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Warming promoted CH₄ absorption compared with precipitation addition in typical steppe in Inner Mongolia

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Introduction: Climate change, characterized by rising temperatures and changing precipitation patterns, has emerged as a significant global concern. Particularly, the warming potential of CH₄ is 28 times greater than that of CO₂, leading to an increased focus on its impact. Among various ecosystems, grasslands exhibit a high vulnerability to climate change. Grassland in Inner Mongolia is an important component of the typical grassland in Eurasian, and there was evidence that warmer and more precipitation in this area in future.

Methods: In this study, we utilized an open-top chamber (OTC) to conduct warming and precipitation experiments on a representative steppe located in Inner Mongolia in 2011. From 2017 to 2019, we monitored various factors, including soil temperature, moisture, CH₄ flux, community characteristics, soil carbon nitrogen content. Subsequently, we analyzed the response of CH₄ flux and its influencing factors to warming and precipitation in this typical steppe.

Results: The soil in the typical steppe acted as a CH₄ sink. In 2018, CH₄ flux during the growing season and t during the non-growing season were -59.31 and -21.21 under C, -56.55 and -31.17 under T, -41.34 and -24.93 under P, -50.09 and -26.51 ug C·m⁻²·h⁻¹ under TP respectively. Warming stimulated absorption of CH₄ during the non-growing season (25.8%), while the addition of precipitation hindered CH₄ absorption during the growing season (76.37%). Warming and precipitation addition decreased the percentage of CH₄ absorbed in growing season and increased that in non-growing season which account 67.66% and 32.34% under C, 59.81% and 40.19% under T, 62.71% and 37.29% under P, 62.03% and 37.97% under TP respectively. Soil temperature exhibited a positive correlation with CH₄ flux ($P < 0.001$), while the dominance of *Leymus chinensis* (IV-L.c.) exhibited a negative correlation with CH₄ flux ($P < 0.01$). Moreover, NH₄⁺-N displayed a positive correlation with CH₄ flux ($P < 0.05$).

Conclusion: The findings suggest that CH₄ absorption in a typical steppe may increase in a warmer future, and warming is conducive to the absorption of CH₄ in the non-growing season. Not only abiotic factors had an impact on CH₄ absorption, but also changes in community composition. Consequently, further exploration of the underlying mechanisms is warranted.

KEYWORDS

climate change, typical grassland, CH₄, growing season, non-growing season

1 Introduction

Global warming has garnered considerable attention worldwide, with the increasing concentration of carbon dioxide (CO₂), methane (CH₄), and nitrous oxide (N₂O) being significant contributors to climate change (IPCC, 2021). CH₄ the second-largest greenhouse gas after CO₂, possesses a potent warming potential and can raise surface temperatures by absorbing long-wave radiation emitted by the Earth's surface. Grasslands represent crucial terrestrial ecosystems, and the Inner Mongolian grassland, situated at the eastern edge of Eurasia, serves as a vital ecological barrier in northern China, making it highly susceptible to climate change. Investigating the variations and influencing factors of greenhouse gas fluxes in typical grasslands and understanding the feedback and response of grassland ecosystems in the context of climate change are of utmost importance.

Scholars have explored CH₄ fluxes during both the growing and non-growing seasons. For instance, CH₄ absorption rates in alpine meadows on the Qinghai-Tibet Plateau are higher in summer and lower in winter (Chen W. et al., 2019). CH₄ oxidative absorption occurs in temperate semi-arid grasslands during winter with a low absorption rate (Wang et al., 2011). Meadows exhibit net CH₄ absorption throughout the year, primarily during the growing season, while the non-growing season weakens the sink's ability to emit CH₄ (Li et al., 2022). Warming affects CH₄-producing and oxidising bacteria by altering environmental factors such as soil temperature, moisture, permeability, and nutrient levels within the ecosystem (Dijkstra et al., 2011; Dijkstra et al., 2013; Lin et al., 2015), consequently affecting soil CH₄ flux. The results showed that the methane oxidation rate was $0.14 \pm 0.04 \text{ mg} \cdot \text{cm}^{-2} \cdot \text{d}^{-1}$ in grasslands with an annual average temperature of -7.8°C (Li et al., 2020). In alpine grasslands with an annual average temperature of 0.08°C , the methane oxidation rate significantly increased with a 1°C temperature rises (Li et al., 2020). In the range of -10 to 30°C , the amount of methane oxidation increases with the increase of temperature (Chen et al., 2010). Furthermore, when the soil temperature rises from 18°C to 28°C , the activity of methanotrophs increases (Ma et al., 2016). Changes in precipitation affect the production or oxidation processes of soil CH₄ and regulate its emission or absorption (Xu et al., 2015a). For example, reduced precipitation promotes CH₄ oxidation in tropical and temperate forest soils, thereby enhancing CH₄ uptake (Savi

et al., 2016; Yan et al., 2019; Wu et al., 2020a; Wu et al., 2021). As the temperature and precipitation vary across different grassland ecosystems, the effects of temperature rise and precipitation fluctuations on CH₄ flux also differ among various grassland types. Furthermore, limited continuous observations of CH₄ fluxes in different seasons in previous studies have resulted in gaps in understanding the influence of temperature and precipitation changes on CH₄ dynamics.

