespective of rainfall category ($P>0.05$). Moreover, mean daily PAR, daily Ta, and daily VPD is the primary drivers of stem sap flow on rainfall and the subsequent three days. Additionally, diurnal variations in half-hourly stem sap flow during the three days post-rainfall showed non-significant deviations compared to pre-rainfall levels or those on the rainfall day. Thus, we conclude that impacts of rainfall variability on the stem sap flow of *T. ramosissima* are primarily driven by meteorological factors, independent of the rainfall category, rather than soil water content as initially hypothesized. We can therefore conclude that the impact of rainfall variability on the stem sap flow of *T. ramosissima* are primarily driven by meteorological factors, independent of the rainfall category, rather than soil water content as initially hypothesized. These findings provide critical insights into how plant stem sap flow responses to rainfall events in arid regions. These findings provide critical insights into plant stem sap flow responses to rainfall events in arid regions, highlighting the necessity of considering meteorological variables and rainfall category characteristics in such assessments.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding authors.

Author contributions

FL: Data curation, Methodology, Writing – original draft, Writing – review & editing. LZ: Formal analysis, Investigation, Methodology, Writing – original draft. QY: Formal analysis, Investigation, Methodology, Supervision, Writing – review & editing. XX: Data curation, Supervision, Writing – review & editing. GL: Resources, Supervision, Writing – review & editing. CF: Conceptualization, Formal analysis, Supervision, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fpls.2025.1563166/full#supplementary-material>

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