Response of Soil Respiration to Short-term Changes in Precipitation and Nitrogen Addition in a Desert Steppe (Postprint)

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Abstract

Changes in precipitation and nitrogen (N) addition may significantly affect the processes of soil carbon (C) cycle in terrestrial ecosystems, such as soil respiration. However, relatively few studies have investigated the effects of changes in precipitation and N addition on soil respiration in the upper soil layer in desert steppes. In this study, we conducted a control experiment that involved a field simulation from July 2020 to December 2021 in a desert steppe in Yanchi County, China. Specifically, we measured soil parameters including soil temperature, soil moisture, total nitrogen (TN), soil organic carbon (SOC), soil microbial biomass carbon (SMBC), soil microbial biomass nitrogen (SMBN), and contents of soil microorganisms including bacteria, fungi, actinomyces, and protozoa, and determined the components of soil respiration including soil respiration with litter (RS+L), soil respiration without litter (RS), and litter respiration (RL) under short-term changes in precipitation (control, increased precipitation by 30%, and decreased precipitation by 30%) and N addition (0.0 and 10.0 g/(m2 a)) treatments. Our results indicated that short-term changes in precipitation and N addition had substantial positive effects on the contents of TN, SOC, and SMBC, as well as the contents of soil actinomyces and protozoa. In addition, N addition significantly enhanced the rates of RS+L and RS by 4.8% and 8.0% ($P<0.05$), respectively. The increase in precipitation markedly increased the rates of RS+L and RS by 2.3% ($P<0.05$) and 5.7% ($P<0.001$), respectively. The decrease in precipitation significantly increased the rates of RS+L and RS by 12.9% ($P<0.05$) and 23.4% ($P<0.001$), respectively. In contrast, short-term changes in precipitation and N addition had no significant effects on RL rate ($P>0.05$). The mean RL/RS+L value observed under all treatments was 27.63%, which suggested that RL is an important component of soil respiration in the desert steppe ecosystems. The results also showed that short-term changes in precipitation and N addition had significant interactive effects on the rates of RS+L, RS, and RL ($P<0.001$). In addition, soil temperature was the most important abiotic factor that affected the rates of RS+L, RS, and RL. Results of the correlation analysis demonstrated that the rates of RS+L, RS, and RL were closely related to soil temperature, soil moisture, TN, SOC, and the contents of soil microorganisms, and the structural equation model revealed that SOC and SMBC are the key factors influencing the rates of RS+L, RS, and RL. This study provides further insights into the characteristics of soil C emissions in desert steppe ecosystems in the context of climate change, which can be used as a reference for future related studies.

Full Text

Preamble

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Response of soil respiration to short-term changes in precipitation and nitrogen addition in a desert steppe

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Abstract: Changes in precipitation and nitrogen (N) addition may significantly affect soil carbon (C) cycling processes in terrestrial ecosystems, such as soil respiration. However, relatively few studies have investigated the effects of precipitation changes and N addition on soil respiration in the upper soil layer of desert steppes. In this study, we conducted a controlled field simulation experiment from July 2020 to December 2021 in a desert steppe in Yanchi County, China. Specifically, we measured soil parameters including soil temperature, soil moisture, total nitrogen (TN), soil organic carbon (SOC), soil microbial biomass carbon (SMBC), soil microbial biomass nitrogen (SMBN), and the contents of soil microorganisms (bacteria, fungi, actinomycetes, and protozoa). We determined the components of soil respiration—including soil respiration with litter (RS+L), soil respiration without litter (RS), and litter respiration (RL)—under short-term precipitation changes (control, increased precipitation by 30%, and decreased precipitation by 30%) and N addition treatments (0.0 and 10.0 $g/(m^2 \cdot a)$). Our results indicated that short-term precipitation changes and N addition had substantial positive effects on TN, SOC, and SMBC contents, as well as on soil actinomycete and protozoan contents. N addition significantly enhanced RS+L and RS rates by 4.8% and 8.0% ($P<0.05$), respectively. Increased precipitation markedly raised RS+L and RS rates by 2.3% ($P<0.05$) and 5.7% ($P<0.001$), respectively. Decreased precipitation significantly increased RS+L and RS rates by 12.9% ($P<0.05$) and 23.4% ($P<0.001$), respectively. In contrast, short-term precipitation changes and N addition had no significant effects on RL rate ($P>0.05$). The mean RL/RS+L value observed across all treatments was 27.63%, suggesting that RL is an important component of soil respiration in desert steppe ecosystems. The results also showed significant interactive effects of precipitation changes and N addition on RS+L, RS, and RL rates ($P<0.001$). Soil temperature was the most important abiotic factor affecting RS+L, RS, and RL rates. Correlation analysis demonstrated that RS+L, RS, and RL rates were closely related to soil temperature, soil moisture, TN, SOC, and soil microorganism contents, while structural equation modeling revealed that SOC and SMBC are the key factors influencing RS+L, RS, and RL rates.

