frontiers | Frontiers in Ecology and Evolution

TYPE Original Research
PUBLISHED 08 March 2023
DOI 10.3389/fevo.2023.1149595

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OPEN ACCESS

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SPECIALTY SECTION
This article was submitted to Population, Community, and Ecosystem Dynamics,
a section of the journal
Frontiers in Ecology and Evolution

RECEIVED 22 January 2023
ACCEPTED 17 February 2023
PUBLISHED 08 March 2023

CITATION
Zheng Z, Wen F, Li C, Guan S, Xiong Y, Liu Y, Qian R, Lv M, Xu S, Cui X, Wang Y, Hao Y and Li L (2023) Methane uptake responses to heavy rainfalls co-regulated by seasonal timing and plant composition in a semiarid grassland.
Front. Ecol. Evol. 11:1149595.
doi: 10.3389/fevo.2023.1149595

Methane uptake responses to heavy rainfalls co-regulated by seasonal timing and plant composition in a semiarid grassland

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Heavy rainfalls caused by global warming are increasing widespread in the future. As the second greenhouse gas, the biological processes of methane (CH_4) uptake would be strongly affected by heavy rainfalls. However, how seasonal timing and plant composition affect CH_4 uptake in response to heavy rainfalls is largely unknown. Here, we conducted a manipulative experiment to explore the effects of heavy rainfall imposed on middle and late growing season stage on CH_4 uptake of constructed steppe communities including graminoid, shrub and their mixture in Inner Mongolia, China. The results of mixed effect model showed that both heavy rainfalls decreased CH_4 uptake. Nevertheless, the effect magnitude and the pathways were varied with seasonal timing. Relatively, the late heavy rainfall had larger negative effects. Structural equation model suggested that late heavy rainfall decreased CH_4 uptake through decreased diffusivity, *pmoA* abundance, and NH_4^+-N content, as products of high soil water content (SWC). However, middle heavy rainfall decreased CH_4 uptake only by increasing SWC. Additionally, aboveground biomass (AGB) had negative effects on CH_4 uptake under both heavy rainfalls. Additionally, plant composition not only affected CH_4 uptake but also regulated CH_4 uptake in response to heavy rainfalls. Late heavy rainfall had less negative effect on CH_4 uptake in graminoid community than in other two communities, in coincidence with less reduction in NH_4^+-N content and less increase in SWC and AGB. In contrast, we did not observe obvious difference in effects of middle heavy rainfall on CH_4 uptake across three communities. Our findings demonstrated that magnitude and pathways of heavy rainfall effects on CH_4 uptake were strongly co-regulated by seasonal timing and plant composition.

KEYWORDS

CH_4, climate extremes, greenhouse gasses, methanotrophs, community composition, precipitation

Introduction

Methane (CH_4) is a powerful greenhouse gas and strongly contributes to global warming and resultant changes in precipitation, as the global warming potential is 28–36 times than that of carbon dioxide (CO_2) at 100-y timescale (Jiang et al., 2012; Fischer and Knutti, 2016; Otto et al., 2018; IPCC, 2021). Aerobic soils are important CH_4 sink, in which 9–47 Tg CH_4 year^{-1} from the atmosphere was oxidated by methanotroph through methane monooxygenase (MMO) (Elango et al., 1997; Fest et al., 2015; Yue et al., 2019, 2022). The subunit genes of MMOs, specifically *pmoA,* are used as biomarker genes for the presence and abundance of bacterial methanotrophs (Fest et al., 2015; Tentori and Richardson, 2020). Therefore, understanding effects of changes in precipitation on CH_4 uptake in drylands and underlying microbial mechanisms have great implications for prediction of future carbon cycling and its feedback to climate changes.

It has been confirmed that precipitation changes are expected to significantly influence the intensity of CH_4 sinks (Aronson et al., 2019; Martins et al., 2021). For example, increased precipitation by 30% significantly increased CH_4 uptake in temperate deserts (Yue et al., 2019). In contrast, CH_4 uptake was decreased and unchanged by increased precipitation in alpine meadows and in degraded steppe grasslands, respectively (Chen W. W. et al., 2013; Wu et al., 2020). Meta-analysis studies suggested that increased precipitation can decrease CH_4 uptake in terrestrial ecosystems at the global scale (Chen H. et al., 2013; Yan et al., 2018). Although these results highlighted the important role of increased precipitation in regulating CH_4 uptake in aerobic soils, to date, there is great uncertainty about the effects of extreme precipitation with several days (e.g., heavy rainfall events), rather than chronic increases in precipitation at seasonal timescale, on CH_4 uptake.

Effects of chronic increases in precipitation and heavy rainfall on CH_4 uptake may be largely different. Soil moisture controlled CH_4 uptake through affecting the methanotroph community and altering air-soil diffusion (Wei et al., 2015). A bell-shaped relationship was observed between soil moisture and CH_4 uptake with CH_4 uptake reached the peak at intermediate soil moisture (Dijkstra et al., 2013; Li et al., 2016; Zhang et al., 2021). Above the optimum soil moisture, soil moisture would limit oxygen (O_2) diffusion in soils and depress the activity of methanotroph communities, inhibiting CH_4 uptake (Curry, 2007; Liptzin et al., 2011; Zhuang et al., 2013). Hence, slight increases in precipitation may promote methanotroph community and thereby increase CH_4 uptake while heavy rainfall caused saturation soil moisture and thereby would reduce CH_4 uptake. Additionally, CH_4 uptake is sensitive to soil ammonium (NH_4^+-N) and nitrate (NO_3^--N). NH_4^+-N had an inhibiting effect on CH_4 uptake mainly through replacing CH_4 to be oxidized by methanotroph (Schnell and King, 1994; Yue et al., 2022), while NO_3^--N had an inhibiting effect on CH_4 uptake through changing methanotroph activity and composition or enhancing soil oxidation potential and environment (Le Mer and Roger, 2001; Yue et al., 2022). Increased precipitation is likely to enhance soil inorganic nitrogen by accelerating mineralization (Cabrera and Kissel, 1988; Bai et al., 2012). In contrast, soil inorganic nitrogen may decline through leaching and runoff under heavy rainfalls (Borken and Matzner, 2009; Cregger et al., 2014). Thus, slight increases in precipitation and heavy rainfall are likely to induce opposite impacts on CH_4 uptake through the pathway of NH_4^+-N and NO_3^--N content.

Furthermore, seasonal timing and plant composition potentially modulate CH_4 uptake in response to heavy rainfalls. Previous studies suggested that seasonal timing strongly regulates effects of heavy rainfall on multiple ecosystem attributes such as soil water, carbon, and nitrogen availability, as well as plant biomass and phenology (Li et al., 2019; Post and Knapp, 2020; Li et al., 2022). Therefore, we except that impacts of heavy rainfall on CH_4 uptake may be also regulated by seasonal timing. Indeed, Zhao et al. (2017) found that CH_4 uptake was reduced by 62% and 45% during the period of middle and late heavy rainfall, respectively. Besides, there were significant differences in the composition and abundance of methanogens in soil with different plant species, resulting in different potential of CH_4 uptake (Dai et al., 2015). For example, CH_4 uptake capacity was stronger in soil of oat than that in native vegetation (Hüppi et al., 2022). Moreover, plant communities with higher-diversity were less negatively affected by floods and mature plants can withstand flooding better than seedlings (Gattringer et al., 2017; Wright et al., 2017). Although several studies had reported that plant community composition and seasonal timing could moderate heavy rainfall effects on CH_4 uptake capacity (Liebner et al., 2015; Tong et al., 2017; Zhao et al., 2017; Yue et al., 2022), it is unknown the interactions on CH_4 uptake in the face of heavy rainfall.

