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REVIEW

Responses and mechanisms of soil greenhouse gas fluxes to changes in precipitation intensity and duration: a meta-analysis for a global perspective

Guoyong Yan, Changcheng Mu, Yajuan Xing, and Qinggui Wang

Abstract: Although extensive manipulative experiments have been conducted to study the effects of altered precipitation intensity and duration on soil greenhouse gas (GHG; carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O)) fluxes, the general patterns of GHGs to altered precipitation have not been globally described across biomes. Thus, we performed a meta-analysis of 84 published studies to examine the general responses of CO_2, CH_4, and N_2O fluxes to altered precipitation. Our results indicated that increased precipitation significantly increased N_2O emissions (+154.0%) and CO_2 fluxes (+112.2%) and significantly decreased CH_4 uptake (−41.4%); decreased precipitation significantly decreased N_2O emissions (−64.7%) and CO_2 fluxes (−8.6%) and significantly increased CH_4 uptake (+32.4%). Moreover, increased precipitation significantly increased litter biomass and microbial biomass and decreased root biomass and the root:shoot ratio. However, decreased precipitation significantly decreased litter biomass and root biomass and significantly increased root:shoot ratio. These results suggest that precipitation changes could alter the carbon distribution patterns in plants. In addition, the CO_2, CH_4, and N_2O fluxes exhibited diverse responses to different ecosystems, durations of precipitation changes, and changes in precipitation intensity. These results demonstrate that there are many factors that regulate the responses of GHG to precipitation changes.

Key words: soil greenhouse gas fluxes, altered precipitation, meta-analysis.

Résumé : On ne compte plus les expériences de manipulation entreprises pour préciser les conséquences d'une modification de l'intensité des précipitations et de la durée des flux de gaz à effet de serre (GES) dégagés par le sol comme le dioxyde de carbone (CO_2), le méthane (CH_4) et l'oxyde nitreux. En revanche, les patrons généraux des émissions de GES résultant d'un changement du régime pluvial n'ont fait l'objet d'aucune description globale à l'échelle du biome. Les auteurs ont effectué une méta-analyse de 84 études publiques afin de vérifier la réaction générale des flux de CO_2, de CH_4 et de N_2O à un nouveau régime pluvial. Les résultats indiquent qu'une hausse des précipitations augmente significativement les émissions de N_2O (+154,0 %) et les flux de CO_2 (+112,2 %) tout en diminuant sensiblement l'absorption de CH_4 (−41,4 %), alors que des précipitations moins abondantes réduisent nettement les dégagements de N_2O (−64,7 %) et les flux de CO_2 (−8,6 %), tout en accroissant significativement l'absorption de CH_4 (+32,4 %). Par ailleurs, une hausse des précipitations augmente sensiblement la biomasse de la litière de même que la biomasse microbienne, mais réduit la biomasse des racines et le rapport racines:pousses. Parallèlement, des précipitations plus faibles réduisent sensiblement la biomasse de la litière et celle des racines, tout en accroissant nettement le rapport racines:pousses. Ces résultats laissent croire qu'un changement du régime pluvial pourrait altérer les modes de répartition de carbone chez les plantes. En outre, les flux de CO_2, de CH_4 et de N_2O réagissent de façon variée, selon l'écosystème, la durée du changement du régime de pluvial et la modification de l'intensité des précipitations. Il semble donc que de nombreux paramètres régulent la réaction des gaz à effet de serre aux altérations subies par les précipitations. [Traduit par la Rédaction]

Mots-clés : flux des gaz à effet de serre du sol, modification des précipitations, méta-analyse.

