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Limited direct impacts of precipitation changes on microbial resource limitation in a moderately saline-alkaline desert steppe

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Abstract. While soil enzyme C:N:P ecological stoichiometry is known to be sensitive to precipitation changes in acidic to slightly alkaline grasslands, its response to long-term precipitation changes in moderately to severely saline-alkaline desert steppes remain unclear. In these ecosystems, the triple stress of soil water limitation, nutrient poor, and salinity-alkalinity complicates enzyme response, especially under extreme regimes. Based on a precipitation manipulation experiment (50% reduction, 30% reduction, ambient, 30% increase, 50% increase) initiated in 2014 in a moderately saline-alkaline desert steppe in northwestern China, this study assesses microbial resource limitation and identifies their driving factors by monitoring the monthly dynamics of soil extracellular enzyme C:N:P stoichiometry after 9-year treatment. Enzyme stoichiometry showed limited responses to both reduced and increased precipitation ($P > 0.05$). However, when responses did occur, they varied depending on the direction and intensity of the precipitation change, as well as the specific index examined. Similarly, enzyme vector length and angle were minimally affected by altered precipitation, with phosphorus being the primary limitation for microbes. The variation in vector length and angle was primarily explained by plant traits and microbial stoichiometry, respectively. Precipitation changes altered vector length and angle by modifying soil properties (moisture, NH_4^+-N concentration, pH), plant traits (diversity, carbon concentration, C:P), and microbial stoichiometry (carbon content, C:N, C:P). Rather than exerting a direct effect on microbial resource limitation, altered precipitation indirectly influenced it through modifying soil resource availability, plant diversity, and the carbon-linked stoichiometry of both plants and microbes.

1 Introduction

Climatic warming has significantly altered the water cycle, increasing global precipitation overall (IPCC, 2023; Sun et al., 2022). However, its spatiotemporal distribution has become more uneven， with a rise in extreme precipitation events (Franzke, 2022; Wang et al., 2021; Zhang and Wang, 2023). Simultaneously, increased atmospheric evaporation demand has exacerbated water imbalance, expanding drought extent, even in humid regions that are experiencing drying trends (Gebrechorkos et al., 2025). In China, while precipitation intensity has generally increased, its uneven distribution exposes some regions to extreme precipitation conditions, particularly in the northwest, where precipitation events are becoming

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more frequent (Dong et al., 2022; Zhang and Zhao, 2022). Precipitation variability affects plant growth and microbial activity by regulating soil water availability, ultimately influencing soil carbon (C) and nutrient cycling (Deng et al., 2021). As key catalysts in soil ecosystems, enzymes play central roles in organic matter decomposition and nutrient cycling (Sinsabaugh et al., 2009). Understanding how soil enzymes respond to precipitation changes, especially under extreme changes, is of great significance for predicting ecosystem responses to climate change and for maintaining their stability.

Numerous studies have demonstrated that the impacts of altered precipitation on soil enzyme activity in grasslands depend on the intensity, direction, and duration of changes. Specifically, a moderate increase in precipitation can enhance enzyme activity by improving soil moisture and promoting substrate diffusion (Akinyemi et al., 2020). In contrast, an extreme increase may cause soil water saturation and O_2 limitation, thereby suppressing the production of aerobic microbial enzymes (Hai et al., 2022). A moderate drought reduces microbial metabolism by limiting water and nutrient availability (Cui et al., 2019), whereas an extreme drought impairs microbial community function and diminishes enzyme activity (Ma et al., 2020b). The double asymmetric model suggests that under moderate precipitation changes, ecosystems respond more strongly to increases than to decreases, whereas the opposite occurs under extreme changes (Knapp et al., 2017). A recent study confirms that soil enzyme activity and stoichiometry also exhibit a "dual-asymmetric" response pattern to altered precipitation and the different responses are strongly linked to experimental duration (Li et al., 2024). A synthesis of recent studies on grassland enzyme responses to the direction and intensity of long-term precipitation change reveals that research has largely concentrated on acidic to slightly alkaline grasslands, while investigations into moderately to severely alkaline ones remain notably limited.

Precipitation regulates soil microbial resource limitations for C, nitrogen (N), and phosphorus (P), yet the underlying mechanisms differ. Drought generally reduces plant productivity and litter input, decreasing microbial C availability and lowering C use efficiency (CUE) (Pei et al., 2024), thereby intensifying C limitation. While drought may also inhibit N transformation processes, reducing available N consumption and temporarily alleviating N limitation in the short term (De Silva et al., 2025). Prolonged drought suppresses P mineralization, which may ultimately exacerbate P limitation despite the potential release of organic P from microbial mortality replenishing the available P pool (Cui et al., 2021). Conversely, moderate water addition can enhance plant photosynthesis and litter return (Gao et al., 2024), thereby alleviating microbial C limitation. In contrast, excessive precipitation can promote N leaching and intensify plant-microbe competition for N, aggravating N limitation (Wan et al., 2024). Although increased precipitation generally helps lower soil pH and promotes the dissolution of bound P, thereby enhancing P availability, extreme precipitation may also lead to the leaching or fixation of particulate P, further intensifying P limitation (Yang et al., 2023). Therefore, microbial resource-limitation responses to altered precipitation are also intensity-direction-duration-dependent.

Desert steppe represents a typical grassland ecosystem in the arid and semi-arid regions of China. The high soil $CaCO_3$ content and intense saline-alkaline conditions of these areas confer a strong abiotic C sequestration potential and inorganic C sink capacity. Although some studies have examined the effects of precipitation changes on soil enzyme stoichiometry and microbial resource limitation in desert steppes, most have focused on neutral to slightly alkaline soils ($pH < 8.5$) and relied

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on short-term observations (<5 years). Consequently, there remains a limited understanding of how grasslands across a wider soil pH gradient respond to altered precipitation regimes. Compared to acidic and neutral soils, the higher pH in saline-alkaline soils greatly inhibits both soil enzyme (Qu et al., 2022) and microbial (He et al., 2025) activities, likely resulting in divergent responses to precipitation change.

To address this, the present study was conducted within a long-term in-situ precipitation manipulation experiment, established in 2014 in a moderately saline-alkaline desert steppe in northwestern China. By monitoring the temporal dynamics of extracellular enzyme stoichiometry, we aimed to investigate microbial resource limitations and their driving factors. Specifically, the study addressed two questions: (1) How do the intensity and direction of long-term precipitation alteration affect soil enzyme activity and microbial resource limitation? (2) Since soil enzymes were secreted from both plant roots and microbes, to what extent can plant traits and microbial stoichiometry explain variations in microbial resource limitation? If their explanatory power is limited, which environmental factors serve as the primary drivers? The findings of this study can provide data to support an in-depth understanding of elemental cycling mechanisms in grasslands with varying soil pH levels under changing precipitation patterns.

2. Materials and Methods

2.1 Study site

The simulated field experiment of changing precipitation was set up in a fenced desert steppe of Yanchi County, Ningxia Hui Autonomous Region, China (107°49′ E, 37°80′ N, Fig. 1). The study area is located at the southwest edge of the Mu Us Sandy Land, with the sandy land proper to the south and the Ordos gently sloping hills to the north. The climate of the area is a temperate continental monsoon climate with low precipitation, high evaporation, and frequent windy and sandy weather. The average temperature in 2014–2022 was 9.7 ℃, and the average annual precipitation was 323.0 mm. The average temperature was 10.0 ℃ in 2022, while the average precipitation was 315.5 mm (Fig. 1). The experimental site is poor in soil nutrients and low in plant cover. The main soil types are gray calcium soil and sandy soil, with poor retention capacities for water and nutrients. The soil displays a high pH (>8.5) and a moderate salinity-alkalinity due to the abundant $CaCO_3$ content in the soils. Plant community composition mainly includes annual and perennial herbaceous plants, e.g., *Astragalus melilotoides*, *Lespedeza potaninii*, *Sophora alopecuroides*, *Thermopsis lanceolata*, *Heteropappus altaicus*, *Artemisia scoparia* (Huang et al., 2021).