To explore the individual and especially interactive effects of heavy rainfall timing and species composition on CH_4 uptake in response to heavy rainfall, we conducted a field experiment in which heavy rainfall occurring in middle and late growing season were imposed on plots with three experimental plant communities of graminoids, shrubs and their combination, respectively. We hypothesized that: (1) Heavy rainfalls would suppress CH_4 uptake due to reduced diffusivity and methanotrophs activity, regardless of seasonal timing, (2) Heavy rainfall occurring in middle growing season with high air temperatures may cause less saturated soil conditions, thus CH_4 uptake is likely to be less decreased by middle heavy rainfall than late heavy rainfall, and (3) Plant community composition would adjust CH_4 uptake in response to heavy rainfalls though soil moisture, inorganic content, aboveground biomass and methanotrophs activities.

Materials and methods

Study site

We carried out the study at the Research Station of Animal Ecology (44°18′ N, 116°45′ E 1079 m.a.s.l) in a semiarid grassland of Inner Mongolia Autonomous Region, China. The study site has a temperate continental semi-arid climate, of which the mean annual precipitation (1953 to 2017) is 281 mm and the mean annual temperature is 2.5°C. The plant species in the study region is mainly dominated by xeric rhizomatous grasses, needle grasses and perennial forbs such as *Leymus chinensis, Stipa grandis* and *Medicago falcata*. The soil type in this experimental region is classified as chestnut soil consisting of 60% sand, 18% clay and 17% silt.

Experiment design

The experiment was began in 2012. In this study, we reported the data measured in 2021. According to the statistical analysis of

~60-year (1953–2012) historical meteorological data provided by The Xilin Gol League Meteorological Administration, the longest continuous rainfall period of daily precipitation (≥ 3 mm) was 20 days during the growing season. The total effective precipitation was calculated over all 20 days periods, which was 250 mm. Thus, heavy rainfall was defined as 250 mm rainfall over 20 d in this study (12.5 mm d^{-1}) (Hao et al., 2017). We used a two-way split-plot experiment design to study the effect of heavy rainfall on CH_4 uptake joint control of seasonal timing and plant composition. The main treatment had 9 plots and each main plot was made up of 3 sub-plots, thus there were total 27 sub-plots in heavy rainfall treatments experiment (Supplementary Figure S1). Specifically, three heavy rainfall treatments were set up in the main plots with three replicates: ambient control, mid-stage heavy rainfall (HR-mid, 15 July-5 August) and late-stage heavy rainfall (HR-late, 15 August-5 September), respectively. Three plant community compositions were set up in the sub-plots: graminoid (*Leymus chinensis* and *Stipa grandis*), shrub (*Caragana microphylla* and *Artemisia frigida*) and their mixture. Plant seeds of dominant local species were cultivated at the start of the study in early May 2012. The total coverage of graminoids, shrub and mixture community were 70, 80, and 75%, respectively.

Twenty-seven 2 m × 2 m sub-plots were established with 1-m intervals between sub-plots. The ambient control sub-plots remained uncovered year-round. Heavy rainfall treatment sub-plots were covered with 27 m^2 rainout shelters (4.5 m × 6 m, height 3 m) to prevent natural rainfall and greenhouse effect during the treatment periods. The rainout shelters were made of transparent polyester fiber material to ensure no significant shading. Non-target plant seedlings in each subplot were weekly removed to maintain fixed plant community composition during the entire growing season.

CH_4 flux and soil water content measurements

Soil water content (SWC) and CH_4 fluxes were measured three times monthly during the growing season in 2021. Time domain reflectometry (TDR 300 Soil Moisture Meter) with 20 cm probe was used to record SWC. CH_4 fluxes were measured by laser-based fast greenhouse gas analyzer with an in-house closed chamber. The data collection frequency of 1 Hz was utilized to measure CH_4 fluxes (Kang et al., 2018). The volume of cube chamber is 1.25×10^5 cm^3, which was equipped with two electric fans in the center of the chamber ceiling to mix air concentration. Laser-based fast greenhouse gas analyzer has two 20-m rubber internal pipes, which were used to connect with the closed chamber through two 2-cm diameter holes on top of the chamber. Two pipes were used to transport gas from the greenhouse gas analyzer to the chamber and return from the chamber to the analyzer. Each subplot had a stainless frame (length × width × height = 50 cm × 50 cm × 10 cm) with 2 cm wide water groove. Each frame was installed and inserted 7 cm deep in soil and retained 3 cm above ground. Enough water should be put into the grooves of frames to guarantee gas tightness before mounting the chamber on the frame. Gas sampling area in each sub-plot was measured between 9:00 am and 10:00 am local time. In each sampling area, the gas in chamber was measured for 10 min, and the chamber should be opened for 2 min before the next measurement. We calculated CH_4 flux from the linear slope.

$$Fc = \frac{dc}{dt} \times \frac{M}{V_0} \times \frac{P}{P_0} \times \frac{T_0}{T} \times H$$

where F is the CH_4 flux rate [mg/(m^2·h)]; dc / dt is the cumulative growth rate of CH_4; M and P represent the molar mass of CH_4 (g/mol) and the air pressure (Pa), respectively; V_0 and P_0 represent the standard molar volume (22.41 m^3/mol) and standard air pressure (101,325 Pa), respectively; T and T_0 represent the absolute temperature inside the chamber (oK) and absolute temperature (oK), respectively; and H is the effective height of the chamber (m).

Above-ground biomass measurement

Harvest method was used to measure above-ground biomass (AGB). We harvested all aboveground living plant tissues in a 50 cm × 50 cm quadrat of each sub-plot on September 21st, 2021. All plant tissues of each quadrat were put in the oven and dried at 65°C until they had constant weight.

Soil property measurement

Three soil cores were taken in 20 cm deep in each plot using an auger (2.5 cm in diameter) on September 21st, 2021. Roots and stones of soil were removed from three core sets and homogenized by 2 mm sieves. The extract was a mixture solution of 10 g fresh soil sample and 40 ml 0.5 M K_2SO_4 solution, which were shaken for 30 min in shaker. After mixing well, $NH_4{}^+$-N and $NO_3{}^-$-N concentration of soil sample were detected by a continuous flow automatic ion analyzer (SEAL Analytical GmbH, Norderstedt, Germany) (Wachendorf et al., 2008).

DNA extraction and qPCR

DNA were extracted from fresh soil of 0.5 g by Power Soil DNA Isolation Kit (MOBIO Laboratories, United States) according to the specification information. DNA quality of soil was assessed by NanoDrop 2000 UV–Vis spectrophotometer (Thermo Scientific, Wilmington, Delaware, USA). The methanotrophic *pmoA* gene abundance was determined by quantitative polymerase chain reaction (qPCR) using Eppendorf Masterpiece realplex sequence detection system (Applied Biosystems 7500/7600). Standard curves were created with plasmid DNA in ten-fold serial dilutions. The primer sets were used for *pmoA*: 5′-GGNGACTGGGACTTCTGG-3′ and 5′-CCGGMGCAACGTCYTTACC-3′. The 20 μL qPCR reaction consisted of 1 μL DNA template, 0.2 μL of front and back primer, 10.4 μL mixture solution of ROX and Takara SYBR®Premix Ex Taq ™ (Perfect RealTime) and 8.4 μL sterile water. After the reaction solution has been thoroughly mixed, the hole in the 96-well plate was filled with 20 μL qPCR reaction solution. Additionally, the contamination was detected by adding 19 μL qPCR reaction solution into the hole of 96-well plate without DNA template during the experiment. The sequential reaction conditions for the *pmoA* gene were set as: an initial denaturation at 95°C for 30 s, followed by 40 cycles at 95°C for 30 s, 60°C for 45 s, and 68°C for 45 s, with a final extension at 80°C for 30 s.

Statistical analyses

We conducted Duncan's multiple comparison to test differences of heavy rainfall with seasonal timing, plant composition and their interaction effects on variables including CH_4 uptake, soil water content, aboveground biomass, *pmoA* abundance, NH_4^+-N and NO_3^--N content. Mixed-effects models were conducted using the NLME package in R v.3.4.4 (R Core Team, 2018) to compare the effects of middle and late growing season heavy rainfall, plant composition, and the interaction effects of plant composition and heavy rainfall on the above variables, respectively. Structural equation model (SEM) analyzes were performed using the piecewise SEM package to explore direct and indirect impacts of heavy rainfall on CH_4 uptake (Domeignoz-Horta et al., 2020). The most variation can explain by this model, including low Akaike Information Criterion (AIC), a nonsignificant Chi-squared test ($p > 0.05$) and high Comparative Fit Index ($CFI > 0.9$).