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Introduction

Soils are important sources and sinks of carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O) (Smith et al. 2018). In previous manipulative field experiments, when precipitation frequency and intensity increased it often resulted in increased greenhouse gas (GHG) emissions (IPCC 2013; Petrakis et al. 2017). However, climate change has begun to affect the frequency, intensity, and duration of both extreme precipitation and droughts (IPCC 2013). Previous studies have shown that precipitation is projected to increase at high latitudes and decrease in most subtropical regions (IPCC 2007). Wet climates are becoming wetter, and the dry climates are becoming drier, intensifying extremes in the soil water cycle (Falloon and Betts 2010). Changes in precipitation regimes (i.e., intensity) have been shown to have a great impact on soil CO_2, CH_4, and N_2O fluxes (Martins et al. 2017; Petrakis et al. 2017). Therefore, examining how changes in precipitation (increase or decrease) affect the GHG flux at the soil–troposphere interface is essential for a better understanding of the terrestrial carbon (C) and nitrogen (N) cycles (Zhou et al. 2016).

Manipulative experiments have been conducted to study the effects of altered precipitation on soil CO_2, CH_4, and N_2O fluxes (Berglund and Berglund 2011; Dinsmore et al. 2013; Wang et al. 2015; Olefeldt et al. 2017; Martins et al. 2017). However, the responses of GHG fluxes to precipitation changes are highly variable between the different experiments. For example, Chen et al. (2013) reported that increased precipitation significantly stimulated CO_2 emissions, but Knorr et al. (2008) showed inconsistent results. Among all experiments, changes in the amount of precipitation were found to substantially stimulate (Petrakis et al. 2017), significantly inhibit (Sanaullah et al. 2012), or have no effect (Knorr et al. 2008) on soil GHG fluxes. The inconsistent results from individual studies likely arise because the magnitude and direction of the change in CO_2, CH_4, and N_2O fluxes are affected by multiple factors, including climate, previous land use and vegetation type, and the different frequency and intensity of precipitation change. A previous meta-analysis focused on the response of the soil C cycle to changes in precipitation; however, they did not focus on trends in soil GHG emissions (Zhou et al. 2016). Although previous studies have provided evidence of changes in GHGs in response to changes in precipitation regimes, these results are not sufficient to understand whether there are globally consistent responses of GHGs to changes in precipitation. This is because studies are usually confined to a particular geographic region and therefore climate, and a particular ecosystem-type. Combining individual study results (including many land use and climate types) into a meta-analysis (Brockwell and Gordon 2001) may help to decipher if there are global-scale changes to GHGs in response to changes in precipitation.

In addition to the response patterns of GHGs to changes in precipitation, the underlying mechanisms of the diverse responses of GHGs to precipitation changes have also been studied. Experimental conditions (e.g., relative changes in precipitation intensity), different ecosystems (e.g., forest and grassland), and forcing factors (e.g., experimental duration and climate factors) may affect the responses of GHGs to changes in precipitation. Previous studies have shown that relative changes in precipitation intensity can exert different effects on GHG emissions. For example, Huang et al. (2015) observed that a 30% increase in precipitation growing season precipitation significantly increased CO_2 emissions (+50%) from soil, whereas a 15% increase in growing season precipitation had less of an effect on CO_2 emissions (+33%) in a temperate desert. In addition, Chen et al. (2008) also found that soil CO_2 emission was higher with 50 mm water addition (+570% compared with control) than with 5 mm water addition (+284% compared with control) in a grassland ecosystem. Different terrestrial ecosystems are also of great significance in regulating the responses of GHGs to changes in precipitation because of how different plant types and climatic factors influence microbial communities and C allocation in roots (Yuan and Chen 2010). Beier et al. (2012) noted that a systematic and holistic approach to investigating how soil and plant community characteristics change with altered precipitation regimes, and the consequent effects on ecosystem processes and functioning within these experiments would greatly increase their value to climate change and ecosystem research. In addition, the duration of precipitation changes can alter the magnitude and direction of GHG responses to changes in precipitation, which may be mainly because of the cumulative effects of simulated precipitation increases or decreases. Therefore, how soil GHG emissions respond to increased or decreased precipitation is largely unclear due to different experimental conditions, ecosystems, and experimental durations of past studies.