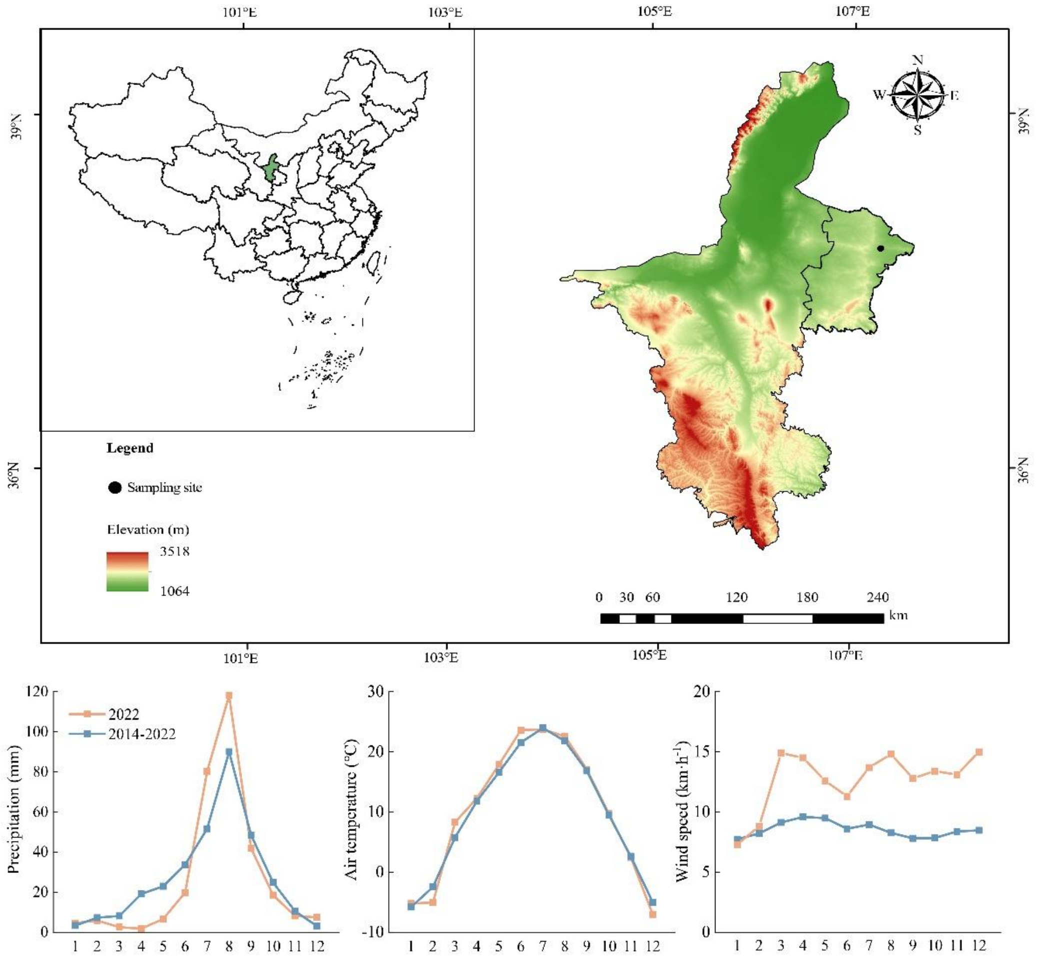

Fig. 1: Geographic location and meteorological factors (mean monthly precipitation, air temperature, wind speed) at the Yanchi County Weather Station, Ningxia, China. Dada was obtained from China Meteorological Data Sharing Service System (https://data.cma.cn/).

2.2 Experimental design

In 2014, a flat area was selected as a simulated field experiment site in the study area, with a 2 m wide buffer zone between each plot. According to the randomized block group experimental design, five precipitation treatments were set up: 50% reduction (extreme reduction, –P50), 30% reduction (moderate reduction, –P30), ambient (control, CK), 30% increase (moderate increase, +P30) and 50% increase (extreme increase, +P50). Each treatment was replicated three times, with a total of 15 plots and each plot was 8 m × 8 m. To reduce surface runoff and underground leakage interference between the adjacent plots, each plot was enclosed by colored steel sheets inserted vertically upwards (20 cm above the ground) and plastic sheets buried vertically downwards (1 m in width) (Fig. S1).

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From 2014 to 2017, reduced precipitation was achieved using rain shelters covered with blue polyvinyl chloride film (>95% light transmittance). The covering period was from May to August each year (abundant precipitation period) (Na et al., 2019). Since January 2018, the treatment method has been improved by installing a U-shaped precipitation reduction frame (with the highest point about 1.8 m above the ground) in each plot. Transparent PolyVinyl Chloride (PVC) panels, equivalent to 50% (–P50) or 30% (–P30) of the precipitation cover area, were built above each frame to achieve a year-round reduction in precipitation.

In the increased precipitation treatments (+P30 and +P50), a self-made device for spraying water, which was installed with a water meter (an accuracy of 0.001 m^3) and three micro-sprinkler belts (an aperture of 1.2 mm), was used to increase the precipitation in each plot. The two water addition treatments increased precipitation by 30% (+86.8 mm) and 50% (+144.7 mm) relative to the local average annual precipitation (289.4 mm). Considering the operability of the field experiment and the abundant period of precipitation distribution in the study area, the increased precipitation required for the two treatments was converted into the amount of water added, which was sprayed once every two weeks from May to August each year.

2.3 Field surveying and sampling

To quantify aboveground plant biomass and diversity, three randomly placed 1 m×1 m subplots were sampled monthly from May to August in 2022. Following Li et al. (2022), we recorded all plant species with each subplot and measured their height and density to calculate species diversity indices (Patrick richness and Shannon-Wiener indices). Subsequently, the aboveground plant in each subplot was clipped and categorized by species. After drying in an oven at 65 °C for 48 h, the total aboveground biomass of each subplot was determined using an analytical balance.

Simultaneously, aboveground part of the plant community was collected to analyze element contents in each subplot. Following the harvest of aboveground plants, a topsoil subsample (0–20 cm) was collected from each subplot using a soil auger (5 cm in diameter). Subsamples from the three subplots were pooled to form a single composite sample, which was immediately transported to the laboratory in an ice box. In the laboratory, each composite sample was first split: one portion was used for immediate soil water content determination. The remaining portion was sieved (2 mm) to remove plant debris and gravel, then subdivided. One subsample was stored at 4 °C for prompt analysis of extracellular enzyme activities, available N (NH_4^+-N and NO_3^--N), available P, and microbial biomass C, N, and P. The other subsample was air-dried for subsequent analysis of soil pH, organic C, total N, and total P.

2.4 Measurement of extracellular enzyme activity and microbial biomass

The enzyme activities, including C-acquiring enzymes (β-1,4-glucosidase, BG; β-D-cellobiosidase, CBH), N-acquiring enzymes (β-1,4-N-acetylglucosaminidase, NAG; L-leucine aminopeptidase, LAP), and P-acquiring enzymes (alkaline phosphatase, AKP), were analyzed using a fluorometric microplate enzyme assay (Sinsabaugh et al., 2009). The three acquiring enzymes were abbreviated as C_e, N_e, and P_e, respectively. Sample suspensions were obtained by mixing 1 g soil with 125 mL of acetate buffer. Aliquots (200 μL) were dispensed into 96-well plate for assay, blank, and standard wells. 50

µL of substrate or buffer was added to the wells (10 mM standard for standard wells). Negative controls had buffer and substrate, while reference standards had buffer and standard. After incubation at 25 °C for 4 h, reactions were terminated with NaOH. Fluorescence was measured at 365/450 nm emission using a microplate reader (M200Pro, Tecan Infinite, Switzerland).