Result

Seasonal dynamics and response of soil moisture content to heavy rainfalls

Total growing season precipitation (GSP) of control, HR-mid and HR-late were 351 mm, 513.16 mm, and 559.02 mm, respectively. Regardless of seasonal timing, SWC was significantly increased by heavy rainfalls in all three communities ($p = 0.01$ and <0.0001 for HR-mid and HR-late, respectively; Figure 1 and Table 1). Overall, SWC in HR-late seems slightly higher than that in HR-mid (Figures 1E,F; Supplementary Figure S2). Plant community composition had no significant effects on SWC ($p = 0.54$ for composition, Table 1). However, the SWC in graminoid community was slightly less increased by heavy rainfalls compared with shrub and mixture communities (Supplementary Figure S2).

Response of CH_4 uptake to heavy rainfalls

Over the growing season, averaged CH_4 uptake significantly decreased by HR-mid ($p = 0.03$) and HR-late ($p < 0.0001$) in all three communities (Figures 2E,F). The reductions were mainly occurred during the period of the heavy rainfalls. Relatively, HR-late had larger negatively effects on CH_4 uptake than HR-mid. There were significant differences of CH_4 uptake among three communities with the least CH_4 uptake in shrub community ($p < 0.0001$, Table 1; Supplementary Figure S3). HR-late effects on CH_4 uptake depended on plant composition ($p = 0.03$ for HR-late × Composition), with the least decreased CH_4 uptake in graminoid community than that in other two communities. There was also a marginally significant interaction between HR-mid × Composition ($p = 0.08$) on CH_4 uptake, but the effects of HR-mid on CH_4 uptake were similar across three communities. Collectively, negative effects of heavy rainfalls on CH_4 uptake modulated by seasonal timing and plant community composition.

Response of *pmoA* abundance, AGB, NH_4^+-N and NO_3^--N to heavy rainfalls

Similarly, heavy rainfalls effects on soil inorganic N content and *pmoA* abundance were changed with seasonal timing and plant community composition. Both two heavy rainfalls significantly declined *pmoA* abundance for three communities but the effects were larger in mixture community than in other two communities ($p = 0.01$ and 0.0001 for HR-mid × Composition and HR-late × Composition) (Figure 3A; Table 1). Regardless of plant composition, HR-mid and HR-late unchanged and significantly increased AGB, respectively (Figure 3B; Table 1), NH_4^+-N was significantly increased by HR-mid but significantly declined by HR-late in three communities (Figure 3C). Similarly, HR-mid significantly increased NO_3^--N content (Figure 3D; Table 1), mainly in graminoid and mixture communities. In contrast, HR-late had little effects on NO_3^--N content.

The influence of abiotic and biotic factors on CH_4 uptake

Structural equation model showed that SWC had directly negative impacts on CH_4 uptake and *pmoA* abundance under two heavy rainfalls. Additionally, CH_4 uptake negatively correlated with AGB under two heavy rainfalls. However, CH_4 uptake positively correlated with *pmoA* abundance in HR-late but not in HR-mid. SWC had significantly positive impact on NH_4^+ under HR-mid, while opposite impact between SWC and NH_4^+ was found in HR-late. Moreover, NH_4^+ positively correlated with *pmoA* abundance only in HR-late. NO_3^- had no significant relationships with CH_4 uptake (Figure 4). In short, heavy rainfalls with different seasonal timing decreased CH_4 uptake through different pathways.

Discussion

Understanding extreme precipitation scenario on CH_4 uptake has important implications for predicting future global climate changes and terrestrial C cycling. To explore how seasonal timing and plant composition affected CH_4 uptake in response to heavy rainfalls, we conducted a manipulative experiment in a semiarid grassland of Inner Mongolia, China. In this study, we identified CH_4 uptake in response to heavy rainfall are regulated by independent and especially interactive effects of heavy rainfall timing and plant composition. Our results demonstrate that seasonal timing strongly controls size and pathway of negative effects of heavy rainfall on CH_4 uptake and importantly the regulating effects of plant composition on CH_4 uptake response to heavy rainfall via soil water content, *pmoA* abundance, NH_4^+-N content and AGB.

Heavy rainfalls decrease CH_4 uptake

CH_4 uptake was significantly decreased by heavy rainfalls, regardless of seasonal timing and plant community composition in our study (Figure 2). Previous study showed that soil moisture and CH_4 uptake had a hump-shaped relationship, where the optimum

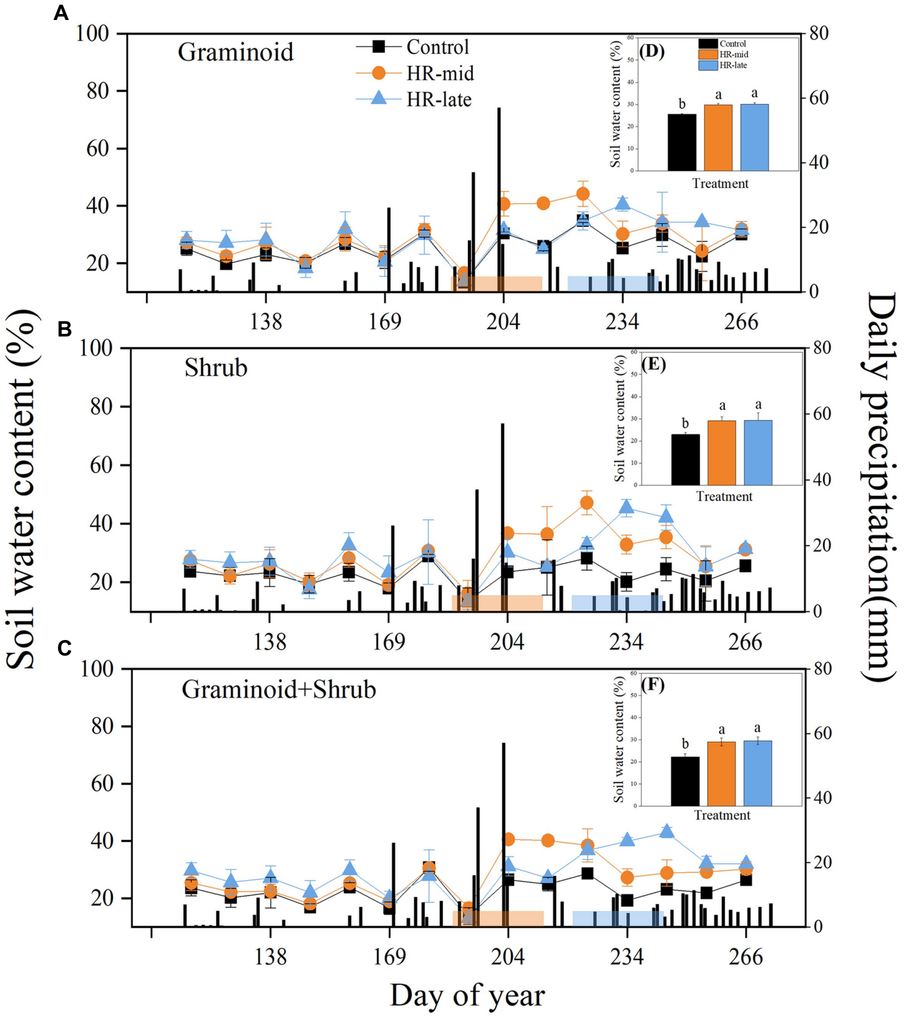

FIGURE 1
Seasonal dynamic and mean of soil water content under heavy rainfall treatments in graminoid **(A,D)**, shrub **(B,E)**, and graminoid +shrub **(C,F)** plots. Different letters above bars in d, e and f indicate significant difference among treatments at $p \leq 0.05$. The orange and blue shaded regions in a–c indicate the periods of the HR-mid (heavy rain imposed in middle of the growing season, orange line) and HR-late (heavy rainfall imposed late in the growing season, blue line) treatments, respectively. Error bars show one standard error of the mean.