To better understand the reasons for the different results and the general patterns of the responses of GHGs to changes in precipitation, we conducted a meta-analysis using data from 84 peer-reviewed published papers consisting of 522 individual experimental observations. Although changes in precipitation include many aspects of precipitation regimes (IPCC 2007), the methods of this study are similar to the methods of Zhou et al. (2016) and focus on the effects of changes in precipitation intensity (increase or decrease) and duration. We hypothesized that (1) increased or decreased precipitation would significantly affect GHG (CO_2, CH_4, and N_2O) fluxes by altering biological and physical soil properties; (2) GHG emissions would show varied responses to increased or decreased precipitation in different ecosystems due to the inherent differences in soil, climate, and vegetation; and (3) differences in precipitation intensity and duration regulate the responses of GHGs to changes in precipitation.

Materials and Methods

Data collection

We searched the ISI (Institute for Scientific Information) Web of Science (Thomson Reuters, New York, NY, USA) for published papers reporting the responses of soil GHG fluxes to precipitation changes. We searched the references by using the search term combinations “rainfall or precipitation or drought or irrigation”, “CO_2 or carbon dioxide or carbon”, “rainfall or precipitation or drought or irrigation”, “CH_4 or methane”, “rainfall or precipitation or drought or irrigation”, “N_2O or nitrous oxide”, “rainfall or precipitation or drought or irrigation”, and “greenhouse gases or GHGs”. Our literature search included papers published (or accepted for publication) between January 1994 and July 2016. A total of 526 articles were first collected by searches using the keywords. Subsequently, to avoid bias in reference selection, the studies were compiled into a database, and the following six criteria were applied: (1) field experiments were selected in which at least one of the selected GHG fluxes was measured; (2) the control and treatment plots were in the same locations in each article (including the same abiotic and biotic conditions); if the studies were conducted at distinct locations (some articles included data from two or more experimental sites) and with different precipitation intensities, they were treated as independent; (3) for the multifactorial studies, only the control and precipitation change treatment data were included, and the interacting effects were excluded; (4) the type of precipitation manipulation (increase or decrease, using only studies with manipulations and excluding studies that did not manipulate but observed changes in precipitation between different years), experiment location, manipulation method, ecosystem type, sampling season, and the length of the experiment were collected for each experiment; (5) the methods used to manipulate precipitation changes, such as magnitude (absolute amounts or relative changes), and the experimental durations of the precipitation changes were clearly indicated; and (6) the means, standard errors (SE) or standard deviations (SD), and sample sizes (n) were clearly reported in the papers. After exclusion of unsuitable studies, a total of 84 published papers were compiled into the literature database from more than 500 papers (Supplementary References[1]).

For each of 84 published papers, the raw data were extracted from the text, tables, and figures. The data were extracted from figures using GetData Graph Digitizer software, version 2.26 (http://www.getdata-graph-digitizer.com/index.php). When the SD was not reported, we calculated it from the SE and sample size (n) ($SD = SE \times \sqrt{n}$). When the SD or SE was not shown, the SD was estimated by multiplying the reported mean by the average coefficient of variance (Bai et al. 2013). The mean, SD, and sample size (n) were recorded for the response variables (e.g., CO_2 flux, CH_4 uptake, and N_2O emission), climate factors (e.g., soil temperature and moisture values), and some soil biological and chemical variables (they can affect GHG fluxes) for each experiment plot and each control plot (Supplementary Table S1[1]). However, in many studies, data were collected with diverse units and different time intervals and frequencies. When response variables were reported in different units, they were converted to the same unit; when response variables were reported for multiple sampling dates, we only collected the monthly means.

The variables of each study were categorized according to the environmental and simulated factors into the following three criteria: (1) ecosystem types were categorized into tropical forests, subtropical forests, temperate forests, boreal forests, grasslands, scrublands, farmlands, deserts, and wetlands; (2) the duration of precipitation change was categorized into ≤1 yr (short term), 1–5 yr (medium term), and >5 yr (long term); and (3) the precipitation intensity was categorized into addition <30% (low intensity), addition 30%–50% (moderate intensity), addition >50% (high intensity), decrease <30% (low intensity), decrease 30%–50% (moderate intensity), or decrease >50% (high intensity), relative to natural precipitation.