Climate change also affects soil carbon and nitrogen pools (Zhang et al., 2018; Wei et al., 2020; Xie et al., 2020; Wang et al., 2022) leading changes in methane flux. Soil soluble carbon and nitrogen act as nutrient sources that influence the activity of methanotrophs and control soil CH₄ oxidation processes (Shukla et al., 2013). For instance, changes in soil dissolved organic carbon content can affect soil CH₄ flux by limiting the carbon mineralization process of methane-oxidizing bacteria, and indirectly impact the soil CH₄ oxidation process by affecting other soil characteristics such as water content and soil inorganic nitrogen content (Tate, 2015). Inorganic nitrogen has long been considered an important factor in regulating soil CH₄ oxidation capacity. The addition of NH₄⁺ may inhibit, promote, or even have no significant effect on the soil CH₄ oxidation process (Bodelier, 2011; Shukla et al., 2013; Tate, 2015). Additionally, variations in biomass, nutrient uptake, and photosynthetic characteristics among different plant species contribute to differences in ecosystem nitrogen and carbon cycles, as well as greenhouse gas fluxes (Han and Chen, 2020). Alterations in plant species composition significantly reduce CH₄ flux, primarily due to a decrease in soil active carbon content (such as microbial biomass carbon) and soil enzyme activity (Luan et al., 2016). The effects of grassland species richness and functional group presence on CH₄ production found that the emission flux of species mixtures can be significantly higher than that of the species monoculture because of the significant increase in biomass (Khalsa et al., 2014). Moreover, plant species richness can significantly increase CH₄ flux (Zhang et al., 2012). However, few studies have examined how simulated climate change affects CH₄ flux through vegetation. While abiotic factors are often considered when explaining the influencing factors of CH₄, the response of biological factors, particularly vegetation community composition, to climate change is intuitively significant. Thus, understanding the impact of climate change on CH₄ flux should not neglect the role of vegetation.

To obtain more accurate observations of the feedback on the CH₄ flux and climate change, long-term monitoring is essential. Therefore, the aim of this study was to conduct warming and precipitation addition experiments in Inner Mongolia, China, in 2011, based on the climate change trend in temperate steppes. The study sought to elucidate (1) how warming and precipitation addition affect CH₄ emission fluxes in temperate steppes, particularly during the growing and non-growing seasons, and (2) the main factors influencing CH₄ fluxes. By monitoring vegetation and soil nutrient changes and analysing their relationship with greenhouse gas fluxes, we aimed to reveal the response of greenhouse gas fluxes to climate change in a typical steppe, providing further insights into the temporal dynamics and influencing factors of CH₄ flux in grassland ecosystems.

2 Research method

2.1 Study site

The study site is located at the Grassland Ecology Research Base of Inner Mongolia University in Mauden Pasture (44°09'N, 116°29' E, 1102 m above sea level), 40 km east of XilinHot (Figure 1). The region experiences a temperate continental climate characterised by cold and dry winters and hot and humid summers. The average annual temperature is 2.6°C, with the lowest temperature occurring in January (−23.8°C) and the highest temperature in July (24.9°C). The average annual precipitation is 271.42 mm, concentrated between May and September, which accounts for 87.3% of the total annual precipitation. The annual evaporation ranges from 1600 to 1800 mm. The soil in the study area is chestnut soil, and the vegetation type is typical steppe dominated by *Stipa krylovii* and *Leymus chinensis*.

2.2 Experimental design

The simulated warming and precipitation addition experiment commenced in July 2011 using open-top chamber (OTC). The OTC were fixed in the plots throughout the year to avoid disturbance. The warming treatment in this experiment was set at 2°C based on the IPCC Fourth Assessment Report. The OTC is a cone-shaped device made of polycarbonate (PC board) with a fan for temperature control. The upper bottom surface diameter of the OTC was 0.7 m, the lower bottom surface diameter was 1.2 m, and the height was 0.4 m. Precipitation addition was conducted twice each month during the growing season, equivalent to 20% of the average monthly precipitation from 1961 to 2010 (Wan et al., 2018). Precipitation was added after 18:00 to avoid damage to plants during high daytime temperatures. Four treatments were applied: control (CK), warming (T), warming and precipitation (TP), and precipitation (P). Each treatment had 4 replicates, resulting in a total of 16 experimental plots (Figure 1).

The greenhouse gas collection in this experiment used the platform of warming and precipitation addition experiment to

collect and measure greenhouse gases in 2017–2018 after 6 years of continuous warming and precipitation addition and continued the warming and precipitation addition experiment.

2.3 Determination method

2.3.1 Determination of soil temperature and moisture

Temperature and moisture measurements were measured using a data collector with a (temperature probe model: DS18B20; humidity probe model: EC-5). Soil temperature and humidity were recorded at 10 cm intervals, and data were automatically recorded every 30 min.