TABLE 1 ***p*-Value from mixed-effect model analyzes of HR-mid and HR-late, community composition and their interactions on soil water content (SWC), aboveground biomass (AGB), CH_4 uptake, abundance of *pmoA*, and content of NH_4^+-N and NO_3^--N.**

Fixed effect	DF		SWC	AGB	CH_4 uptake	*pmoA*	NH_4^+-N	NO_3^--N
	Num	Den						
HR-mid	1	24	**0.01**	0.44	**0.04**	**<0.0001**	**<0.0001**	**0.04**
HR-late	1	24	**<0.0001**	**0.05**	**<0.0001**	**<0.0001**	**0.004**	0.77
Composition	2	24	0.27	**<0.0001**	**<0.0001**	**0.001**	**0.03**	0.21
HR-mid × Composition	2	24	0.85	0.85	0.08	**0.01**	0.22	0.10
HR-late × Composition	2	24	0.49	0.95	**0.03**	**0.0001**	0.58	0.96

p-Values in bold are statistically significant to an alpha value of 0.05.

moisture is 10 % -12 % for highest CH_4 uptake in a semiarid and arid soils (Dijkstra et al., 2011; Li et al., 2016; Yue et al., 2022). Moderate soil moisture could significantly promote CH_4 uptake, which could be significantly inhibited by too- low or too- high soil moisture (Van den Pol-van Dasselaar et al., 1998; Dijkstra et al., 2011). In our study, SWC were above 12% in all treatments throughout the growing season. High soil moisture induced by heavy rainfalls would cause anaerobic soil conditions, low soil oxygen (O_2) concentrations and CH_4 diffusion (Figure 1). Additionally, *pmoA* abundance decreased in both two heavy rainfalls (Figure 3A). Taken together, these results

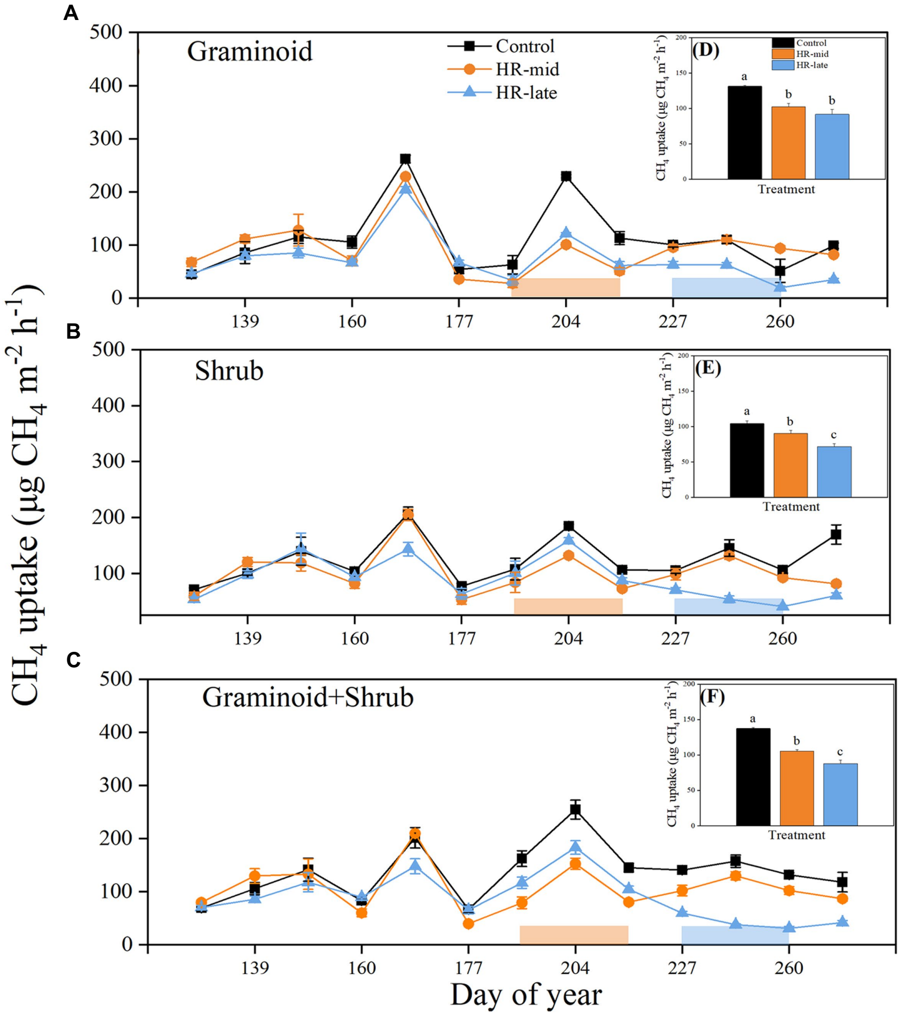

FIGURE 2
Seasonal dynamic and mean of CH_4 uptake under heavy rainfall treatments in graminoid **(A,D)**, shrub **(B,E)**, and graminoid +shrub **(C,F)** plots. Different letters above bars in d, e and f indicate significant difference among treatments at $p \leq 0.05$. The orange and blue shaded regions in a–c indicate the periods of the HR-mid (heavy rain imposed in middle of the growing season, orange line) and HR-late (heavy rainfall imposed late in the growing season, blue line) treatments, respectively. Error bars show one standard error of the mean.

suggested that experimental heavy rainfalls continuously decreased CH_4 diffusivity and O_2 availability and thus inhibited the activity of methanotrophs, supporting our first hypothesis. As a result, SWC showed negatively relationship with CH_4 uptake under two heavy rainfalls in our study (Figure 4).

Magnitude and pathways of heavy rainfall effects on CH_4 uptake depend on seasonal timing

Although two heavy rainfalls had negative effects on CH_4 uptake, the effect magnitude varied with seasonal timing. Consistent with the second hypothesis, CH_4 uptake is less decreased by HR-mid than HR-late in all three communities (Figure 2). This may be because HR-mid received less precipitation than HR-late (513.16 mm vs. 559.02 mm, Figure 1). In addition, higher air temperatures during the period of HR-mid would induce larger evapotranspiration. As a result, HR-mid caused less saturated soil conditions than HR-mid, which was reflected by slightly lower SWC in HR-mid than in HR-late (Figure 1F). As discussed above, SWC had negative impacts on CH_4 uptake in our study. Thus, lower SWC and corresponding less saturated soil conditions under HR-mid induced less reduction in CH_4 uptake.

Structural equation model showed that SWC and resultant anaerobic conditions were main controller of CH_4 uptake (Wei et al., 2015; Zhou et al., 2021). AGB also had direct negative effects on CH_4 uptake under both heavy rainfalls (Figure 4B). Previous studies showed similar trends that increased AGB may contribute to increasing soil water-holding capacity, maintaining high soil moisture and inhibiting soil substrate availability. As a result, methanotrophs activities and CH_4 oxidation in soil were inhibited (Robson et al., 2007; Zhang et al., 2012; Tang et al., 2018). Besides, high SWC directly and indirectly inhibited *pmoA* abundance through decreasing NH_4^+-N content, ultimately, suppressing CH_4 uptake in HR-late. CH_4 was oxidated by methanotroph, thus, it is not surprising that low *pmoA*