This study provides further insights into the characteristics of soil C emissions in desert steppe ecosystems under climate change and can serve as a reference for future related research.

Keywords: soil respiration; litter respiration; nitrogen deposition; soil carbon; soil microorganisms; climate change; desert steppe ecosystems

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1 Introduction

Soil respiration is the primary process controlling carbon (C) emissions from soil to the atmosphere and plays a crucial role in regulating the response of terrestrial ecosystem C cycles to natural and anthropogenic disturbances (Yu et al., 2020; Qin et al., 2023; Wang et al., 2023). Hanson et al. (2000) demonstrated that plant roots, soil microorganisms, and litter respiration (RL) constitute the primary components of soil respiration. As the second largest C flux process in terrestrial ecosystems, soil respiration accounts for approximately 68–98 Pg C annually (Bond-Lamberty and Thomson, 2010). Moreover, soil respiration serves as a sensitive indicator of soil microbial metabolic activity, litter decomposition processes, and the conversion of soil C to atmospheric C (Harper et al., 2005; Borken et al., 2006; Zhou et al., 2014). However, soil respiration is highly vulnerable to global climate change, including nitrogen (N) deposition and alterations in temperature and precipitation (Shi et al., 2019; Song et al., 2020; Xiao et al., 2020). Therefore, investigating soil respiration dynamics and their influencing factors is essential for understanding the relationship between soil C emission dynamics and climate change.

Atmospheric N deposition, a major factor in global climate change, substantially impacts ecosystem structure and function, including C cycling in grassland ecosystems (Chen et al., 2020; Yang et al., 2022a; Yang et al., 2022c). Previous studies have reported that N deposition affects soil respiration by altering plant growth and development, litter decomposition, and soil microenvironments (Peng et al., 2011; Zhang et al., 2019a). However, other studies have revealed inconsistent results, demonstrating that N addition can either facilitate (Song et al., 2011; Wang et al., 2019a), inhibit (Phillips and Fahey, 2007; Mo et al., 2008; Yan et al., 2010), or have no effect on soil respiration (Qi et al., 2014; Zhu et al., 2015). This inconsistency may be attributed to N-induced C fixation patterns and differences in soil microbial metabolic activity among ecosystems (Lee and Jose, 2003). Wang et al. (2019a) highlighted how the positive effects of N addition increase aboveground litter input, which may promote belowground C utilization and soil respiration, particularly in desert steppes. Therefore, investigating the effects of N addition on soil respiration is crucial for accurately predicting C emission characteristics from desert steppes under increasing global N deposition.

As a key driver of ecological processes, precipitation change can substantially affect C cycling in terrestrial ecosystems and the source-sink functions of these ecosystems, particularly in desert steppe regions (Zhang et al., 2019b; Legesse et al., 2022; Zhang et al., 2022a). Zhang et al. (2019d) demonstrated the substantial effects of precipitation changes in promoting soil respiration in arid ecosystems. These effects are enhanced through several ecological processes (Talmon et al., 2011; Liu et al., 2016), including plant growth (Zhou et al., 2016), soil microorganisms (Ren et al., 2018), soil enzyme activity (Zhao et al., 2016), and the temperature sensitivity of soil respiration rates (Suseela et al., 2012). However, some studies have reported that precipitation changes can inhibit soil respiration (Harper et al., 2005; Liu et al., 2018), possibly related to substrate availability and the activity of extracellular enzymes that degrade C (Knapp et al., 2002; Ren et al., 2017). Therefore, more detailed studies are needed on soil respiration responses to precipitation changes in desert steppe ecosystems.

Litter plays an important role in the C cycle of grassland ecosystems (Schlesinger and Andrews, 2000; Zhang et al., 2012). Wang et al. (2009a) demonstrated that litter is one of the sources of the soil C pool in desert steppe ecosystems. Litter provides nutrients for soil microorganisms, improves microbial community composition, and enhances microbial respiration (Zhao et al., 2020; Craig et al., 2022). Moreover, litter can alter soil microenvironments, change soil nutrient use efficiency, and affect soil respiration (Sun et al., 2019; Connell et al., 2022).