2.3.2 Determination of greenhouse gas concentration

Static chamber gas chromatography was used to measure greenhouse gas concentration. The static chamber material was a PVC cylinder with a diameter of 0.4 m and a height of 0.3 m, were. The static chamber was placed at the base to collect the gas. Gas samples were collected at 0, 10, 20, and 30 minutes and injected into sealed glass gas cylinders. The sampling time was from May 2017 to February 2019, with measurements taken every 7 days during the growing season (May to early September) was measured every 7 days. During the spring freeze–thaw period (March to April), it was measured every 4 days, in late September to October every 15 days, and once a month from November to February of the following year. The collected samples were analyzed for CH₄ concentration using gas chromatography (HP6890N, Agilent Company). The CH₄ flux was calculated based on the difference in gas concentration within the time range of the static chamber (70).

2.3.3 Investigation of community characteristics

The community characteristics and biomass were determined using quadrat surveys. Monthly surveys were conducted during the growing season (May to August) in each plot, with a sampling area of 1×1m². The surveys included assessments of community species composition, density, and height.

At the end of August, the growing season, the quadrat was selected outside the sample plot, and the plants in the quadrat were cut off on the ground and seeded into envelopes. They were then oven-dried at 65°C for 48 h to determine peak above-ground biomass (Xu et al., 2015b). A regression equation was used to calculate the biomass in the plot (Table S1).

2.3.4 Determination of soil carbon and nitrogen

Soil samples were collected at the end of August in 2017 and 2018, with the top 10 cm of soil collected using a 3 cm diameter soil drill. Fresh soil samples were partially air-dried and passed through a 0.15 mm sieve. The sieved soil was placed in tin cups for sample packaging. The total carbon and nitrogen content of the soil were determined using an elemental analyzer (Thermo Fisher, Thermo Fisher Scientific, USA). The microbial biomass, carbon, and nitrogen were determined using the chloroform fumigation

method. After sieving the fresh soil through a 2 mm sieve, three portions of fresh soil (20 g each) were weighed. One portion was placed in an aluminum box and dried in an oven at 70°C to determine dry weight. The remaining two soil samples were placed in a 50 ml beaker. One of the beakers was placed into a vacuum pumping vessel and, at the same time, placed in a beaker containing 25 ml of chloroform. The chloroform was vacuum boiled for 5 min, and the piston and air pump were closed. The beaker was covered with black cloth, fumigated in the dark for 24 h, removed, vacuumed three times for 5 min each time, and vacuum chloroform was added. Another beaker was used as a control without the fumigation treatment; the other treatments were consistent and placed under the same conditions. After 24 h, the treated soil samples were transferred to centrifuge tubes, and each bottle was injected with 50 ml 0.5 mol/L K₂SO₄ solution, shocked for 30 min, centrifuged, and filtered, and the filtrate was analyzed using a Multi N/C 3000 DOC analyzer (German Jena company). The extractable carbon and nitrogen were converted to MBC and MBN using conversion factors (K_{ec} and K_{en}) of 0.45 both (Xu et al., 2010). NH₄⁺-N and NO₃⁻-N were determined by a continuous flow analyzer with 2 mol·L⁻¹ KCL solution and water–soil ratio of 5:1. The soil samples (10 g) were weighed, and distilled water was added according to the ratio of water to soil (2:1). The soil samples were shaken at 25°C for 30 min and filtered with 0.45 μm filter membrane. The DOC and DON in the filtrate were determined using a Multi N/C 3000 DOC analyzer (Jena, Germany).

2.4 Data calculation and analysis

2.4.1 Greenhouse gas flux calculation

$$F = \rho \times h \times \frac{\Delta C}{\Delta t} \times \frac{273.15}{273.15 + T} \quad \text{Formula 1}$$

In the formula, F is the greenhouse gas flux, CH₄ flux unit is (ug·m⁻²·h⁻¹). A positive value represents emissions, and a negative value represents absorption. ρ is the density of a greenhouse gas under standard conditions, h is the height of the sampling static

chamber (m), $\frac{\Delta C}{\Delta t}$ is the rate of change of a gas concentration with time, and T is the air temperature (°C) at the time of sampling.

2.4.2 Data analysis method

Microsoft Excel 2016 and IBM SPSS Statistics 24.0 (SPSS Inc., Chicago, IL, USA) were utilized for data processing and analysis. One-way analysis of variance (ANOVA) was employed to analyze the significance of differences between different treatments, and multiple comparisons were conducted using Duncan's method. Correlation analysis was performed to analyze the relationship between greenhouse gas fluxes, environmental factors, and nutrients (results of soil carbon and nitrogen used in correlation heat map analysis in Table S2; results of community characteristics used in correlation heat map analysis in Tables S3 and S4). We used piecewise structural equation modelling (SEM) with AMOS 21.0 (Amos Development Co., Armonk, New York, USA) to evaluate the effects of temperature and moisture changes on CH₄ emissions by affecting vegetation and soil carbon and nitrogen pools. Before establishing SEM, we conducted a stepwise regression analysis of CH₄ flux and its influencing factors, and established formulas, CH₄ = -337.40 + 146.27 IV-L.c + 3.03 MBN (F = 10.92, P = 0.001). Finally, we verify the feasibility of the model through P > 0.05.