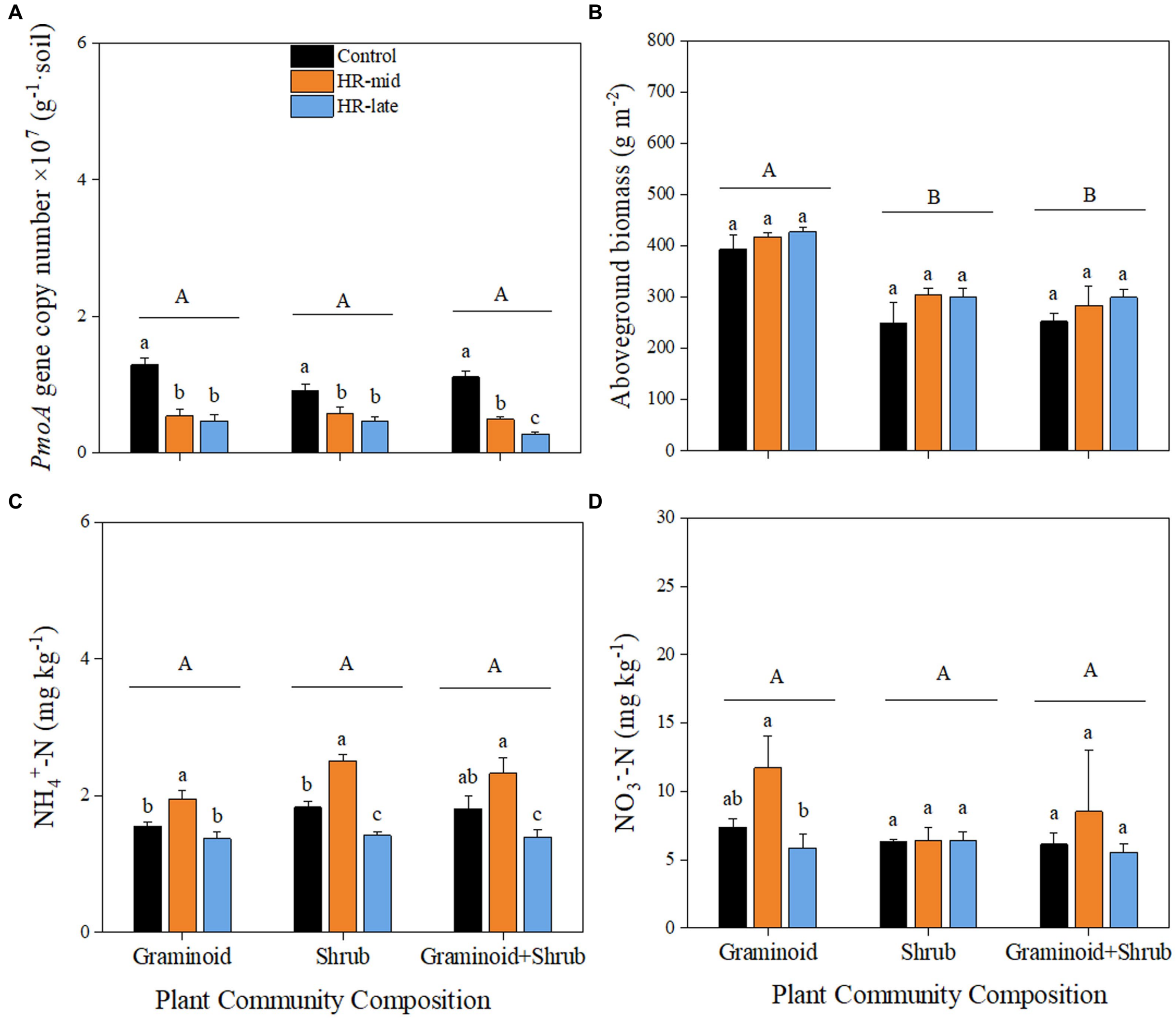

FIGURE 3
Responses of *pmoA* abundance **(A)**, above-ground biomass (AGB) **(B)**, NH_4^+-N **(C)** and NO_3^--N **(D)** to heavy rainfall treatments in three plant communities. Different letters above bars indicate significant difference among treatments at $p \leq 0.05$.

abundance would limit CH_4 uptake (Degelmann et al., 2010; Zhang et al., 2019; Kaupper et al., 2021;). Previous studies have found that the process of methanotrophs using CH_4 as both an energy and carbon source generally requires soil NH_4^+-N as N source (Rigler and Zechmeister-Boltenstern, 1999; Schimel and Weintraub, 2003; Bürgmann, 2011), resulting in decreased soil NH_4^+-N content can inhibit methanotrophs activities and *pmoA* abundance (Le Mer and Roger, 2001; Xu and Inubushi, 2007; Yue et al., 2016, 2022). However, some findings of other studies suggest that decreased NH_4^+-N availability in soils can promote CH_4 oxidation as higher NH_4^+-N can replace CH_4 to be oxidized by methanotroph (Song et al., 2020; Yue et al., 2022). Therefore, the net effects of NH_4^+-N on CH_4 uptake depend on the relative size of the two processes. Nevertheless, the mechanism was not suitable for HR-mid. Similar to HR-late, HR-mid declined *pmoA* abundance, however, it had no significant correlation with CH_4 uptake. This may be because increased NH_4^+-N content under HR-mid leaded to the oxidation of NH_4^+-N instead of CH_4 by methanotrophs, thus resulting in the most decreased CH_4 uptake in mixture community, although the largest reduction of *pmoA* abundance were found in graminoid community. As NO_3^--N content was little impacted by heavy rainfalls, it had no effects on CH_4 uptake in this study. Our results are consistent with the finding that soil NO_3^--N concentrations and CH_4 uptake had no correlation in a subtropical plantation forest ecosystem (Wang et al., 2014). Taken together, our study proved that the pathways underlying CH_4 uptake in response to heavy rainfall depend on seasonal timing.

Plant composition regulates responses of CH_4 uptake to heavy rainfalls

Multiple lines of evidence proved that plant composition is a controlling factor in regulation of soil CH_4 oxidation. CH_4 uptake would increase with enhanced plant diversity as high plant biodiversity promoted microbial activities (Altor and Mitsch, 2006; Bouchard et al., 2007; Schultz et al., 2011; Hassan et al., 2019). Niklaus et al. (2016) showed that the presence of legume plants inhibited soil CH_4 oxidation capacity due to decline in plant N acquisition. Likewise, CH_4

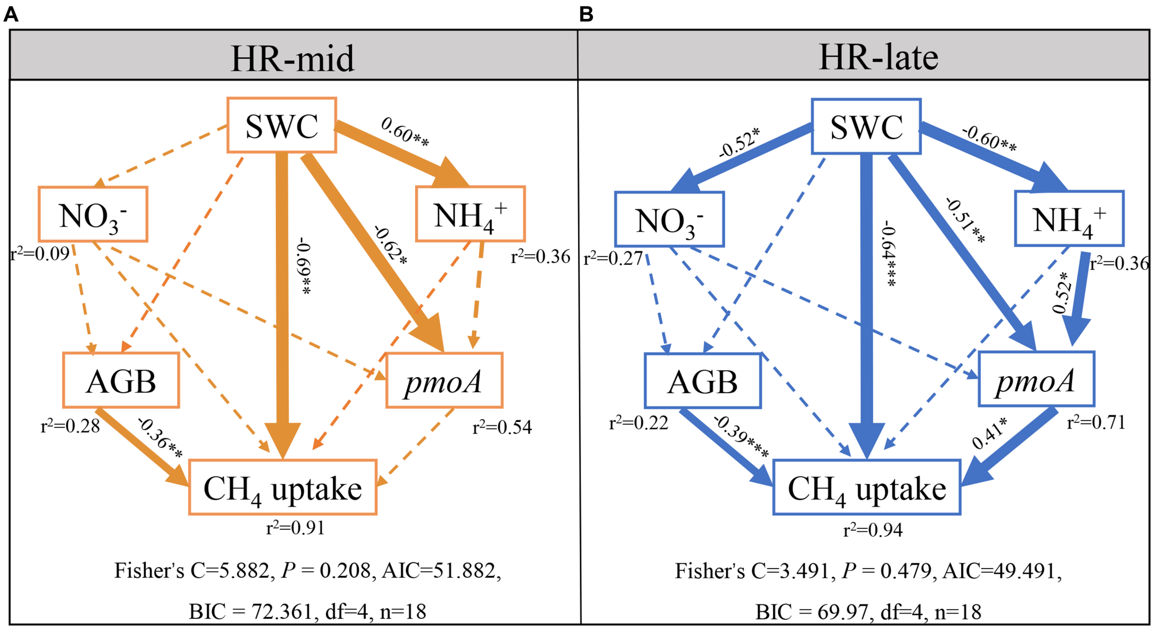

FIGURE 4
Structural equation models analysis of the direct and indirect effects of soil, microbe and plant variables on CH_4 uptakes under HR-mid **(A)** and HR-late **(B)** treatment. SWC: soil water content; AGB: aboveground, biomass; NH_4^+ and NO_3^-: soil ammonium and nitrate content. Solid and dashed lines indicate significant ($p \leq 0.05$) and nonsignificant ($p > 0.05$) relationships, respectively. Width of the line is proportional to the strength of path coefficients expressed by the numbers adjacent on lines. r^2 values denote the proportion of variance explained for each variable.

uptake had significant differences among three communities, where CH_4 uptake was less in shrub community than in graminoid and mixture communities in our study (Supplementary Figure S3; Table 1). It may be because shrubs had harmful effects on methanotrophs activities and CH_4 uptake through the chemistry of root exudates and N competition among plants and microbes (Zak et al., 2003; Hassan et al., 2019).