Niu et al. (2019) demonstrated that litter removal or addition to soils could alter soil organic C (SOC) content, thereby significantly reducing or increasing soil respiration. The contribution of litter to soil respiration is one of the most important indicators of litter's role in the soil C cycle (Huang et al., 2017) and reflects the mechanism of C allocation to aboveground and belowground plant parts to some extent (Wang et al., 2009b). Therefore, comprehensively investigating litter's contribution to soil respiration is important for revealing the role of litter in material cycling and energy flow processes between plants and soil.

Desert steppe is a typical ecosystem vulnerable to environmental changes such as precipitation changes and N addition (Olive et al., 2019; Wang et al., 2019b; Zhang et al., 2022b). However, the responses of soil respiration with litter (RS+L) to precipitation changes and N addition in desert steppes remain unclear (Zhang et al., 2020; Zhang et al., 2022c). Furthermore, most observational studies on soil respiration in desert steppes have focused primarily on the effects of plant community and nutrient addition on soil respiration (Zhang et al., 2015). To date, few studies have monitored soil respiration and investigated litter effects on soil respiration (Han et al., 2007; Wen et al., 2020). Analyzing the characteristics of carbon dioxide (CO_2) emissions derived from litter in the upper soil layer of a desert steppe in China provides basic information for estimating the C balance and studying the primary mechanisms controlling the C cycle in desert steppe ecosystems, thereby accelerating the improvement and restoration of desert steppes (Wang et al., 2019a). In this study, we investigated the impacts of short-term precipitation changes, N addition, and their interaction on RS+L, soil respiration without litter (RS), and RL, as well as the effects of biotic (soil microorganisms) and abiotic (soil physical-chemical properties) factors on soil respiration (RS+L, RS, and RL) under different treatments in a desert steppe in Yanchi County, China. We hypothesized that: (1) increased precipitation and N addition would accelerate soil respiration due to increased soil nutrients and enhanced soil microbial activity, while decreased precipitation would restrain soil respiration; and (2) soil respiration rates would be strongly associated with soil temperature, moisture, and microbial community. Our research will help understand soil respiration dynamics in desert steppes and provide a scientific basis for studying the C cycle in desert steppe ecosystems.

2.1 Study area

The study area (37°04 –38°10 N, 106°30 –107°47 E; 1600 m a.s.l.) is located in Yanchi County in the eastern part of Ningxia Hui Autonomous Region, China. This county is an important agro-pastoral transition zone comprising vast dry grasslands and desert steppes from southeast to northwest. The area is characterized by a mid-temperate continental monsoon climate with semi-arid to arid transition zones. The annual average temperature and precipitation are 8.4°C and 280 mm, respectively. Gray calcium soil is the dominant soil type in the study area (Spaargaren and Deckers, 1998), and vegetation types are primarily composed of shrub, sandy vegetation, and desert vegetation. Dominant plant species in fields that do not produce litter include *Pennisetum centrasiaticum*, *Astragalus melilotoides*, *Cleistogenes squarrosa*, *Setaria viridis*, *Gueldenstaedtia verna*, *Lespedeza potaninii*, *Euphorbia esula*, *Oxytropis racemosa*, *Bassia dasyphylla*, *Eragrostis pilosa*, and *Polygala tenuifolia*. Dominant species that produce litter include *Artemisia scoparia*, *Sophora alopecuroides*, *Stipa breviflora*, and *Agropyron mongolicum* (Table S1).

2.2 Experimental design

Experiments were conducted from July 2020 to December 2021 using a randomized complete block design with six treatment plots (2 m × 6 m each) and three replicates per treatment. The experiment included three precipitation levels: control (CK), increased precipitation by 30% (IP), and decreased precipitation by 30% (DP), as well as two N addition rates: 0.0 $g/(m^2 \cdot a)$ (N0) and 10.0 $g/(m^2 \cdot a)$ (N10) (Bai et al., 2010). We utilized self-made V-shaped gutters made of transparent plexiglass to achieve the decreased precipitation in corresponding treatment plots. Increased precipitation was achieved by collecting rainwater from the gutters after precipitation events using buckets and then spraying it evenly onto the treatment plots with a watering can. N was applied as urea (CH_4N_2O) at a rate of 2.5 g/m^2 in September 2020, March 2021, June 2021, and September 2021. The urea was first dissolved in clear water. The treatment without N addition received the same amount of water as the N addition treatment. All treatments were therefore: CK+N0, IP+N0, DP+N0, CK+N10, IP+N10, and DP+N10. Polyvinyl chloride (PVC) boards were installed 30 cm deep in the soil around each treatment plot to prevent water and nutrient exchange. Six PVC collars for respiration measurements (10 cm height and 20 cm diameter) were installed in each treatment plot. Living plants were irregularly removed from each treatment plot. In one half of each treatment plot (1 m × 6 m), three collars with litter were arranged to measure RS+L, while in the other half (1 m × 6 m), three collars without litter were arranged to measure RS.