3 Results and analysis

3.1 Effects of warming and precipitation addition on CH₄ flux in typical steppe

Typical steppe soil acts as a sink for CH₄, with higher CH₄ absorption during the growing season compared to the non-growing season (the percentage of CH₄ absorption during the growing season to the non-growing season ranges from 1.27 to 2.47) (Figures 2, 3, 4B). The average CH₄ flux during the growing season accounted for 55.80% to 69.71% of the entire year under different treatments (Figure 4A), while the non-growing season contributed 30.29% to 44.2% of the annual CH₄ flux (Figure 4A). Warming and precipitation addition decreased the percentage of

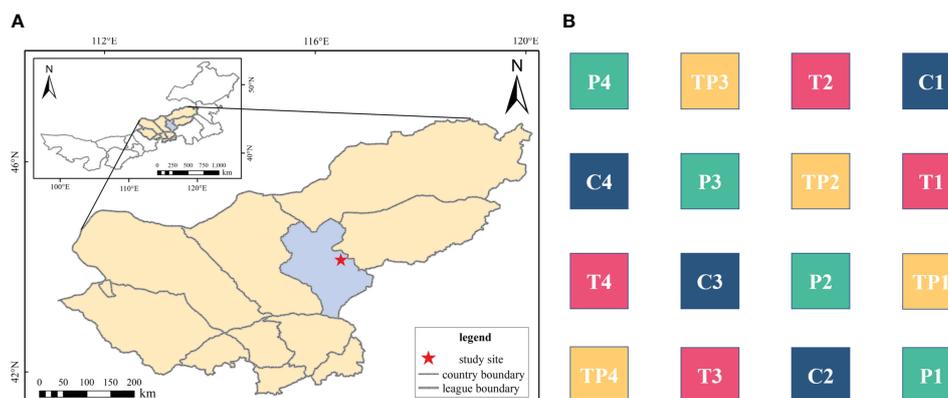


FIGURE 1

Study site (A) and the schematic diagram of experimental warming design (B). Control (C), warming (T, warming 2 °C), warming plus precipitation addition (TP, warming 2 °C plus precipitation addition 20%), and precipitation (P, precipitation addition 20%).

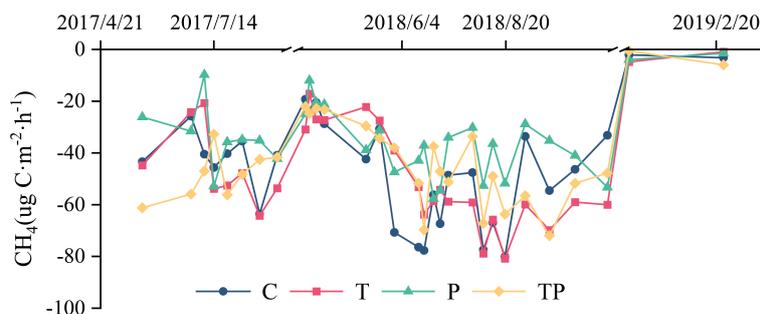


FIGURE 2
Effect of warming and precipitation addition on CH_4 flux.

CH_4 absorbed in growing season and increased that in non-growing season which account 67.66% and 32.34% under C, 59.81% and 40.19% under T, 62.71% and 37.29% under P, 62.03% and 37.97% under TP respectively. The addition of precipitation (P treatment) reduced the absorption of CH_4 by the soil, likely due to decreased soil permeability caused by increased precipitation, which hinders the diffusion of CH_4 into the soil. On the other hand, warming promoted the absorption of CH_4 in typical steppe ecosystems.

3.2 Relationships between CH_4 and environmental factors

Warming and precipitation addition significantly affected soil temperature and moisture. Warming increased soil temperature and decreased soil moisture, while precipitation addition decreased soil temperature and increased soil moisture. Combined warming and precipitation addition can alleviate the adverse effects of individual warming on the soil environment (Wan et al., 2018). Soil temperature showed a significant positive correlation with CH_4 flux ($P < 0.001$). In this study, the variation in soil surface temperature explained the variation in CH_4 flux well ($R^2 = 0.52$) (Figure 5). With seasonal changes, the decrease in soil moisture caused by warming led to increased soil permeability (Juc'a and Maciel, 2006; Lu et al., 2023), promoting the diffusion of CH_4 from the atmosphere into the deep soil and thereby enhancing CH_4 absorption. In a typical steppe in semiarid areas, the increase in

water may not reach the threshold level that affects methanotrophs, hence no significant correlation between CH_4 flux and soil surface moisture was noted.