Importantly, plant composition regulated CH_4 uptake to heavy rainfalls, reflected by significant interactions between plant composition and heavy rainfalls (Table 1). Negative effects of HR-late on CH_4 uptake was the least in graminoid community than in other two communities. The potential explanation may be that HR-late had larger positive effects on SWC and AGB and larger negative effects on *pmoA* abundance and NH_4^+-N content in shrub and mixture communities (Figures 1F, 3A), although the interactions were only significant on SWC and *pmoA* abundance. This finding supports the third hypothesis that plant composition would regulate CH_4 uptake in response to heavy rainfalls though soil moisture, inorganic content, aboveground biomass and methanotrophs activities. Although previous studies proved that plant communities with higher-diversity are less negatively affected by floods (Gattringer et al., 2017; Wright et al., 2017), the least increase in SWC, AGB and the least decrease NH_4^+-N content were observed in graminoid community under HR-late. Previous studies have reported that precipitation infiltration and evaporation rate vary with plant species composition. Evaporation and transpiration can remove water from shallow soil layers after rainfall and thus decrease soil moisture (Coughenour, 1984; Weltzin et al., 2003; Springer et al., 2006; MacIvor and Lundholm, 2011; Moore et al., 2022). Graminoids are shallower rooting with deeper and faster infiltration and faster evaporation rate, leading to lower soil moisture and the duration of soil saturation in graminoid community (Springer et al., 2006). Therefore, HR-late had the least negative effect on CH_4 uptake in graminoid community under HR-late. Overall, SWC, *pmoA* abundance and NH_4^+-N content had the least reduction in graminoid, leading to the least decreased CH_4 uptake in HR-late. However, HR-mid had similar negative effects on CH_4 uptake across three communities although the interaction between HR-mid and plant composition on CH_4 uptake was statistically significant ($p = 0.08$). Therefore, we concluded that CH_4 uptake in response to climate extremes jointly controlled by interaction of seasonal timing and plant composition.

Conclusion

Our results highlight the vital role of seasonal timing and plant composition in regulating heavy rainfall effects on CH_4 uptake. Specifically, although both heavy rainfalls reduced CH_4 sink, late heavy rainfall had larger negative effects than middle heavy rainfall. This is because decreased NH_4^+-N induced by late heavy rainfall had negative effects on *pomA* abundance and further suppressing CH_4 sink, in addition to directly negative effects of high soil moisture induced by heavy rainfall. Besides, shrub community had lower CH_4 uptake than graminoid and mixture communities. Moreover, late heavy rainfall had the least negative effects on CH_4 uptake in graminoid communities than in other two communities, indicating that climate extremes-driven shifts in dominant species would in turn alter ecosystem feedbacks. Therefore, to improve prediction accuracy of terrestrial ecosystems feedbacks to climate changes, we encourage future studies to further quantify the interactive effects between seasonal timing and plant on regulating carbon cycling in response to climate extremes.

Data availability statement

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

Author contributions

LL designed the experiments. ZZ and FW performed the experiments. ZZ and LL analyzed the data. ZZ wrote the manuscript. ZZ, FW, CL, SG, YX, YL, RQ, ML, SX, XC, YW, YH, and LL provided the editorial advice. All authors contributed to the article and approved the submitted version.

Funding

This project was funded by the funds for the National Natural Science Foundation of China (42041005 and 32101313), China Postdoctoral Science Foundation (2021M693138), and the Fundamental Research Funds for the Central Universities (E1E40607 and E1E40511).

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.

Publisher's note

Supplementary material

The Supplementary material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2023.1149595/full#supplementary-material

References

Altor, A., and Mitsch, W. (2006). Methane flux from created riparian marshes: relationship to intermittent versus continuous inundation and emergent macrophytes. *Ecol. Eng.* 28, 224–234. doi: 10.1016/j.ecoleng.2006.06.006

Aronson, E. L., Goulden, M. L., and Allison, S. D. (2019). Greenhouse gas fluxes under drought and nitrogen addition in a Southern California grassland. *Soil Biol. Biochem.* 131, 19–27. doi: 10.1016/j.soilbio.2018.12.010

Bai, J., Gao, H., Xiao, R., Wang, J., and Huang, C. (2012). A review of soil nitrogen mineralization as affected by water and salt in coastal wetlands: issues and methods. *CLEAN–Soil Air Water* 40, 1099–1105. doi: 10.1002/clen.201200055

Borken, W., and Matzner, E. (2009). Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. *Glob. Chang. Biol.* 15, 808–824. doi: 10.1111/j.1365-2486.2008.01681.x

Bouchard, V., Frey, S., Gilbert, J., and Reed, S. (2007). Effects of macrophyte functional group richness on emergent freshwater functions. *Ecology* 88, 2903–2914. doi: 10.1890/06-1144.1

Bürgmann, H. (2011). "Methane oxidation (aerobic)" in *Encyclopedia of Geobiology*. eds. J. Reitner and V. Thiel (Amsterdam: Springer)

Cabrera, M. L., and Kissel, D. E. (1988). Evaluation of a method to predict nitrogen mineralized from soil organic matter under field conditions. *Soil Sci. Soc. Am. J.* 52, 1027–1031. doi: 10.2136/sssaj1988.03615995005200040024x

Chen, W. W., Zheng, X. H., Chen, Q., Wolf', B., Butterbach-Bahl, K., Bruggemann, N., et al. (2013). Effects of increasing precipitation and nitrogen deposition on CH_4 and N_2O fluxes and ecosystem respiration in a degraded steppe in Inner Mongolia, China. *Geoderma* 192, 335–340. doi: 10.1016/j.geoderma.2012.08.018

Chen, H., Zhu, Q., Peng, C., Wu, N., Wang, Y., Fang, X., et al. (2013). The impacts of climate change and human activities on biogeochemical cycles on the Qinghai-tibetan plateau. *Glob. Chang. Biol.* 19, 2940–2955. doi: 10.1111/gcb.12277

Coughenour, M. B. (1984). A mechanistic simulation analysis of water use, leaf angles, and grazing in east African graminoids. *Ecol. Model.* 26, 203–230. doi: 10.1016/0304-3800(84)90070-X

Cregger, M. A., McDowell, N. G., Pangle, R. E., Pockman, W. T., and Classen, A. T. (2014). The impact of precipitation change on nitrogen cycling in a semi-arid ecosystem. *Funct. Ecol.* 28, 1534–1544. doi: 10.1111/1365-2435.12282

Curry, C. L. (2007). Modeling the soil consumption of atmospheric methane at the global scale. *Glob. Biogeochem. Cycles* 21:GB4012. doi: 10.1029/2006GB002818

Dai, Y., Zhen, W., Xie, S., and Liu, Y. (2015). Methanotrophic community abundance and composition in plateau soils with different plant species and plantation ways. *Appl. Microbiol. Biotechnol.* 99, 9237–9244. doi: 10.1007/s00253-015-6782-z