2.3 Methods of measurement

Soil respiration was measured using an LI-8100 Automated Soil CO_2 Flux System (LI-COR Inc., Lincoln, NE, USA). Soil temperature and moisture in the 0–5 cm soil layer were measured simultaneously using a portable 8100-201 soil temperature probe (LI-COR Inc., Lincoln, NE, USA) and an 8100-204 soil moisture probe (LI-COR Inc., Lincoln, NE, USA), respectively. Soil respiration was measured on sunny days during 15–18 April, 19–22 July, 12–15 October, and 17–20 December 2021. Measurements were taken from 12:00 to 10:00 the following day (local standard time) at 2-hour intervals. Mean values from the three sunny days in April, July, October, and December were calculated and used as representative values for spring, summer, autumn, and winter, respectively (Yang et al., 2020). Due to low nighttime temperatures in winter, the LI-8100 system could not reliably determine soil respiration at 00:00–04:00, so measurements at 00:00, 02:00, and 04:00 were excluded from winter data. RL was estimated as the difference between RS+L and RS, and litter respiration contribution (RL/RS+L) represented the contribution of litter respiration to total soil respiration.

Additionally, three replicate soil samples (0–5 cm depth) were randomly collected from half of each treatment plot (1 m × 6 m) in July 2021. Samples were passed through a 2-mm sieve and stored at −4°C until analysis. SOC was analyzed using the H_2SO_4–$K_2Cr_2O_7$ oxidation method followed by titration with $FeSO_4$ (Liu et al., 2017). Total nitrogen (TN) content was determined using the micro-Kjeldahl digestion procedure (Kjeltec 8400, FOSS, Koebenhavn, Denmark) (Liu et al., 2017). Soil microbial biomass carbon (SMBC) and nitrogen (SMBN) were analyzed using the chloroform fumigation-extraction method, with extraction efficiency factors of 0.38 and 0.54, respectively (Guckert et al., 1986). Soil microbial communities (bacteria, fungi, actinomycetes, and protozoa) were determined using the phospholipid fatty acid method (Frostegård et al., 1991) combined with the approach described by Bligh and Dyer (1959). Bacterial content was indicated by the sum of phospholipid fatty acids 12:0, 13:0, 14:0, 15:0, 16:0, 22:0, and 24:0 (Zelles, 1997); fungal content by the sum of 18:1$ 9c, 21 : 0, 23 : 0, and18 : 2 6c(Ngosongetal., 2012); actinomycetecontentbythesumof10Me17 : 0, 10Me18 : 1 7c, 10Me19 : 1 7c, 10Me17 : 1 7c, and10Me18 : 0(Lechevalier, 1977); andprotozoancontentbythesumof20 : 4 6c, 20 : 3 6c, 20 : 5 3c, and19 : 3 $6c (Massaccesi et al., 2015).

2.4 Statistical analysis

A linear model (Eq. 1) and an exponential model (Eq. 2) were used to analyze relationships between soil respiration and soil moisture and temperature. Equation 3 was used to analyze the combined effect of soil temperature and moisture on soil respiration:

$$R_{(S+L,S,L)} = a_{1W} + b_1$$

$$R_{(S+L,S,L)} = a_{2e}^{b_{2T}}$$

$$R_{(S+L,S,L)} = a_{3W} + b_{3T} + c$$

where $R_{(S+L,S,L)}$ indicates each type of soil respiration (RS+L, RS, and RL) in mol/($m^2 \cdot s$); W is soil moisture (%); T is soil temperature (°C); a_1, b_1, a_2, b_2, a_3, and b_3 are regression coefficients; and c is the regression constant.

Data were processed and analyzed using Microsoft Excel (Redmond, WA, USA) and SPSS 24.0 (IBM Inc., NY, USA). One-way analysis of variance (ANOVA) was used to compare differences in soil respiration and soil parameters among treatments. Least significant difference (LSD) tests were performed to assess differences at a significance level of 0.05. Two-way ANOVA was applied to analyze the effects of precipitation changes, N addition, and their interaction on soil respiration and soil parameters. Origin 2023 (OriginLab, Northampton, MA, USA) was used for fitting, correlation analysis, and graphing. A structural equation model (SEM) was constructed using AMOS 24.0 (IBM Inc., NY, USA) based on maximum likelihood estimation to reveal key factors influencing RS+L, RS, and RL rates.