3.3 Relationships between CH_4 flux with soil factors and community factors

Community species diversity decreased, *Leymus chinensis* biomass increased, and *Stipa krylovii* biomass decreased due to warming and precipitation addition (community factors, soil carbon, and nitrogen under warming and precipitation are shown in Tables S2–S4).

The correlation heat map of CH_4 flux, which used negative values (higher absolute value indicating higher absorption), revealed that IV-L. c. is positively correlated with CH_4 flux ($P < 0.01$). The Simpson and Shannon indices were negatively correlated with CH_4 flux ($P < 0.05$). $\text{NH}_4^+ - \text{N}$ was negatively correlated with CH_4 flux ($P < 0.05$). The increase in the dominance of *Leymus chinensis* hampered CH_4 absorption, whereas an increase in species diversity and NH_4^+ content promoted CH_4 absorption. CH_4 flux was not only affected by soil carbon and nitrogen but also by vegetation species diversity and dominant species dominance (Figure 6).

Warming mainly affected CH_4 flux by influencing IV-L. c. Precipitation addition primarily affected CH_4 flux through its influence on soil nitrogen (Figure 7).

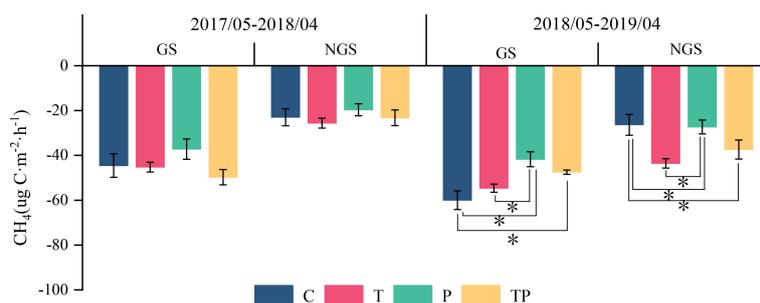


FIGURE 3
Effects of warming and precipitation addition on CH_4 flux in growing and non-growing seasons.

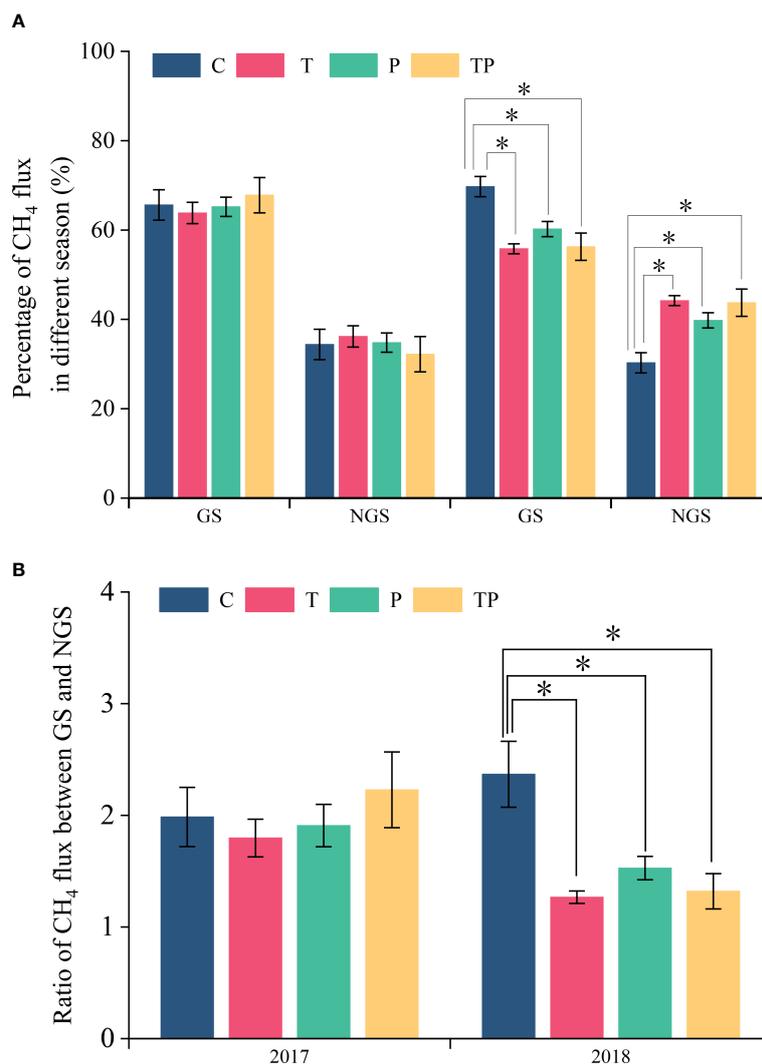


FIGURE 4

Percentage of CH₄ flux in growing season and non-growing season in the whole year and CH₄ emission of GS to NGS. C, Control, no warming and no precipitation addition; W, warming; P, precipitation addition; WP, warming plus precipitation addition; GS, growing season; NGS, non-growing season; * significant at P<0.05.