Degelmann, D. M., Borken, W., Drake, H. L., and Kolb, S. (2010). Different atmospheric methane-oxidizing communities in European beech and Norway spruce soils. *Appl. Environ. Microbiol.* 76, 3228–3235. doi: 10.1128/AEM.02730-09

Dijkstra, F. A., Morgan, J. A., Follett, R. F., and Lecain, D. R. (2013). Climate change reduces the net sink of CH_4 and N_2O in a semiarid grassland. *Glob. Chang. Biol.* 19, 1816–1826. doi: 10.1111/gcb.12182

Dijkstra, F. A., Morgan, J. A., Von Fischer, J. C., and Follett, R. F. (2011). Elevated CO_2 and warming effects on CH_4 uptake in a semiarid grassland below optimum soil moisture. *J. Geophys. Res. Atmos.* 116, 79–89. doi: 10.1029/2010JG001288

Domeignoz-Horta, L. A., Pold, G., Liu, X. J. A., Frey, S. D., Melillo, J. M., and DeAngelis, K. M. (2020). Microbial diversity drives carbon use efficiency in a model soil. *Nat. Commun.* 11, 3684–3610. doi: 10.1038/s41467-020-17502-z

Elango, N. A., Radhakrishnan, R., Froland, W. A., Wallar, B. J., Earhart, C. A., Lipscomb, J. D., et al. (1997). Crystal structure of the hydroxylase component of methane monooxygenase from Methylosinus trichosporium OB3b. *Protein Sci.* 6, 556–568. doi: 10.1002/pro.5560060305

Fest, B., Wardlaw, T., Livesley, S. J., Duff, T. J., and Arndt, S. K. (2015). Changes in soil moisture drive soil methane uptake along a fire regeneration chronosequence in a eucalypt forest landscape. *Glob. Chang. Biol.* 21, 4250–4264. doi: 10.1111/gcb.13003

Fischer, E. M., and Knutti, R. (2016). Observed heavy precipitation increase confirms theory and early models. *Nat. Clim. Change* 6, 986–991. doi: 10.1038/NCLIMATE3110

Gattringer, J. P., Donath, T. W., Eckstein, R. L., Ludewig, K., Otte, A., and Harvolk-Schoning, S. (2017). Flooding tolerance of four floodplain meadow species depends on age. *PLoS One* 12:e0176869. doi: 10.1371/journal.pone.0176869

Hao, Y. B., Zhou, C. T., Liu, W. J., Li, L. F., Kang, X. M., Jiang, L. L., et al. (2017). Aboveground net primary productivity and carbon balance remain stable under extreme precipitation events in a semiarid steppe ecosystem. *Agric. For. Meteorol.* 240-241, 1–9. doi: 10.1016/j.agrformet.2017.03.006

Hassan, M. K., McInroy, J. A., and Kloepper, J. W. (2019). The interactions of rhizodeposits with plant growth-promoting rhizobacteria in the rhizosphere: a review. *Agriculture* 9:142. doi: 10.3390/agriculture9070142

Hüppi, R., Horváth, L., Dezső, J., Puhl-Rezsek, M., and Six, J. (2022). Soil nitrous oxide emission and methane exchange from diversified cropping Systems in Pannonian Region. *Front. Environ. Sci.* 10:857625. doi: 10.3389/fenvs.2022.857625

IPCC, (2021). *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, England pp. 3–32.

Jiang, Z., Song, J., Li, L., Chen, W., Wang, Z., and Wang, J. (2012). Extreme climate events in China: IPCC-AR4 model evaluation and projection [J]. *Clim. Chang.* 110, 385–401. doi: 10.1007/s10584-011-0090-0

Kang, X., Yan, L., Cui, L., Zhang, X., Hao, Y., Wu, H., et al. (2018). Reduced carbon dioxide sink and methane source under extreme drought condition in an alpine peatland. *Sustainability* 10:4285. doi: 10.3390/su10114285

Kaupper, T., Mendes, L. W., Lee, H. J., Mo, Y., Poehlein, A., and Jia, Z. (2021). When the going gets tough: emergence of a complex methane-driven interaction network during recovery from desiccation-rewetting. *Soil Biol. Biochem.* 153:108109. doi: 10.1016/j.soilbio.2020.108109

Le Mer, J., and Roger, P. (2001). Production, oxidation, emission and consumption of methane by soils: a review. *Eur. J. Soil Biol.* 37, 25–50. doi: 10.1016/S1164-5563(01)01067-6

Li, L., Fan, W., Kang, X., Wang, Y., Cui, X., Xu, C., et al. (2016). Responses of greenhouse gas fluxes to climate extremes in a semiarid grassland. *Atmos. Environ.* 142, 32–42. doi: 10.1016/j.atmosenv.2016.07.039

Li, L., Hao, Y., Zheng, Z., Wang, W., Biederman, J. A., Wang, Y., et al. (2022). Heavy rainfall in peak growing season had larger effects on soil nitrogen flux and pool than in the late season in a semiarid grassland. *Agric. Ecosyst. Environ.* 326:107785. doi: 10.1016/j.agee.2021.107785

Li, L., Zheng, Z., Biederman, J. A., Xu, C., Xu, Z., Che, R., et al. (2019). Ecological responses to heavy rainfall depend on seasonal timing and multi-year recurrence. *New Phytol.* 223, 647–660. doi: 10.1111/nph.15832

Liebner, S., Ganzert, L., Kiss, A., Yang, S., Wagner, D., and Svenning, M. M. (2015). Shifts in methanogenic community composition and methane fluxes along the degradation of discontinuous permafrost. *Front. Microbiol.* 6:356. doi: 10.3389/fmicb.2015.00356

Liptzin, D., Silver, W. L., and Detto, M. (2011). Temporal dynamics in soil oxygen and greenhouse gases in two humid tropical forests. *Ecosystems* 14, 171–182. doi: 10.1007/s10021-010-9402-x

MacIvor, J. S., and Lundholm, J. (2011). Performance evaluation of native plants suited to extensive green roof conditions in a maritime climate. *Ecol. Eng.* 37, 407–417. doi: 10.1016/j.ecoleng.2010.10.004

Martins, C. S., Nazaries, L., Delgado-Baquerizo, M., Macdonald, C. A., Anderson, I. C., and Singh, B. K. (2021). Rainfall frequency and soil water availability regulate soil methane and nitrous oxide fluxes from a native forest exposed to elevated carbon dioxide. *Funct. Ecol.* 35, 1833–1847.

Moore, P. A., Pypker, T. G., Hribljan, J. A., Chimner, R. A., and Waddington, J. M. (2022). Examining the peatland shrubification-evapotranspiration feedback following multi-decadal water table manipulation. *Hydrol. Process.* 36:e14719. doi: 10.1002/hyp.14719

Niklaus, P. A., Le Roux, X., Poly, F., Buchmann, N., Scherer-Lorenzen, M., Weigelt, A., et al. (2016). Plant species diversity affects soil–atmosphere fluxes of methane and nitrous oxide. *Oecologia* 181, 919–930. doi: 10.1007/s00442-016-3611-8

Otto, F. E., van der Wiel, K., van Oldenborgh, G. J., Philip, S., Kew, S. F., and Uhe, P. (2018). Climate change increases the probability of heavy rains in northern England/southern Scotland like those of storm Desmond-a real-time event attribution revisited [J]. *Environ. Res. Lett.* 13:024006. doi: 10.1088/1748-9326/aa9663

Post, A. K., and Knapp, A. K. (2020). The importance of extreme rainfall events and their timing in a semi-arid grassland. *J. Ecol.* 108, 2431–2443. doi: 10.1111/1365-2745.13478

Rigler, E., and Zechmeister-Boltenstern, S. (1999). Oxidation of ethylene and methane in forest soils-effect of CO_2 and mineral nitrogen. *Geoderma* 90, 147–159. doi: 10.1016/S0016-7061(98)00099-8

Robson, T. M., Lavorel, S., Clement, J. C., and Rouxc, X. L. (2007). Neglect of mowing and manuring leads to slower nitrogen cycling in subalpine grasslands. *Soil Biol. Biochem.* 39, 930–941. doi: 10.1016/j.soilbio.2006.11.004