Five goodness-of-fit indices evaluated the SEM: chi-square to degrees of freedom ratio (^{2}/df), root mean square error of approximation (RMSEA), goodness-of-fit index (GFI), adjusted goodness-of-fit index (AGFI), and P-value. Model fit was considered good when ^{2}/df < 3, RMSEA < 0.05, GFI > 0.9, AGFI > 0.9, and P > 0.05.

3.1 Characteristics of soil parameter variations

Soil moisture and temperature in the 0–5 cm layer showed obvious diurnal and seasonal dynamics under different treatments (Fig. S1). Soil temperature exhibited a clear single-peaked curve compared to soil moisture. N addition significantly increased soil moisture by 14.2% (P<0.05) but had no significant effect on soil temperature (P>0.05; Fig. 1a [Figure 1: see original paper]). Both increased and decreased precipitation significantly affected soil temperature and moisture (P<0.001; Fig. 1a).

N addition significantly reduced SMBN by 27.7% (P<0.05) but had no significant effect on SMBC (Fig. 1b). Both precipitation increase and decrease enhanced SMBN and SMBC (P>0.05; Fig. 1b). N addition increased TN and SOC contents by 12.0% (P<0.05) and 6.8% (P>0.05), respectively (Fig. 1c). Decreased precipitation significantly increased TN and SOC contents by 17.8% (P<0.001) and 26.3% (P<0.001), respectively, while increased precipitation did not significantly affect TN and SOC contents (P>0.05; Fig. 1c). N addition markedly increased soil actinomycete content by 20.2% (P<0.05) but had no significant effects on soil bacteria, fungi, or protozoa (P>0.05; Fig. 1d). Increased precipitation reduced soil actinomycete and protozoan contents by 16.4% (P<0.001) and 9.6% (P<0.001), respectively, while decreased precipitation significantly increased these contents by 16.8% (P<0.001) and 31.3% (P<0.001), respectively (Fig. 1d). However, precipitation changes had no significant effects on soil bacterial or fungal contents (P>0.05; Fig. 1d). Precipitation changes and N addition showed significant interactive effects on soil temperature, SMBN, soil bacteria, and soil actinomycetes (P<0.05), but no significant interactive effects on soil moisture, SMBC, TN, SOC, soil fungi, or soil protozoa (P>0.05; Table 1).

3.2 Characteristics of soil respiration and component variations

RS+L and RS exhibited similar diurnal dynamics throughout the experimental period (Figs. 2 and 3). The highest and lowest soil respiration rates were observed at 12:00–14:00 and 02:00–04:00, respectively. RL dynamics were more complex, with maximum and minimum rates not appearing at consistent times across seasons (Fig. 4 [Figure 4: see original paper]). Seasonal dynamics followed the order: summer > spring > autumn > winter (Fig. S2). The daily average RS+L rate across all treatments ranged from 0.08 ($±0.01)to0.51(±0.03)μmol/(m^{2·s)acrossseasons(Fig.2[Figure2 : seeoriginalpaper]).RS + Lratedifferedsignificantlyamong seeoriginalpaper]),withsignificantdifferencesamongNadditiontreatmentsinspring(P < 0.05; Fig.3a)andamongprecipitationchangetreatmentsinspring, autumn, andwinter(P < 0.05; Fig.3b, f, andh).ThedailyaverageRLraterangedfrom0.01(±0.00)to0.08(±0.01)μmol/(m^{2}$· s) across seasons (Fig. 4), with significant differences among precipitation change treatments across all seasons (P<0.05; Fig. 4b, d, f, and h).

N addition markedly increased RS+L and RS rates by 4.8% and 8.0%, respectively, compared to the treatment without N addition (P<0.05; Fig. 5a [Figure 5: see original paper]). Increased precipitation raised RS+L and RS rates by 2.3% (P<0.05) and 5.7% (P<0.001), respectively (Fig. 5a). Decreased precipitation significantly increased RS+L and RS rates by 12.9% (P<0.05) and 23.4% (P<0.001), respectively (Fig. 5a). In contrast, precipitation change and N addition treatments had no significant effects on RL rate (Fig. 5a). RL/RS+L across treatments ranged from 24.85% ($±2.56±$2.92%) (Fig. 5b). A significant interactive effect of precipitation changes and N addition was identified on RS+L, RS, and RL rates (P<0.001; Table 2).

3.3 Relationships between soil respiration and soil parameters

Figure 6 [Figure 6: see original paper] shows relationships between soil respiration (RS+L, RS, and RL) and soil temperature and moisture. RS+L, RS, and RL rates showed significant positive exponential relationships with soil temperature, with R^2 values of 0.60 (P<0.001), 0.45 (P<0.001), and 0.37 (P<0.001), respectively (Fig. 6a, c, and e). Additionally, RS+L, RS, and RL rates exhibited significant linear relationships with soil moisture (P<0.05; Fig. 6b, d, and f). These rates also showed significant linear relationships with the interaction of soil temperature and moisture ($P<0.001$; Table S2). The results demonstrated that soil temperature was the primary abiotic factor affecting changes in RS+L, RS, and RL rates compared to soil moisture.