Microbial biomass C, N and P contents were determined using the chloroform fumigation-extraction method (Vance et al., 1987). For each soil sample, one 10 g fresh soil portion was subjected to chloroform fumigation at 25 °C for 24 h , while an equivalent portion served as an unfumigated control. C and N contents were extracted from both sets with 0.5 M K_2SO_4 (100 mL), and P content with 0.5 M $NaHCO_3$ (200 mL). The measured contents were converted to microbial biomass using established factors (0.45 for C, 0.54 for N, and 0.40 for P).

2.5 Measurement of environmental variables

In the laboratory, dried leaf samples were pulverized and sieved through a 0.425 mm mesh. The plant community C, N, and P concentrations were examined using the $K_2Cr_2O_7$ method, Kjeldahl method, and molybdenum blue colorimetry method, respectively. Soil water content was determined gravimetrically after drying at 105 °C for 24 h; pH was measured in a 1:5 soil-water suspension using an acidity meter. The organic C, total N, total P and available P contents were determined by the $K_2Cr_2O_7$ method, Kjeldahl method, $HClO_4$-H_2SO_4 method and 0.5 mol L^{-1} $NaHCO_3$ method, following the standard procedures outlined by Sparks et al. (1996). The NH_4^+-N and NO_3^--N concentrations were analyzed using a continuous analytical system (Liu et al., 2020). The climate data (mean monthly precipitation, air temperature, and wind speed) in Yanchi County from 2014 to 2022 were obtained from the China Meteorological Data Sharing Service System (https://data.cma.cn/).

2.6 Data calculation

Microbial resource limitation was assessed via vector analysis of soil extracellular enzyme activities (Moorhead et al., 2016). Vector length reflects microbial C limitation, which quantifies relative C acquisition versus nutrient acquisition. A longer vector length reflects a stronger C limitation. Vector angle indicates microbial nutrient limitation, which quantifies relative P acquisition versus N acquisition. Vector angle > 45° denotes a stronger P limitation, whereas < 45° denotes a stronger N limitation. The degree of P and N limitation increases with larger and smaller angles, respectively. Vector length and angle were calculated as follows:

$$\text{Vector length} = \text{Sqrt}\ (x2+y2) \quad (1)$$

$$\text{Vector angle}\ (°) = \text{Degrees}\ (\text{ATAN2}(y, x)) \quad (2)$$

$$x = \ln\ (BG+CBH)/\ln\ (NAG + LAP) \quad (3)$$

$$y = \ln\ (BG+CBH)/\ln\ (AKP) \quad (4)$$

Based on the concept of double asymmetry model (Knapp et al., 2017), the asymmetry index (ASI) was calculated between increased precipitation (+P30 and +P50) and reduced precipitation (–P30 and –P50) treatments, as well as moderate precipitation changes (–P30 and +P30) and extreme precipitation changes (–P50 and +P50) treatments to quantify the asymmetry of soil enzyme activities in response to precipitation changes. The positive ASI values indicate that soil enzymes responded more strongly to the increased precipitation (extreme precipitation changes) than to the reduced precipitation (moderate precipitation changes), and vice versa. The ASI was calculated as following:

$$ASI=[(V_{IP}-V_C)-(V_C-V_{DP})]/V_C \quad (5)$$

$$ASI=[(V_{50}-V_C)-(V_C-V_{30})]/V_C \quad (6)$$

where V_C, V_{IP}, V_{DP}, V_{50} and V_{30} represent soil enzyme activity under the ambient precipitation, increased precipitation, reduced precipitation, extreme precipitation changes, and moderate precipitation changes, respectively.

Microbial CUE was calculated based on the stoichiometry of organic matter, microbial biomass and enzyme (Sinsabaugh and Follstad Shah 2012):

$$CUE = CUE_{max} \times ((S_{C:N} \times S_{C:P})/[(K_{C:N} + S_{C:N}) \times (K_{C:P} + S_{C:P})])^{0.5} \quad (7)$$

$$S_{C:N} = C{:}N_m / C{:}N_s \times 1/ C{:}N_e \quad (8)$$

$$S_{C:P} = C{:}P_m / C{:}P_s \times 1/ C{:}P_e \quad (9)$$

where the half-saturation constants $K_{C:N}$ and $K_{C:P}$ (0.5) account for the stoichiometric availability of C relative to N and P in the substrate. CUE_{max} represents the upper limit of microbial growth efficiency, which was set as 0.6 (Sinsabaugh et al., 2016). $C{:}N_m$ and $C{:}P_m$ were the microbial biomass C:N and C:P, respectively. $C{:}N_s$ and $C{:}P_s$ were estimated as soil C:N and C:P, respectively. $C{:}N_e$ was calculated as (BG+CBH)/(NAG + LAP), while $C{:}P_e$ was calculated as (BG+CBH)/AKP.

2.7 Statistical analysis

A two-way analysis of variance (ANOVA) was used to analyze the interaction between changing precipitation and sampling month on soil enzyme activities, microbial resource limitation, and CUE. Differences in enzyme activities and microbial resource limitation among the five treatments in different months were assessed unsing One-way ANOVA. Data were Log-transformed prior to analysis if necessary (Legendre and Gallagher 2001). These analyses were performed in SPSS 26.0 (IBM Corp.), and all figures were generated using Origin 2021 (OriginLab Corp.). To quantify the asymmetry in enzyme activities in response to precipitation changes, the ASI of enzyme stoichiometry was calculated in Microsoft Excel. The confidence intervals for the ASI were computed using Rmisc package in R4.1.2. The results were presented as means ± 95% confidence intervals, with responses considered significant when the intervals did not exceed zero. Linear regression was applied to determine the relationships between vector characteristics (length and angle) with CUE.

The variation partition analysis was performed using the vegan package in R to disentangle the effects of precipitation treatment, soil physicochemical property (water content, pH, electric conductivity, NO_3^--N, NH_4^+-N, available P, C:N:P stoichiometry), microbial stoichiometry and plant trait (biomass, diversity, and C:N:P stoichiometry) on microbial resource limitation and CUE. Pearson's correlation analysis was performed to identify the key environmental factors influencing microbial resource limitation and CUE. Following the theoretical framework, the structural equation model was constructed using the plspm package in R to screen latent variables and standardize the data, during which soil factors with standardized loadings < 0.7 were excluded. See abbreviations in Table 1.

Table 1 The abbreviation of each index in the text.