R Core Team. (2018). R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing. [WWW document] URL https://www.r-project.org/

Schimel, J. P., and Weintraub, M. N. (2003). The implications of exoenzyme activity on microbial carbon and nitrogen limitation in soil: a theoretical model. *Soil Biol. Biochem.* 35, 549–563. doi: 10.1016/S0016-7061(98)00099-8

Schnell, S., and King, G. M. (1994). Mechanistic analysis of ammonium inhibition of atmospheric methane consumption in Forest soils. *Appl. Environ. Microbiol.* 60, 3514–3521. doi: 10.1128/aem.60.10.3514-3521.1994

Schultz, R., Andrews, S., O'Reilly, L., Bouchard, V., and Frey, S. (2011). Plant community composition more predictive than diversity of carbon cycling in freshwater wetlands. *Wetlands* 31, 965–977. doi: 10.1007/s13157-011-0211-6

Song, W. M., Chen, S. P., Zhou, Y. D., and Lin, G. H. (2020). Rainfall amount and timing jointly regulate the responses of soil nitrogen transformation processes to rainfall increase in an arid desert ecosystem. *Geoderma* 364:114197. doi: 10.1016/j.geoderma.2020.114197

Springer, A. E., Amentt, M. A., Kolb, T. E., and Mullen, R. M. (2006). Evapotranspiration of two vegetation communities in a high-elevation riparian meadow at hart prairie, Arizona. *Water Resour. Res.* 42:3. doi: 10.1029/2004WR003863

Tang, S., Zhang, Y., Zhai, X., Wilkes, A., Wang, C., and Wang, K. (2018). Effect of grazing on methane uptake from Eurasian steppe of China. *BMC Ecol.* 18, 11–17. doi: 10.1186/s12898-018-0168-x

Tentori, E. F., and Richardson, R. E. (2020). Methane monooxygenase gene transcripts as quantitative biomarkers of methanotrophic activity in Methylosinus trichosporium OB3b. *Appl. Environ. Microbiol.* 86, e01048–e01020. doi: 10.1128/AEM.01048-20

Tong, C., Cadillo-Quiroz, H., Zeng, Z. H., She, C. X., Yang, P., and Huang, J. F. (2017). Changes of community structure and abundance of methanogens in soils along a freshwater–brackish water gradient in subtropical estuarine marshes. *Geoderma* 299, 101–110. doi: 10.1016/j.geoderma.2017.03.026

Van den Pol-van Dasselaar, A., Van Beusichem, M. L., and Oenema, O. (1998). Effects of soil moisture content and temperature on methane uptake by grasslands on sandy soils. *Plant Soil* 204, 213–222. doi: 10.1023/A:1004371309361

Wachendorf, C., Lampe, C., Taube, F., and Dittert, K. (2008). Nitrous oxide emissions and dynamics of soil nitrogen under 15N-labeled cow urine and dung patches on a sandy grassland soil. *J. Plant Nutr. Soil Sci.* 171, 171–180. doi: 10.1002/jpln.200625217

Wang, Y., Cheng, S., Fang, H., Yu, G., Xu, M., Dang, X., et al. (2014). Simulated nitrogen deposition reduces CH_4 uptake and increases N_2O emission from a subtropical plantation forest soil in southern China. *PLoS One* 9:e93571. doi: 10.1371/journal.pone.0093571

Wei, D., Xu-Ri, T.-T., Wang, Y. S., and Wang, Y. H. (2015). Considerable methane uptake by alpine grasslands despite the cold climate: in situ measurements on the central Tibetan plateau, 2008–2013. *Glob. Chang. Biol.* 21, 777–788. doi: 10.1111/gcb.12690

Weltzin, J. F., Loik, M. E., Schwinning, S., Williams, D. G., Fay, P. A., Haddad, B. M., et al. (2003). Assessing the response of terrestrial ecosystems to potential changes in precipitation. *Bioscience* 53, 941–952. doi: 10.1641/0006-3568(2003)053

Wright, A. J., de Kroon, H., Visser, E. J., Buchmann, T., Ebeling, A., Eisenhauer, N., et al. (2017). Plants are less negatively affected by flooding when growing in species-rich plant communities. *New Phytol.* 213, 645–656. doi: 10.1111/nph.14185

Wu, H., Wang, X., Ganjurjav, H., Hu, G., Qin, X., and Gao, Q. (2020). Effects of increased precipitation combined with nitrogen addition and increased temperature on methane fluxes in alpine meadows of the Tibetan plateau. *Sci. Total Environ.* 705:135818. doi: 10.1016/j.scitotenv.2019.135818

Xu, X., and Inubushi, K. (2007). Effects of nitrogen sources and glucose on the consumption of ethylene and methane by temperate volcanic forest surface soils. *Chin. Sci. Bull.* 52, 3281–3291. doi: 10.1007/s11434-007-0499-z

Yan, G. Y., Mu, C. C., Xing, Y. J., and Wang, Q. G. (2018). Responses and mechanisms of soil greenhouse gas fluxes to changes in precipitation intensity and duration: a meta-analysis for a global perspective. *Can. J. Soil Sci.* 98, 591–603. doi: 10.1139/cjss-2018-0002

Yue, P., Cui, X., Wu, W., Gong, Y., Li, K., Goulding, K., et al. (2019). Impacts of precipitation, warming and nitrogen deposition on methane uptake in a temperate desert. *Biogeochemistry* 146, 17–29. doi: 10.1007/s10533-019-00606-0

Yue, P., Li, K., Gong, Y., Hu, Y., Mohammat, A., Christie, P., et al. (2016). A five-year study of the impact of nitrogen addition on methane uptake in alpine grassland. *Sci. Rep.* 6:32064. doi: 10.1038/srep32064

Yue, P., Zuo, X., Li, K., Li, X., Wang, S., and Misselbrook, T. (2022). Precipitation changes regulate the annual methane uptake in a temperate desert steppe. *Sci. Total Environ.* 804:150172. doi: 10.1016/j.scitotenv.2021.150172

Zak, D. R., Holmes, W. E., White, D. C., Peacock, A. D., and Tilman, D. (2003). Plant diversity, soil microbial community, and ecosystem function: are there any links? *Ecology* 84, 2042–2050. doi: 10.1890/02-0433

Zhang, L., Adams, J. M., Dumont, M. G., Li, Y., Shi, Y., He, D., et al. (2019). Distinct methanotrophic communities exist in habitats with different soil water contents. *Soil Biol. Biochem.* 132, 143–152. doi: 10.1016/j.soilbio.2019.02.007

Zhang, L., Guo, D., Niu, S., Wang, C., Shao, C., and Li, L. (2012). Effects of mowing on methane uptake in a semiarid grassland in northern China. *PLoS One* 7:e35952. doi: 10.1371/journal.pone.0035952

Zhang, Z., Wang, G., Wang, H., Qi, Q., Yang, Y., and He, J. S. (2021). Warming and drought increase but wetness reduces the net sink of CH_4 in alpine meadow on the Tibetan plateau. *Appl. Soil Ecol.* 167:104061. doi: 10.1016/j.apsoil.2021.104061

Zhao, H., Li, T., Li, L., and Hao, Y. (2017). A stable CH_4 sink responding to extreme precipitation events in a fenced semiarid steppe. *J. Soils Sediments* 17, 2731–2741. doi: 10.1007/s11368-017-1798-x

Zhou, X., Smaill, S. J., Gu, X., and Clinton, P. W. (2021). Manipulation of soil methane oxidation under drought stress. *Sci. Total Environ.* 757:144089. doi: 10.1016/j.scitotenv.2020.144089

Zhuang, Q., Chen, M., Xu, K., Tang, J., Saikawa, E., Lu, Y., et al. (2013). Response of global soil consumption of atmospheric methane to changes in atmospheric climate and nitrogen deposition. *Glob. Biogeochem. Cycles* 27, 650–663. doi: 10.1002/gbc.20057