Correlation analysis revealed significant positive correlations between RS+L rate and TN ($P<0.05$), SOC ($P<0.001$), and SMBC ($P<0.01$) (Fig. 7 [Figure 7: see original paper]). RS rate significantly and positively correlated with TN ($P<0.01$), SOC ($P<0.001$), SMBC ($P<0.05$), soil actinomycetes ($P<0.05$), and soil protozoa ($P<0.01$) (Fig. 7). RL rate only positively correlated with SOC ($P<0.05$) and SMBC ($P<0.05$) (Fig. 7).

SEM results showed that precipitation changes and N addition had positive effects on soil hydrothermal factors (temperature and moisture) but negative effects on soil C (SOC and SMBC) and microorganisms (actinomycetes and protozoa). Soil C positively affected RS+L rate, while soil hydrothermal factors, C, and microorganisms positively affected RS rate. Precipitation changes, N addition, and soil C positively affected RL rate. SMBC and SOC were the key factors controlling RS+L (Beta=0.59; Fig. 8a1 and a2 [Figure 8: see original paper]), RS (Beta=0.39; Fig. 8b1 and b2), and RL (Beta=0.37; Fig. 8c1 and c2).

4.1 Effects of precipitation changes and N addition on soil parameters

Arid and semi-arid desert steppes are typical ecosystems with limited water resources and soil nutrients (Hooper and Johnson, 1999; Yan et al., 2011). Soil microenvironments, particularly soil temperature and moisture, are extremely sensitive to climate change. This study found similar diurnal and seasonal patterns of soil temperature and moisture under different treatments (Fig. S1), consistent with previous related studies (Cui and Zhang, 2016; Zhao et al., 2020). We hypothesized that soil temperature and moisture varied largely with atmospheric temperature and precipitation. However, N addition can enhance litter-soil contact (Li et al., 2016) and prevent soil moisture loss, explaining the significant effects of N addition on average soil moisture in this study (Fig. 1a). Additionally, precipitation changes significantly influenced average soil temperature and moisture values (Fig. 1a), consistent with previous grassland studies (Zhao et al., 2014; Zhao et al., 2020).

Many studies have highlighted the importance of soil nutrients and microbial communities in assessing soil fertility (Sun et al., 2014; Gao et al., 2018). Xiao et al. (2020) demonstrated the key role of N addition in promoting soil microbial activity and enhancing microbial nutrient utilization efficiency, consistent with our results showing significant effects of N addition on increasing SMBC, TN, SOC, and soil microbial community contents (Fig. 1b–d). This may be because N addition promoted litter decomposition and accelerated nutrient flow in soil (Miao et al., 2020; Wilcots et al., 2022), as demonstrated by significant positive correlations among soil microorganisms, temperature, moisture, TN, SOC, SMBN, and SMBC in this study ($P<0.05$; Fig. 7). Additionally, due to limited nutrient leaching under low precipitation, decreased precipitation increased soil nutrient and microbial biomass contents compared to normal and increased precipitation (Fig. 1b–d), thereby accumulating nutrients in the upper soil layer. Similar findings were reported by Fang et al. (2017) and Zhao et al. (2020). However, some studies have highlighted that low precipitation can reduce soil moisture infiltration and decrease organic matter utilization by soil microorganisms, potentially reducing soil microbial biomass contents (Li et al., 2020; Ondier et al., 2020).

4.2 Effects of precipitation changes and N addition on soil respiration

The obvious diurnal and seasonal variations in soil respiration rates demonstrated that desert steppe ecosystems are highly vulnerable to environmental changes (Gao et al., 2018; Tiruvaimozhi and Sankaran, 2019; Wang et al., 2020). Precipitation changes and N addition caused similar diurnal and seasonal dynamics in soil respiration rates (Figs. 2–4 and S2), suggesting that soil respiration dynamics might be related to other factors (Wang et al., 2013; Li et al., 2021). We also found that RS+L and RS rate dynamics closely matched soil temperature patterns, indicating that soil temperature is closely related to soil respiration (Ondier et al., 2020).