Full names	Abbreviations
Soil C-acquiring enzymes (BG+CBH)	C_e
Soil N-acquiring enzymes (NAG+LAP)	N_e
Soil P-acquiring enzymes (AKP)	P_e
Soil enzyme C:N:P ecological stoichiometry	C_e, N_e, P_e, $C:N_e$, $C:P_e$, and $N:P_e$
Microbial carbon use efficiency	CUE
Mean monthly precipitation	MMP
Mean monthly temperature	MMT
Soil C:N:P ecological stoichiometry	C_s, N_s, P_s, $C:N_s$, $C:P_s$, and $N:P_s$
Soil water content	SWC
Soil pH	pH
Soil electric conductivity	EC
Soil NH_4^+-N concentration	AN
Soil NO_3^--N concentration	XN
Soil available P concentration	AP
Microbial biomass C:N:P ecological stoichiometry	C_m, N_m, P_m, $C:N_m$, $C:P_m$, and $N:P_m$
Plant C:N:P ecological stoichiometry	C_p, N_p, P_p, $C:N_p$, $C:P_p$, and $N:P_p$
Plant community biomass	B
Plant Patrick richness index	R
Plant Shannon-Wiener diversity index	H

3. Results

3.1 Effects of precipitation treatments on soil enzyme C:N:P ecological stoichiometry

Changing precipitation and its interaction with sampling month did not greatly affect enzyme stoichiometry in most cases ($P > 0.05$), whereas sampling month had great effects on the six indices of enzyme stoichiometry ($P < 0.05$; Table 2). Across the four sampling months, both reduced and increased precipitation had little effect on enzyme stoichiometry (Fig. 2). Compared with the control (CK), –P50 decreased C_e and P_e in July ($P < 0.05$), –P30 decreased $C:P_e$ in May ($P < 0.05$), +P30 increased P_e in June ($P < 0.05$) but decreased the latter in July ($P < 0.05$), +P50 increased N_e and P_e, in June ($P < 0.05$). When soil enzyme activity was subjected to the moderate precipitation changes, the ASIs of C_e, N_e, P_e, $C:N_e$, $C:P_e$, and $N:P_e$ were –0.05, 0.02, 0.06, –0.06, –0.07, and –0.01, respectively (Fig. 3). However, under extreme precipitation changes, those of six indices increased to –0.01, 0.15, 0.09, –0.09, –0.08, and 0.01, respectively (Fig. 3).

Table 2 Effects of precipitation change (P), sampling month (M), and their interaction (P×M) on soil enzyme C:N:P stoichiometry (Two-way ANOVA).

Sources of variation	Degrees of freedom	*F* value					
		C_e	N_e	P_e	C:N_e	C:P_e	N:P_e
P	4	2.262	4.514**	2.040	0.969	0.893	1.862
M	3	27.072***	26.873 ***	144.853***	19.317***	29.891***	3.106*
P×M	12	0.826	1.055	1.290	0.931	1.459	0.612

**, $P < 0.01$. ***, $P < 0.001$. See abbreviations in Table 1.

3.2 Effects of precipitation treatments on soil microbial resource limitation and carbon use efficiency

Sampling month influenced enzyme vector length and angle and CUE ($P < 0.001$), whereas changing precipitation and its interaction with sampling month showed no significant impacts ($P > 0.05$; Table 3). Across the four sampling months, both reduced and increased precipitation had generally little effect on vector length (Fig. 4a), angle (Fig. 4b), and CUE (Fig. 5a), except for a significant effect of +P30 on vector angle in June ($P < 0.05$) and of +P50 on CUE in July ($P < 0.05$). Overall, vector length under ambient precipitation was higher than under decreased or increased precipitation.

Vector angle exceeded 45° and all data points fell above the 1:1 line, indicating that P limitation occurred in microbial communities across all treatments (Fig. 4c). Linear regression analysis showed CUE was significantly negatively correlated with vector length ($P < 0.001$; Fig. 5b) and significantly positively correlated with vector angle ($P < 0.05$; Fig. 5c).

Table 3 Effects of precipitation change (P), sampling month (M), and their interaction (P×M) on microbial resource limitation (vector length and angle) and carbon use efficiency (CUE) (Two-way ANOVA).

00Sources of variation	Degrees of freedom	*F* value		
		Vector length	Vector angle	CUE
P	4	0.626	1.156	1.772
M	3	25.368***	17.593 ***	21.461***
P×M	12	0.863	1.007	1.556

***, $P < 0.001$. See abbreviations in Table 1.

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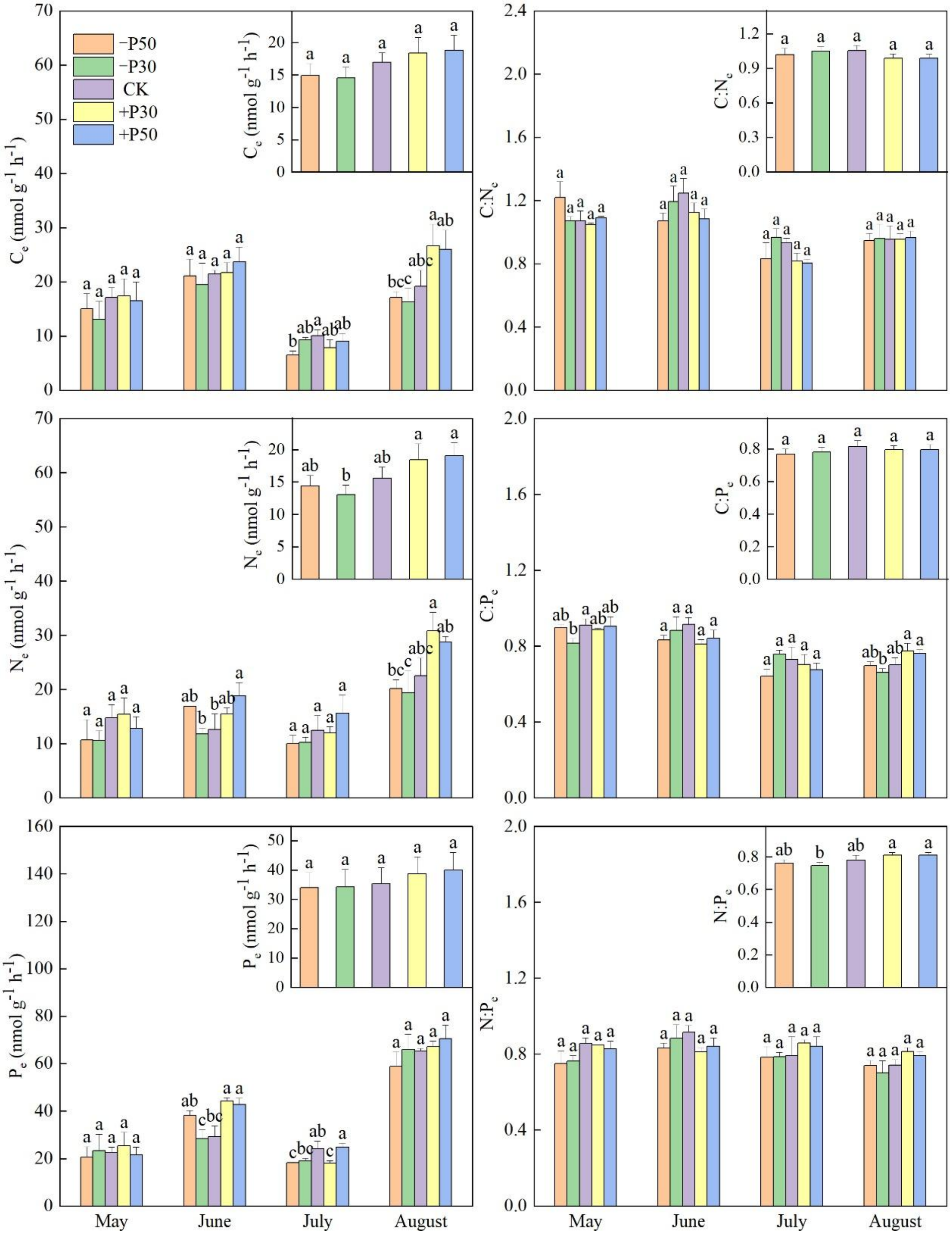

Fig. 2: Differences in soil enzyme C:N:P ecological stoichiometry between the precipitation treatments in the four sampling months. See observations in Table 1. The data are means ± SE. Different lowercase letters represent significant differences in the same sampling month ($P < 0.05$).