4 Discussion

4.1 Effects of warming and precipitation addition on greenhouse gas flux in typical steppe

Grassland ecosystems act as sinks for CH₄. Air temperature is an important factor that affects soil CH₄ uptake, it can affect the activity of methanotrophs in the soil. Within a certain temperature range, the oxidation rate of CH₄ in the soil increases with rising temperature. Additionally, warming leads to reduced soil water content through increased evaporation (Bokhorst et al., 2008), and soil water can exert physiological pressure on methanotrophs, which in turn affects the diffusion of CH₄ in the soil (Luo et al., 2013; Li et al., 2015). In addition to soil temperature, soil moisture is also an important factor influencing CH₄ flux. Decreased water content results in thinner

plant roots, increased soil nitrogen cycling rates, enhanced methanotrophic community, reduced methanogen community, and increased CH₄ uptake (Konda et al., 2010; Lawrence et al., 2015; Liu et al., 2015). Water addition, on the other hand, reduces soil permeability, hinders CH₄ transmission from the atmosphere to the soil, and decreases CH₄ absorption (Conrad, 2007). However, an increase in soil water content creates an anaerobic environment favorable for CH₄-producing bacteria, resulting in reduced CH₄ absorption and increased CH₄ emissions (Dijkstra et al., 2013). In dry years, the increase in soil moisture caused by the addition of precipitation did not reach the threshold level to affect methanotrophs, thus having no significant impact on CH₄ uptake (Zhang et al., 2017). However, other studies have suggested that net methane uptake increases with humidity under drought conditions (Von et al., 2009). The results differed in 2017, which was a more drought-prone year with higher temperatures and lower precipitation

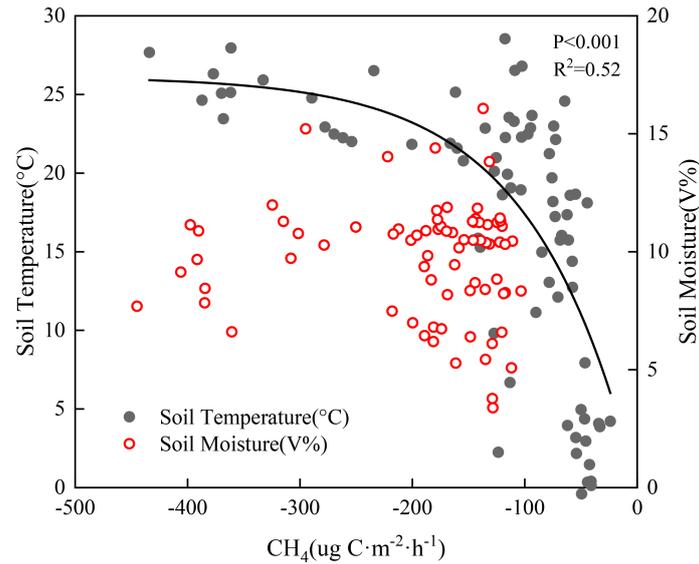


FIGURE 5
Correlation between soil temperature, soil moisture, and CH₄ flux under warming and precipitation addition conditions.

compared to the period of 2012–2022. Additionally, warming can promote CH₄ absorption, while precipitation had an inhibitory effect on CH₄ absorption, which is consistent with the results of Zhu et al. (2015) and Xu et al. (2015a). This indicates that temperature and water jointly regulate CH₄ fluxes in typical steppes in arid and semi-arid regions, with increasing temperature strengthening CH₄ absorption in the area. Warming increased CH₄ absorption was closely correlated with soil temperature and soil moisture (Wang

et al., 2021a). Warming-induced increase in soil temperature directly enhances methanotrophic and decreases methanogen abundance (Zheng et al., 2012; Peltoniemi et al., 2016), thus resulting in an enhancement of soil CH₄ absorption. Furthermore, a lower soil water content was found under warming, which could have decreased anaerobic conditions by increasing air permeability and O₂ diffusion in the soil (Chen et al., 2017), favoring microbial oxidation of CH₄ (Dijkstra et al., 2013).