Enhanced soil respiration from N addition may result from increased available N content, which promotes soil microbial activity and productivity (Hasselquist et al., 2012; Deng et al., 2018; Wang et al., 2019b). Other studies suggest N addition may increase soil N content, thereby reducing microbial N utilization rates and decreasing soil respiration to some extent (Janssen et al., 2010; Sun et al., 2014). This study revealed that N addition significantly increased RS+L and RS rates by 4.8% and 8.0%, respectively ($P<0.05$; Fig. 5a). However, N addition decreased RL rate by 8.6% ($P>0.05$; Fig. 5a), consistent with Schlesinger and Andrews (2000) and Lee and Jose (2003). Han et al. (2019) highlighted N addition's role in promoting litter decomposition and enhancing soil nutrient utilization efficiency, thereby increasing microbial respiration. Our results showed a greater increase in RS rate than RS+L rate under N addition, possibly caused by decreased RL rate (Fig. 5a). This might be due to soil microorganisms utilizing soil nutrients to synthesize their compounds, promoting soil C sequestration. Additionally, this could be attributed to the presence of Gramineae (e.g., *Agropyron mongolicum* and *Stipa breviflora*) and Leguminosae (e.g., *Sophora alopecuroides*) in plant litter, which decreased soil respiration sensitivity to N compared to other plant communities (Xu et al., 2015). Other studies have shown that N addition effects are often dependent on soil moisture, demonstrating the critical role of precipitation changes in weakening N addition effects on soil respiration (Hooper and Johnson, 1999; Li et al., 2011).

Precipitation changes can affect soil respiration by altering SMBC, soil temperature, moisture, and total C (Zhou et al., 2016; Deng et al., 2017). However, factors influencing soil respiration vary across ecosystems (Zhang et al., 2019b). In this study, we removed living plants and roots from surface soil to ensure that microorganisms primarily obtained nutrients from litter. Increased precipitation raised RS+L and RS rates by 2.3% and 5.7%, respectively (Fig. 5a), but the magnitude of increase was higher in plots without litter than in those with litter, consistent with Liu et al. (2016) and Song et al. (2019). Zhou et al. (2019) highlighted that increased precipitation substantially enhances soil C utilization efficiency and stimulates soil respiration. The small magnitude of RS+L rate increase might be due to C immobilization from litter by soil microorganisms.

Many studies have found that low precipitation can limit soil moisture, restraining belowground C distribution and C substrate supply (Peng et al., 2020; Yang et al., 2022b), thereby inhibiting soil enzymes, microbial activities, and microbial respiration (Or et al., 2007; Suseela and Dukes, 2013). In this study, decreased precipitation increased RS+L and RS rates by 12.9% and 23.4%, respectively (Fig. 5a), indicating a greater magnitude of increase than under increased precipitation. Previous studies have shown that low precipitation can reduce soil moisture accumulation and nutrient leaching (Liu et al., 2009; Zhang et al., 2019c; Zhang et al., 2021). These findings demonstrate that decreased precipitation substantially increased soil nutrients and microorganism contents (Fig. 1b–d). In arid and semi-arid desert steppes, intense precipitation events occur primarily during the growing season, enhancing soil compaction and limiting soil aeration (Knapp et al., 2008). Grote et al. (2010) demonstrated that increased precipitation significantly limits oxygen transport with water in arid ecosystems, thereby inhibiting soil respiration. These results are consistent with our findings showing reduced soil actinomycete and protozoan contents under increased precipitation (Fig. 1d).

4.3 Correlations between soil respiration and soil parameters under precipitation change and N addition treatments

Ondier et al. (2020) found that soil respiration is closely related to surface soil temperature. In this study, soil temperature showed a significant exponential relationship with soil respiration compared to soil moisture (Fig. 6a, c, and e), inconsistent with Yu et al. (2022). These findings highlight soil temperature as the key factor affecting soil respiration changes in arid and semi-arid ecosystems. This may be due to decreased surface soil moisture from drastic precipitation changes, lessening moisture effects on respiration (Deng et al., 2017). Additionally, large diurnal soil temperature variations in desert steppes can decrease surface soil moisture independently of soil respiration (Wang et al., 2019a). In contrast, suitable soil temperature can promote soil enzyme and microorganism activity (Feng et al., 2018), potentially enhancing soil C utilization efficiency and affecting soil respiration. Our results showed that precipitation changes significantly and positively correlated with soil temperature and moisture ($P<0.001$; Fig. 7), consistent with SEM results ($P<0.001$; Fig. 8a–c). SEM also demonstrated positive effects of soil temperature and moisture on RS rate (Fig. 8b), indicating that litter removal reduced soil nutrient inputs (Chen et al., 2012). This might be due to antagonistic actions among different factors: soil respiration increased with temperature but negatively correlated with moisture (Fig. 6c and d). However, SEM also indicated that hydrothermal factors positively affect RS rate (Fig. 8b).