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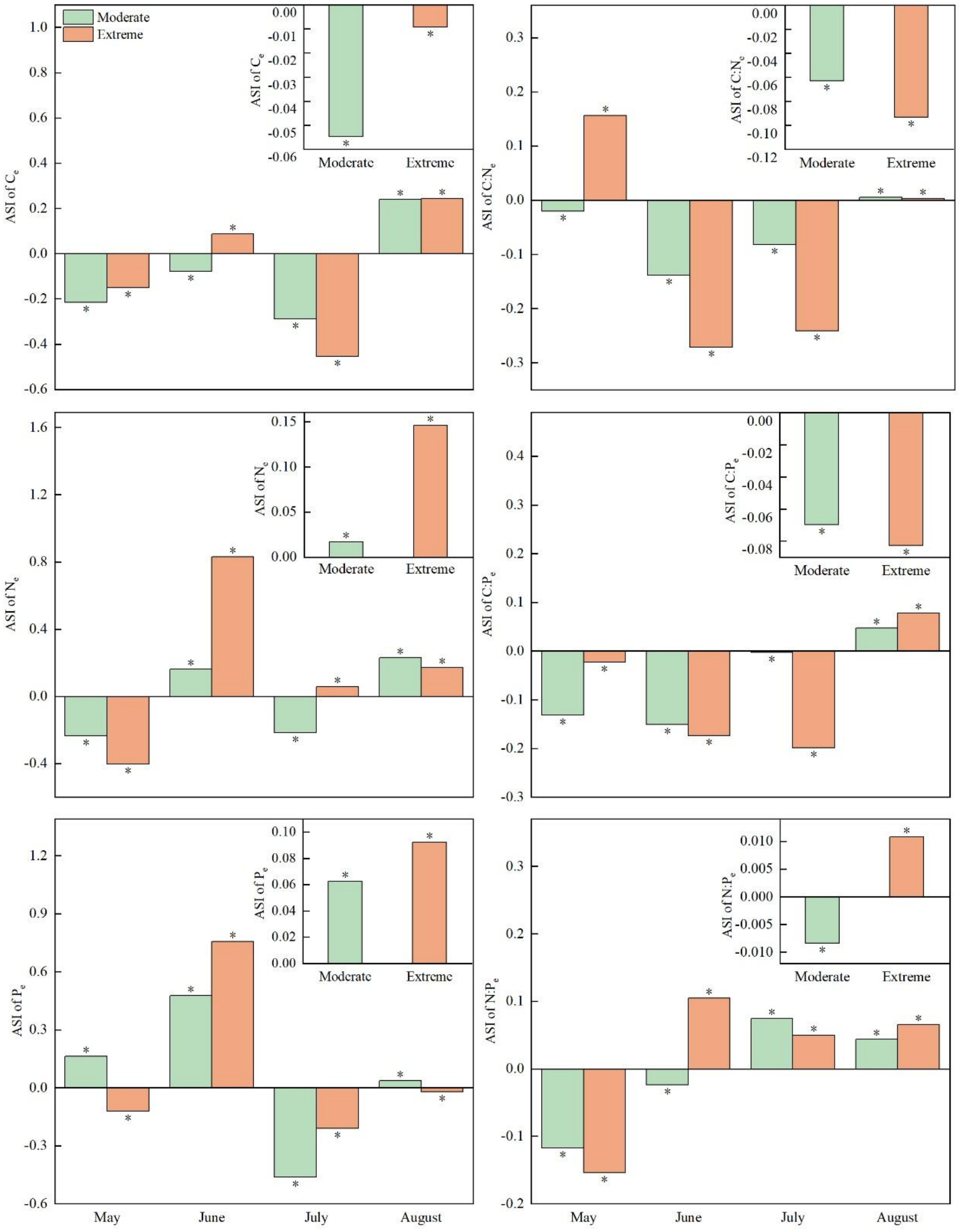

Fig. 3: Asymmetry index (ASI) of soil enzyme C:N:P ecological stoichiometry under moderate and extreme precipitation treatments. Error bars indicate 95% confidence intervals and asterisks suggest significant asymmetries under the condition that the 95% confidence intervals did not override zero. The positive ASI values indicate that soil enzymes responded more strongly to the increase than to the reduction, and vice versa.

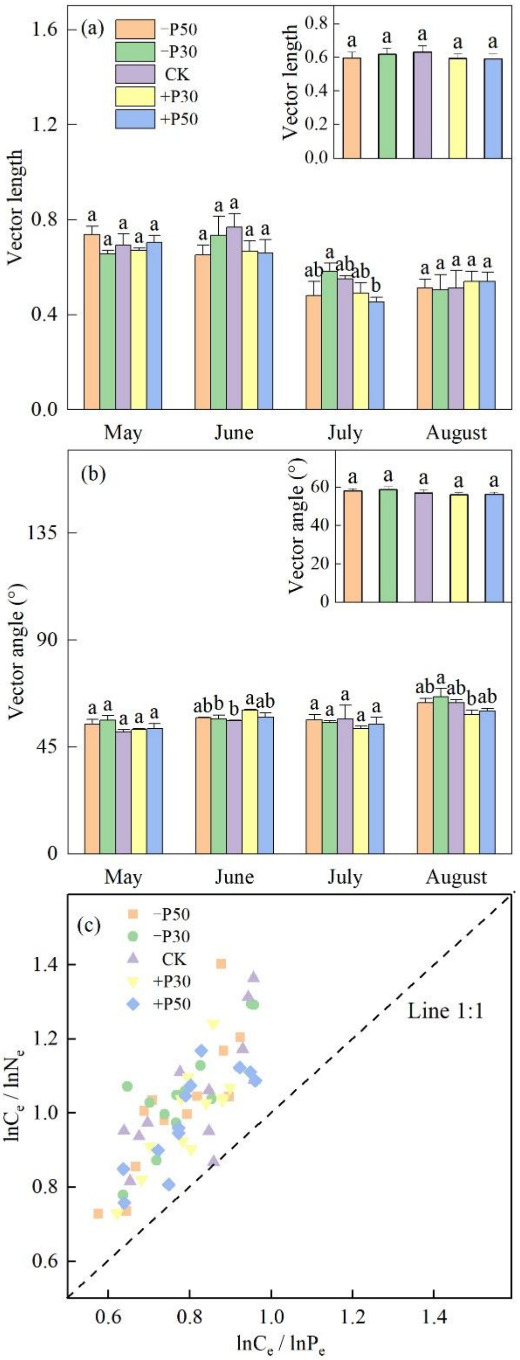

Fig. 4: Differences in soil enzyme vector length (a) and angle (b) between the precipitation treatments in the four months, ecological stoichiometry of the relative proportions of C to N acquisition versus C to P acquisition (c). Different lowercase letters represent significant differences in the same month ($P < 0.05$).

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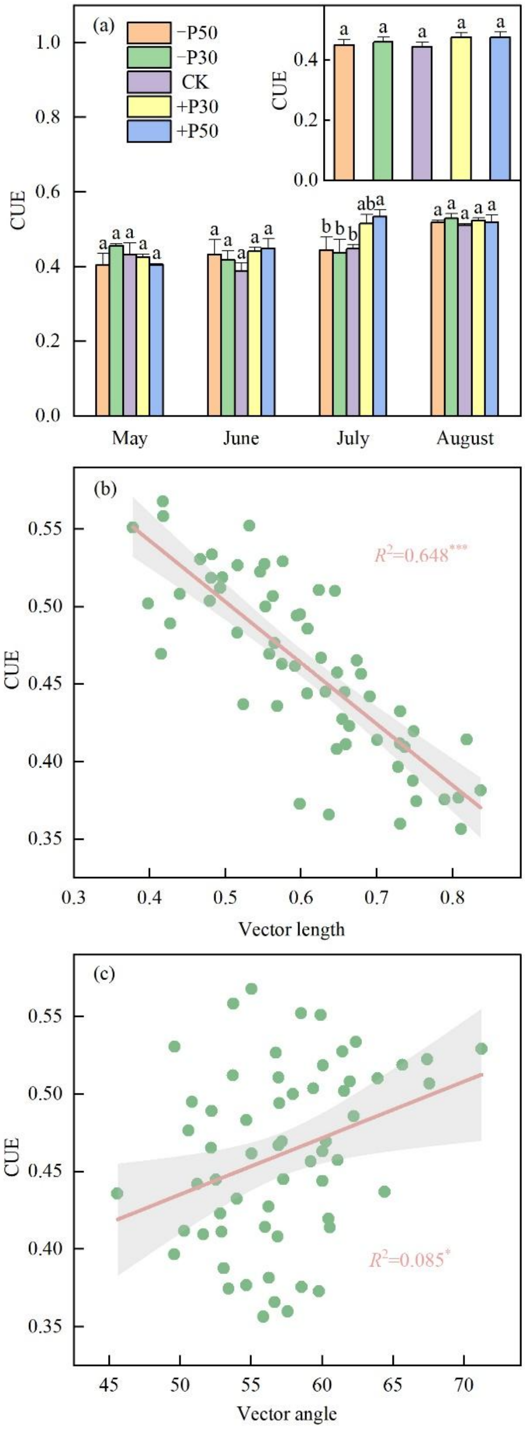