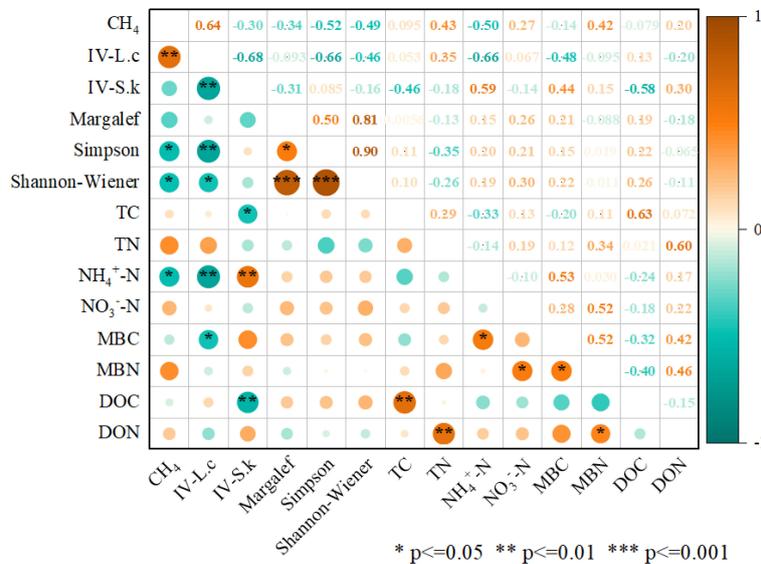


FIGURE 6
Correlation heat map of CH₄ flux with soil factors and community factors. Significant differences shown at * P<=0.05; ** P<=0.01; ***P<=0.001. IV-L.c, important value of *Leymus chinensis*; IV-S.k, important value of *Stipa krylovii*; Margalef, Margalef richness index; Simpson, Simpson's diversity; TC, Total carbon; TN, Total nitrogen; NH₄⁺-N, Ammoniacal nitrogen; NO₃⁻-N, Nitrate nitrogen; MBC, Microbial carbon; MBN, Microbial nitrogen; DOC, Dissolved organic carbon; DON, Soluble organic nitrogen.

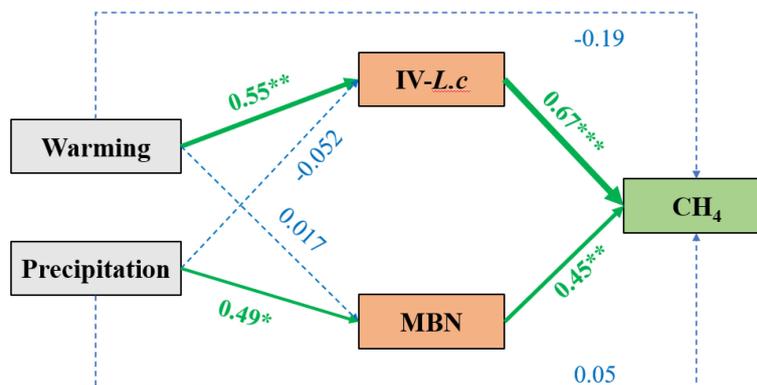


FIGURE 7

SEM model analysis of the influence mechanism of warming and precipitation on CH_4 emission. Chi-square = 0.034; Probability level = 0.854. Significant differences shown at * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. IV-L.c, important value of *Leymus chinensis*; MBN, microbial biomass nitrogen. The thickness of the lines indicated the strength of the correlation. Green lines represent a significant positive correlation; red line represents a significant negative correlation; blue lines indicate that the correlation is not significant.

4.2 Effects of vegetation and soil carbon and nitrogen on greenhouse gas fluxes under warming and precipitation addition conditions

Simulated warming and precipitation have significant effects on soil carbon and nitrogen pools (Zhang et al., 2018; Wei et al., 2020; Wang et al., 2022), and greenhouse gas emissions are closely related to the stability of these pools (Wu et al., 2020b). Grasslands act as sinks for CH_4 , and therefore, increased soil nitrogen can inhibit CH_4 oxidation by raising NH_4^+ concentration, resulting in reduced CH_4 absorption. However, more soil nitrogen can alleviate the nitrogen limitation in grassland soil microorganisms, enhance microbial activity, and promote CH_4 absorption. Thus, the effect of soil nitrogen on grassland CH_4 flux is complex and depends on multiple factors. Previous studies have yielded different conclusions, with some reporting that in Inner Mongolian grasslands, nitrogen addition reduces soil CH_4 uptake (Zhang et al., 2017). In the Tianshan grassland, nitrogen addition promotes CH_4 uptake in (Li et al., 2012). Furthermore, the addition had no significant effect on CH_4 emissions (Zhao et al., 2017). In the present study, soil NH_4^+ promoted CH_4 absorption, while soil NO_3^- inhibited it. Soil NO_3^- increases soil redox potential, exerting osmotic pressure on methanotrophs and exhibiting toxic effects on them. Long-term nitrogen addition leads to changes in the methanotroph community and reduced abundance, ultimately inhibiting CH_4 absorption (Treseder, 2008; Li et al., 2020). Thus, high concentrations of NO_3^- in soil can suppress methanotroph activity (Yue et al., 2016; Chen S. et al., 2019; Zhang et al., 2019; Pan et al., 2022), affecting their abundance and reducing CH_4 absorption. Warming and precipitation affected CH_4 flux by influencing soil nitrogen. Direct and indirect positive correlations were observed between precipitation enhancement and soil N and CH_4 fluxes. However, increased temperature did not facilitate the effect of soil nitrogen or promote greenhouse gas emissions. Considering the warming and drying trends expected under future climate change, increasing CH_4

absorption in the typical steppe area of Inner Mongolia would be beneficial.