Numerous studies have found that soil respiration responses to climate change result from combined soil parameter effects, including antagonistic and synergistic effects (Liu et al., 2009; Zhang et al., 2019; Miao et al., 2020). Our results showed that SOC and SMBC are key factors affecting RS+L, RS, and RL rates (Fig. 8a and b). Several field control experiments have highlighted soil microorganisms as primary indicators reflecting litter effects on soil respiration (Muraskiene et al., 2020), due to microbial ability to fix C from litter (Sui and Zhou, 2013; Xun et al., 2016). This ability could explain the positive effects of soil microorganisms on RS rate and negative effects on RS+L and RL rates (Fig. 8). Additionally, SOC and SMBC are easily mineralized and utilized by soil microorganisms, resulting in CO_2 release (Zhou et al., 2016; Deng et al., 2017). Correlation analysis indicated positive correlations between soil microorganisms and nutrients (Fig. 7). The mean RL/RS+L value in this study was 27.63% (Fig. 5b), consistent with Boone et al. (1998) and Zhao et al. (2020). This finding is mainly because litter decomposition increases soil nutrients and provides substrates for soil heterotrophic respiration (Zhao et al., 2020). Litter is the primary C source for surface soil respiration. Indeed, some C can be decomposed by soil microorganisms, releasing CO_2, while the remaining C can be immobilized by microorganisms to form soil organic matter (Ngao et al., 2005). SEM showed positive effects of precipitation changes and N addition on RL rate (Fig. 8c), explained by their key roles in promoting litter decomposition that leads to C loss from litter in soil (Chimney and Pietro, 2006).

5 Conclusions

This study assessed variation characteristics of soil respiration and its components (RS+L, RS, and RL) in a Yanchi County desert steppe under short-term precipitation changes and N addition treatments, and identified primary factors affecting soil respiration under climate change. The results demonstrated significant effects of N addition, increased precipitation, and decreased precipitation in promoting RS+L and RS rates. In contrast, precipitation changes and N addition had no significant effects on RL rate. The mean RL/RS+L value across treatments was 27.63%, indicating that RL is one of the most important components of soil respiration in desert steppe ecosystems. Soil microorganisms, temperature, moisture, TN, and SOC were the primary factors controlling soil respiration in the desert steppe, with soil temperature, SOC, and SMBC being the most important. Since litter decomposition is a long-term process, continued long-term monitoring is necessary to explore soil respiration responses to climate change and provide more evidence for C emissions in desert steppe ecosystems.

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Appendix

Fig. S1 Diurnal dynamics of soil temperature and moisture in spring (a and e), summer (b and f), autumn (c and g), and winter (d and h) under different treatments. N0 and N10 indicate nitrogen (N) addition rates at 0.0 and 10.0 g/($m^2 \cdot$ a), respectively. CK, IP, and DP indicate precipitation levels of control, increased precipitation by 30%, and decreased precipitation by 30%, respectively. N0×P indicates treatments of CK+N0, IP+N0, and DP+N0; N10×P indicates treatments of CK+N10, IP+N10, and DP+N10; DP×N indicates treatments of DP+N0 and DP+N10; CK×N indicates treatments of CK+N0 and CK+N10; IP×N indicates treatments of IP+N0 and IP+N10. Bars represent standard errors.

Fig. S2 Seasonal dynamics in (a and b) soil respiration with litter (RS+L), (c and d) soil respiration without litter (RS), and (e and f) litter respiration (RL) under different treatments. Bars represent standard errors.

Table S1 Characteristics of litter indices of four typical plant species in the study area

Index	*Stipa breviflora*	*Sophora alopecuroides*	*Agropyron mongolicum*	*Artemisia scoparia*
Cellulose content (g/100 g)	14.14±0.10*d*	10.08±0.20*c*	15.44±0.08*b*	16.18±0.14*a*
Hemicellulose content (g/100g)	18.23±0.39*a*	11.4		

Note: TN, total nitrogen; TP, total phosphorus; TC, total carbon. Different lowercase letters indicate significant differences among litter indices at P<0.05 level based on Duncan's test. Mean±SE.

Table S2 Composite functional parameters of soil respiration with litter (RS+L), soil respiration without litter (RS), and litter respiration (RL) with soil temperature and moisture

Soil respiration	Equation	R^2	P-value
RS+L	RS+L = 0.020T + 0.019W − 0.107	0.60	<0.001
RS	RS = 0.014T + 0.016W − 0.010	0.45	<0.001
RL	RL = 0.005T + 0.003W − 0.007	0.37	<0.001

Note: T, soil temperature; W, soil moisture. ***, significance at P<0.001 level.