Fig. 5: Differences in soil microbial carbon use efficiency (CUE) between the precipitation treatments (a) in the four months and the relationship between CUE and vector length (b) and angle (c). Different lowercase letters represent significant differences in the same month ($P < 0.05$).

3.3 Factors driving soil microbial resource limitation and carbon use efficiency

Variation partition analysis showed that plant trait served as the main contributor to variations in vector length (Fig. 6a), while microbial stoichiometry constituted the main factor explaining variations in vector angle (Fig. 6b). The interaction among soil physicochemical property, plant trait, and microbial stoichiometry acted as a secondary determinant of variations in vector angle (Fig. 6b). Collectively, soil physicochemical property, plant trait, and microbial stoichiometry jointly explain a large variation in CUE (Fig. 6c).

Based on correlation analyses (Fig.7c), structural equation models were developed (Fig. 8). The model revealed that precipitation indirectly reduced vector length by modifying soil properties (moisture and NH_4^+-N concentration) and plant traits (Patrick richness index, Shannon-Wiener diversity index, C concentration, C:P). In contrast, precipitation exerted an indirect positive effect on the vector angle through changes in soil properties (moisture, pH, NH_4^+-N), plant traits (Patrick richness index, Shannon-Wiener diversity index, C concentration, C:P), and microbial stoichiometry (C content, C:N, C:P). Additionally, precipitation positively influenced CUE via its effects on soil properties (moisture and NH_4^+-N concentration), plant traits (Patrick richness index, Shannon-Wiener diversity index, C concentration, C:P), microbial stoichiometry (C content, C:N, C:P), and vector length (Fig. 6c).

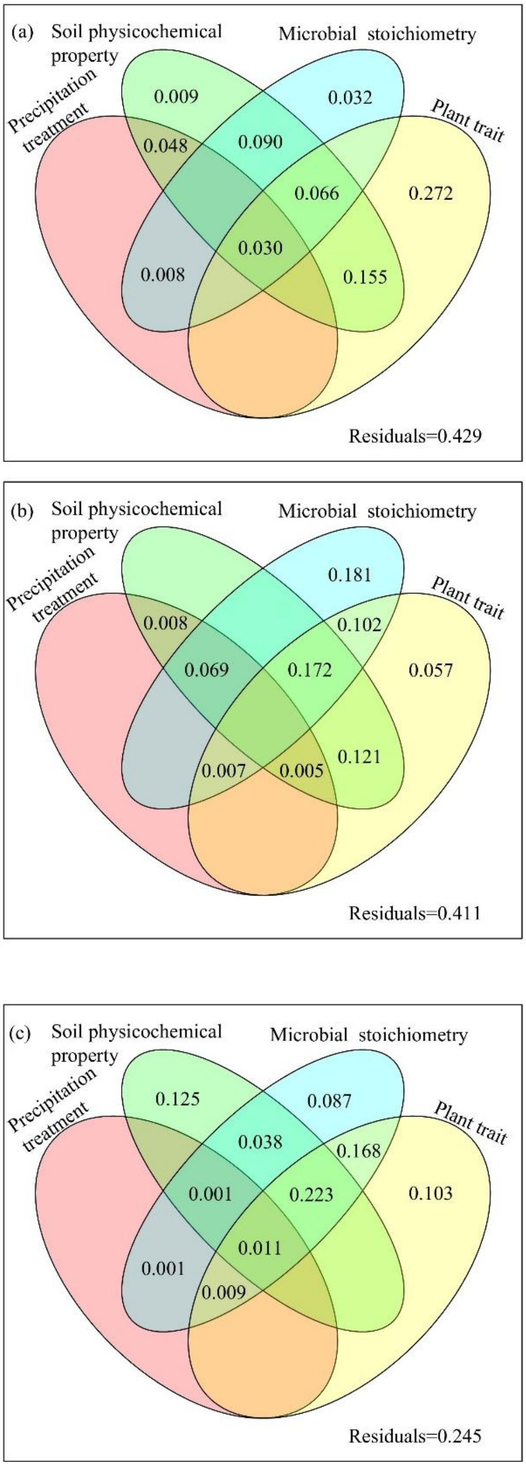
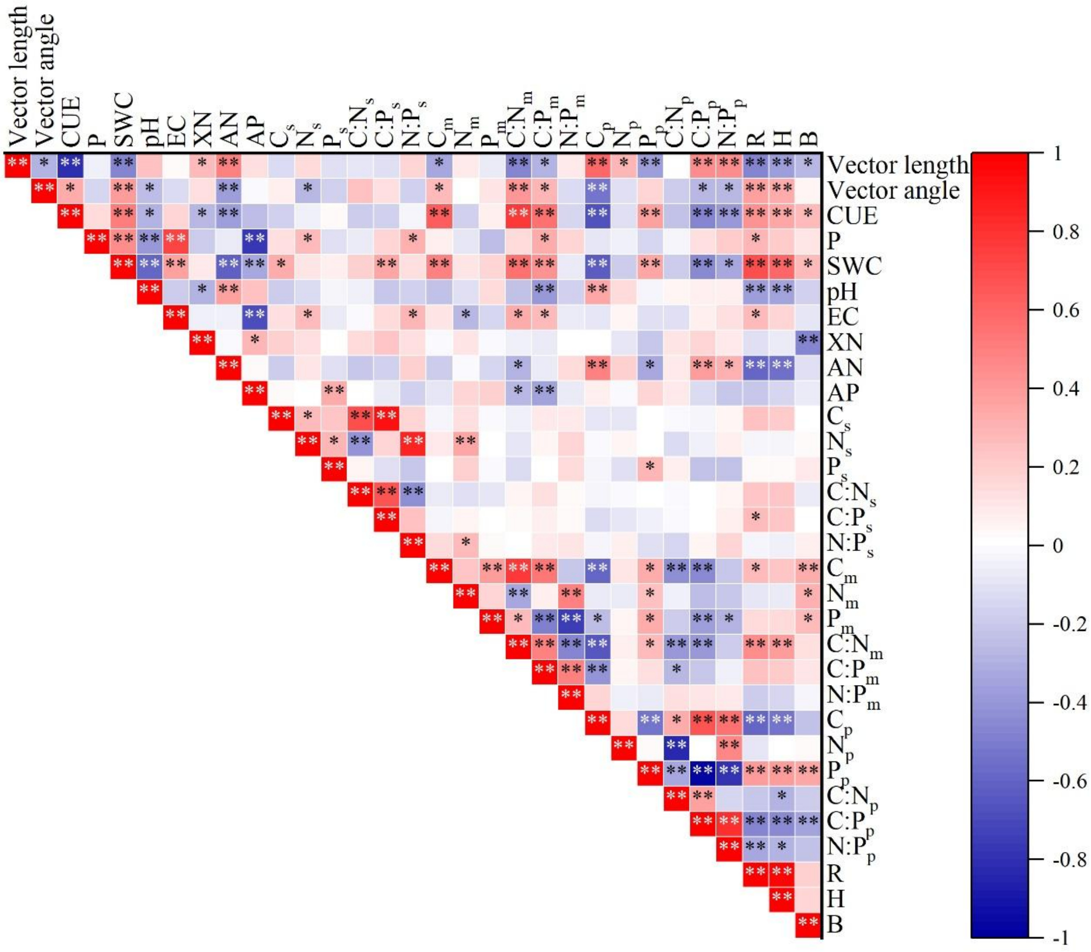


Fig. 6: Variation partition analysis showing the effects of precipitation treatment, soil physicochemical property, microbe C:N:P ecological stoichiometry, and plant trait on soil enzyme vector length (a), vector angle (b) and microbial carbon use efficiency (c).