Soil temperature and moisture explain most of the seasonal variations in CH_4 fluxes, but the effects of environmental factors on greenhouse gas emissions and uptake are not only direct but also indirect through their influence on soil nutrients and vegetation growth (Shaver et al., 2000; Sampson et al., 2007; Aires et al., 2008; Xu and Wan, 2008; Kuzyakov and Gavrichkova, 2010; Nakano and Shinoda, 2010; Potthast et al., 2010; Phillips et al., 2012). Warming can impact species richness by altering soil nutrient content and plant interspecific relationships (Nogueira et al., 2017), while increased water availability improves soil water availability, alleviating the inhibitory effects of water deficit on plant growth (Xu et al., 2014), thereby affecting species diversity. Higher species diversity can promote biomass growth and significantly increase CH_4 flux (Zhang et al., 2012). Plant phenology, which influences plant growth (Fu and Shen, 2022; Jiang et al., 2022; Han et al., 2023a), also indirectly affects CH_4 flux. Although this study did not consider the impact of plant phenology on productivity and CH_4 flux, it examined productivity and community structure under relatively stable plant growth conditions, which can still reflect community changes in response to environmental changes. Warming increased the Simpson, Shannon–Wiener, and Pielou indices (Table S3), and both the Simpson and Shannon indices were negatively correlated with CH_4 flux ($P < 0.05$). Community composition may also be related to plant production (Li et al., 2014; Wang et al., 2021b; Wang et al., 2021c; Han et al., 2023b), and changes in community composition and productivity have a significant impact on CH_4 flux (Zhang et al., 2012; Khalsa et al., 2014). In this study, warming and precipitation addition significantly increased the dominance of the *Leymus chinensis* population and decreased the dominance of *Stipa krylovii* population (Table S4), and IV-L.c was significantly positively correlated with the CH_4 flux ($P < 0.01$). Warming primarily affected CH_4 flux through changes in species dominance. As a dominant species, the increased biomass of *Leymus chinensis* in the

community and its inhibitory effect on CH₄ absorption was stronger. This showed that the dominance of *Leymus chinensis* increases and the species diversity index decreases, which aggravates the inhibition of CH₄ absorption and weakens the function of the CH₄ sink under a warmer future in typical grasslands.

It is well known that soil CH₄ fluxes are determined by the balance between CH₄ production from methanogens and CH₄ oxidation from methanotrophs (Prabhu et al., 2013; Christiansen et al., 2015). Multiple studies have shown that soil microbial community structure was influenced by warming and precipitation changes (Yu et al., 2019; Zhang et al., 2021; Han et al., 2022; Zhong and Fu, 2022). Methanogenic bacteria typically exist in anaerobic environments, and long periods of soil water deficiency, increase contact with soil oxygen, making it difficult to establish low oxidation reduction potential for CH₄ absorption through anaerobic respiration (Yang et al., 2017). The lower soil moisture under warming could lead to higher potential redox conditions, in which microbes degraded SOC by gradually using electron acceptors with higher redox potentials, leading to conditions less suitable for methanogenesis (Johnston et al., 2019; Tano et al., 2020). Meanwhile, soil oxygen content could increase with the decline of soil moisture, resulting in more favorable conditions for methane oxidation (Li et al., 2020). While this study mainly considered the impact of environmental factors and plant community characteristics on CH₄, future research could improve our ability for projecting future CH₄ absorption changes via a better understanding of microbial mechanisms in response to climate changes (Cavicholi et al., 2019; Guo et al., 2020).

5 Conclusion

1) The typical grassland soil was sink of CH₄. CH₄ flux during non-growing seasons accounted for a large proportion of whole year, which account for 30.29% ~ 44.20% under different treatments and was an indispensable part of CH₄ flux. Warming promoted the CH₄ absorption flux during the non-growing seasons, while precipitation addition inhibited that during the growing seasons compared with C. Warming and precipitation addition both reduced the proportion of CH₄ flux in the growing season to the whole year, and increased the proportion in the non-growing season, and the effect of warming was stronger than that of precipitation addition on that. Warming and precipitation addition increased the percentage of CH₄ absorbed in non-growing season which account 32.34% under C, 40.19% under T, 37.29% under P, 37.97% under TP respectively.

2) Increase of soil temperature, soil NH₄⁺-N content and species diversity were conducive to CH₄ absorption, but the increase of *Leymus chinensis* dominance was not conducive to that. Under future climate warming, the increase in *Leymus chinensis* population dominance and decrease in the species diversity index will further inhibit the absorption of CH₄ and weaken the function

of the CH₄ sink in a typical steppe. However, there are many other ways in which warming affects CH₄ absorption, and the results showed that warming promoted CH₄ absorption. Therefore, we need to explore the mechanisms by which different factors affect CH₄ flux in the future.

Data availability statement

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

Author contributions

HG and QG designed the research; ZW and RG performed the experiments; ZW and XMC analyzed the data and wrote the draft; ZW, XMC, HZ, XC, and CH revised the manuscript.

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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 reviewer YY declared a past co-authorship with the author ZW to the handling editor.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2023.1193939/full#supplementary-material>

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