Soil physicochemical property includes water content, pH, electric conductivity, NO_3^--N, NH_4^+-N, available P, C:N:P stoichiometry. Plant trait includes community biomass, diversity, and C:N:P stoichiometry.



265 **Fig. 7: Relationship between soil enzyme vector length, vector angle and microbial carbon use efficiency with environmental factors. ****P* **< 0.05, *****P* **< 0.01, ******P* **< 0.001. See abbreviations in Table 1.**

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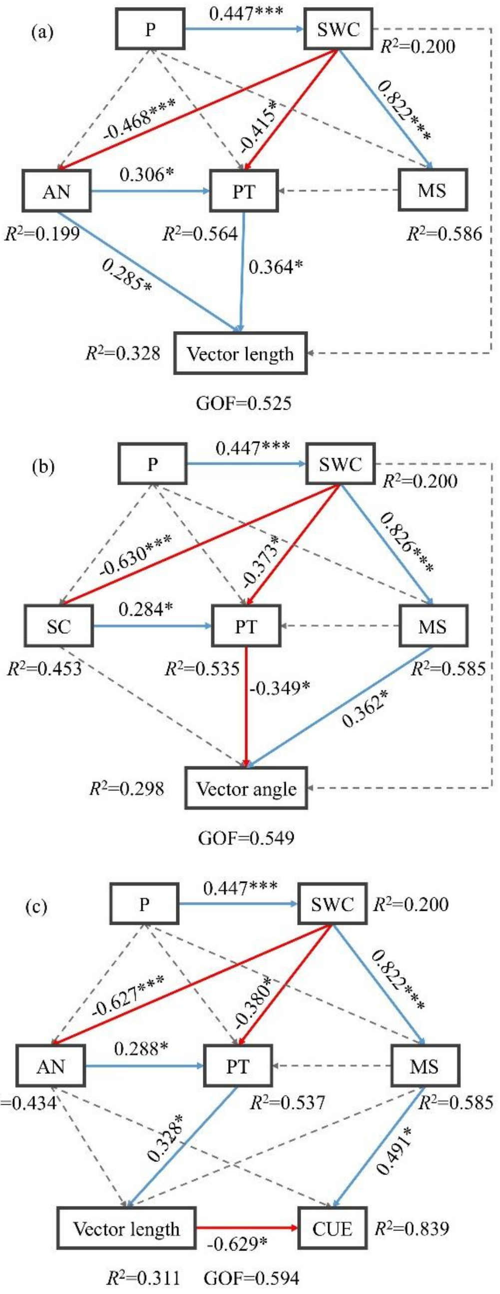

Fig. 8: Structural equation model illustrating the major pathways of environmental factors influencing enzyme vector length (a), vector angle (b), and microbial carbon use efficiency (CUE, c). The solid blue lines represent significantly positive impacts, the solid red lines represent significantly negative impacts, and the dotted grey lines indicate that paths are insignificant. Numbers connected arrows are standardized path coefficients (*P < 0.05; **P < 0.01; ***P < 0.001). R2 values represent the percentage of the variance explained by the model. MS (microbial stoichiometry) includes Cm, C:Nm, and C:Pm. PT (plant trait) includes R, H, Cp, and C:Pp. See abbreviations in Table 1.

4. Discussion

4.1 Little effect of altered precipitation on enzyme C:N:P ecological stoichiometry

In arid and semi-arid regions, water resources are a key limiting factor for plant growth and microbial metabolism (Wang et al., 2022; Yu et al., 2023). Consequently, changes in precipitation can affect soil enzyme activities and their stoichiometry (Akinyemi et al., 2020; Feng et al., 2019). However, in this study, changing precipitation did not significantly alter enzyme stoichiometry (Fig. 2 and Table 2), a finding consistent with that of Steinweg et al. (2013). This non-significant response may be attributed to two key factors. First, through long-term evolution, plants and microbes in water limited regions have developed ecophysiological adaptations to drought. For instance, plants root structure expands their water-absorbing range (Kirschner et al., 2021), and microbes reduce water consumption by entering dormancy (Imminger et al., 2024). These adaptations allow them to maintain normal ecophysiological functions even under reduced precipitation. Second, the desert steppe's soil is mainly sandy loam with poor water and nutrient retention. Although increased precipitation could enhance soil resource availability, it also raises the risk of water infiltration and nutrient leaching (particularly NO_3^--N) (Ma et al., 2020a), thereby stabilizing the microenvironment for plant roots and microbes. In contrast, enzyme C:N:P stoichiometry varied significantly across sampling months ($P < 0.05$) and showed strong correlations with most environmental factors (Fig. S2). This confirms that monthly fluctuations in hydrothermal conditions, plant growth status, and soil properties drive temporal dynamics in enzyme stoichiometry (Akinyemi et al., 2020; Ren et al., 2016; Wallenstein et al., 2009).

Previous studies have reported that enzyme stoichiometry responds asymmetrically to both the direction (decrease or increase) and intensity (moderate or extreme) of precipitation change (Sun and Chen, 2024; Li et al., 2024). In this study, under different precipitation change directions (Fig.3), C_e, $C:N_e$, and $C:P_e$ exhibited greater sensitivity to precipitation reduction (negative asymmetry), suggesting that drought stress intensifies soil water limitation and thereby suppresses microbial synthesis of C-acquiring enzymes (Qu et al., 2023). In contrast, N_e and P_e were more sensitive to precipitation increase (positive asymmetry), as increased water availability facilitates organic matter mineralization and plant nutrient uptake (Zhang et al., 2020), thereby exacerbating microbial nutrient limitation and stimulating enzyme production. Regarding precipitation change intensity, previous studies have demonstrated that soil enzyme activity peaks under moderate increases and reaches its lowest level under moderate decreases (Akinyemi et al., 2020), with greater responsiveness to moderate than to extreme changes (Li et al., 2024). Our results further indicate that $C:N_e$ and $N:P_e$ were more sensitive to moderate increases, whereas C_e, N_e, P_e and $C:P_e$ responded more strongly to extreme increases (Fig. S3), highlighting the importance of precipitation increase intensity in shaping enzyme responses. Conversely, C_e, N_e and $N:P_e$ were more sensitive to moderate reduction, whereas P_e, $C:N_e$ and $C:P_e$ were more affected by extreme reduction, implying that the response of enzyme stoichiometry to precipitation reduction is less dependent on the reduction intensity.

4.2 Minimal impacts of altered precipitation on microbial resource limitation and dominant P-limitation

Microbial C limitation is widespread globally (Soong et al., 2020). In this study, the average enzyme vector length was 0.61 (Fig.4), matching the theoretical optimum of 0.61 for microbial C limitation (Cui et al., 2024). However, this value is notably lower than those reported for typical (0.84 ± 0.04; Cui et al., 2019) and alpine (1.10 ± 0.05; Pan et al., 2024) grasslands, indicating a weaker microbial C limitation in the studied desert steppe. In arid regions, plants reduce leaf stomatal aperture to minimize water loss, which also suppresses photosynthetic capacity and C assimilation, thereby limiting belowground C allocation and exacerbating microbial C shortage (Huang and Hall, 2017). Increased precipitation can mitigate such limitations by improving soil moisture and nutrient availabilities (Akinyemi et al., 2020; Hai et al., 2022). In this study, however, neither decreased nor increased precipitation during the entire growing season had a significant effect on enzyme vector length compared to ambient conditions (Fig. 5), consistent with findings in Loess Plateau grasslands (Hai et al., 2022). It appears that microbial communities maintain functional homeostasis by adjusting their community composition and metabolic strategies under long-term drought stress (Yu et al., 2023). Furthermore, microbial enzyme activity exhibits a threshold response to soil water availability. As long as precipitation-induced changes in soil moisture remain below this threshold, enzyme activity remains relatively stable (Vo and Kang, 2013). Consequently, the low soil water retention capacity at our study site prevents increased precipitation from surpassing the threshold required to alter enzymatic activity.

In this study, an enzyme vector angle >45° together with a left-upper quadrant distribution of the enzyme C:N versus C:P relationship (Fig. 4c) indicated that microbial communities in the study area were primarily P-limited under altered precipitation regimes, which aligns with the widely reported P limitation in arid and semi-arid ecosystems globally (Cui et al., 2025). Across the whole growing season, neither reduced nor increased precipitation had a significant effect on the enzyme vector angle (Fig. 5). Microbial communities may have developed stable P-acquisition strategies under long-term drought stress (Yu et al., 2023). Furthermore, although increased precipitation stimulates plant growth and intensifies plant-microbe competition for P (Ren et al., 2015), the rate of plant P uptake may synchronize with microbial P release, thereby buffering changes in the vector angle under varying precipitation (Yao et al., 2023). In contrast, sampling month had a significant influence on the vector angle (Table 3), confirming distinct seasonal dynamics in microbial nutrient limitation in desert steppes (Schnecker et al., 2023). These seasonal shifts are likely driven by monthly variations in hydrothermal conditions, plant growth status, and soil properties. Thus, under changing precipitation, microbial nutrient limitation in the study area is jointly regulated by soil physicochemical properties, microbial stoichiometry, and plant traits (Fig. 6b).

4.3 Plant trait and microbial stoichiometry well explained the variations in microbial nutrient limitation under altered precipitation

In the present study, plant trait (biomass, diversity, stoichiometry) primarily explained the variation in vector length, whereas microbial stoichiometry largely accounted for that in vector angle (Fig. 6 a and b), confirming their close association with microbial resource limitation under changing precipitation regimes (Cui et al., 2019; Hai et al., 2022; Wan et al., 2024; Zhang et al., 2023). The further analysis revealed that although precipitation did not directly affect vector length, it exerted an indirect negative effect through soil properties (water content and NH_4^+-N) and plant traits (Patrick richness index, Shannon-Wiener diversity index, C concentration, C:P) (Fig. 8a), indicating that increased precipitation tends to alleviate microbial C limitation. The finding aligns with observations from the Tibetan Plateau (Pan et al., 2024). In these regions, altered precipitation regimes modified microbial C limitation by affecting soil water availability and N dynamics (transformation and availability), which in turn regulated plant productivity and microbial activity. In contrast, precipitation had an indirect positive effect on vector angle (Fig. 8b), suggesting that increased precipitation is prone to intensify microbial P limitation. This is likely due to the inherently low availability of soil P in desert steppes. Increased precipitation stimulates plant growth, thus intensifying competition for P between microbes and plants (Ren et al., 2015).

Microbial CUE governs microbial C allocation in a given resource environment, with higher values indicating a greater proportion of assimilated C directed toward biomass synthesis rather than respiration or other metabolic processes (Sinsabaugh et al., 2016). This study found that precipitation enhanced CUE by modulating soil properties (moisture and NH_4^+-N availability), plant traits (Patrick richness index, Shannon-Wiener diversity index, C concentration, C:P), microbial stoichiometry (C content, C:N, C:P), and vector length (Fig. 6c). This aligns with finding from temperate grassland study (Hai et al., 2022). Enhanced water availability improves the physiological status of microbes and increases nutrient supply, thereby promoting the C allocation toward microbial biomass (Oram et al., 2023; Sinsabaugh et al., 2016). Moreover, excessive soil water content reduced plant Patrick richness and the Shannon–Wiener diversity index while increasing the dominance of key species within the community. This shift in plant community structure provided a more stable and abundant C source for microbes, potentially lowering the energy cost of C acquisition (Hou et al., 2023), and thus further supporting efficient microbial C utilization.

4.4 Limitations and future prospects

Our findings demonstrate that both reduced and increased precipitation have minimal direct effects on microbial resource limitation, while highlighting the significant roles of soil water and N availability, plant diversity and stoichiometry, and microbial C-linked stoichiometry in driving the variation of microbial resource limitation. However, certain limitations of this study should be acknowledged.

First, global analyses suggest that the effects of precipitation changes are time-dependent, with short-term responses often deviating from long-term trends (Li et al., 2024). Although this study accounted for precipitation-treatment duration and monitored monthly enzyme stoichiometry dynamics, it did not examine annual-scale variations in enzyme stoichiometry. Extending monitoring periods in future studies would help verify and more accurately characterize long-term impact patterns. Second, existing evidence indicates that belowground plant traits (e.g., fine root characteristics) (Chen et al., 2026) and microbial diversity (He et al., 2023) play key regulatory roles in microbial resource limitation under changing precipitation regimes. While this study measured aboveground plant traits and microbial biomass, it did not incorporate belowground root dynamics or microbial community composition and function attributes. This omission limits a more mechanistic understanding of the biological drivers underlying microbial resource limitation. Future studies should integrate these aspects to systematically clarify the interactions among microbial resource limitation, plants, and microbial communities.

5. Conclusion

While both enzyme stoichiometry and microbial resource limitation exhibited significant monthly variation ($P < 0.05$), they showed little direct response to either precipitation reduction or increase. However, when responses did occur, they depended on the direction (reduction or increase) and intensity (moderate or extreme) of the precipitation change, as well as the specific index examined. Microbes were primarily limited by P rather than C and N. Variation in microbial C limitation was largely explained by plant trait (biomass, diversity, and stoichiometry), while that in microbial N and P limitation was primarily explained by microbial stoichiometry. Altered precipitation could indirectly affect microbial C limitation by modifying soil moisture and NH_4^+-N availability, as well as plant traits (Patrick richness index, Shannon-Wiener diversity index, C concentration, C:P). Similarly, it could influence microbial N and P limitation through changes in soil properties (moisture, pH, NH_4^+-N), plant traits (Patrick richness index, Shannon-Wiener diversity index, C concentration, C:P), and microbial stoichiometry (C content, C:N, C:P). Therefore, although altered precipitation exerted limited direct effects on microbial resource limitation, it could indirectly alter limitation patterns by modulating soil resource availability, plant diversity and C-related stoichiometry, and microbial C-related stoichiometry in moderately saline-alkaline desert steppes.

Data availability.

The data generated in this study are available from the first or corresponding author upon reasonable request.

Supplement link

The supplement related to this article is available online.

Author contributions

Methodology, Data curation, Writing –review & editing, Writing – original draft,: XW. Investigation, Supervision, Formal analysis, Super-vision: BL Formal analysis, Investigation: HY. Investigation, Methodology, Supervision, Funding acquisition, Visualization, Writing – revie&editing: JH.

Competing interests

The contact author has declared that none of the authors has any competing interests.

Disclaimer

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Review statement

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