Meta-analysis

In our study, we used a meta-analysis approach according to the methods in Hedges et al. (1999) to calculate the response ratio (RR) of each variable in the individual studies to show the effects of increased or decreased precipitation. The natural log-transformed RR was defined as the “effect size” (Hedges et al. 1999). Hedges et al. (1999) noted that the logarithm of the RR was utilized to improve its statistical behavior in meta-analyses. The RR was calculated as the ratio of the mean value of a variable in the treatment group (X_t) to that in the control group (X_c) (eq. 1).

$$(1) \qquad \mathrm{RR} = \ln(X_t/X_c) = \ln X_t - \ln X_c$$

The variance (v) of the RR was calculated using eq. 2.

$$(2) \qquad v = \frac{S_t^2}{n_t X_t^2} + \frac{S_c^2}{n_c X_c^2}$$

where S_t and S_c are the standard deviations for the treatment and control groups, respectively, and n_t and n_c are

[1]Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjss-2018-0002.

Table 1. Effects of precipitation changes on between-group heterogeneity (Q_b) of soil greenhouse gas fluxes (CO_2 flux, CH_4 uptake, and N_2O emission).

	CO_2 flux		CH_4 uptake		N_2O emission	
Categories	Q_b	*P* value	Q_b	*P* value	Q_b	*P* value
Ecosystem type	13.02	0.0003**	21.10	<0.0001***	2.39	0.1224
Treatment type	97.20	<0.0001***	63.45	<0.0001***	61.96	<0.0001***
Treatment duration	23.59	<0.0001***	0.01	0.97	6.51	0.0107*

Note: Ecosystem types include subtropical forests, temperate forests, boreal forests, grasslands, shrublands, farmlands, deserts, and wetlands. Treatment types include precipitation addition and precipitation removal. Treatment durations include short-term treatments (<1 yr), medium-term treatments (>1 yr, <5 yr), and long-term treatments (>5 yr). *, **, and *** indicate significance at $p < 0.05$, $p < 0.001$, and $p < 0.0001$, respectively.

the sample sizes for the treatment and control groups, respectively.

Not all of the studies in our database reported the sampling variance (e.g., SE), but all reported the sample size. To derive the overall response effect of each treatment group relative to the control group, individual observations were weighted by the inverse of the variance, and individuals with a lower variance were weighted higher. Thus, we weighted the RR (RR_{++}) by sample size (eq. 3), as defined in

$$\text{(3)} \qquad \text{Weight}_n(RR_{++}) = n_t n_c/(n_t + n_c)$$

where n_t and n_c are the sample sizes for the control and treatment groups, respectively. The details of the methods were described by Peng et al. (2017).

A fixed-effects model (fixed-effects models are discussed in more detail in Brockwell and Gordon (2001)) was used to determine whether precipitation changes significantly affected each variable. Bootstrapping with 9999 iterations was used to generate the 95% confidence intervals (CIs) of the RR and was calculated with MetaWin statistical software, version 2.0 (Rosenberg et al. 2000). If the 95% CI did not overlap zero, this suggested that the treatments had a significant impact (positive or negative) on the variable; if not, the treatments were assumed to have no significant impact on the variable. To further analyze the effects of precipitation among the different subgrouping categories (based on above three criteria), between-group heterogeneity (Q_b) was examined across all data for a given response variable (Hedges et al. 1999). The percentage transformed from the average RR of each variable was used to explain the response to precipitation changes (eq. 4).

$$\text{(4)} \qquad \text{Percentage change} = [\exp(RR_{++}) - 1] \times 100\%$$

In this study, all figures were created using Stata software, version 12.0 (Stata Corp, College Station, TX, USA).

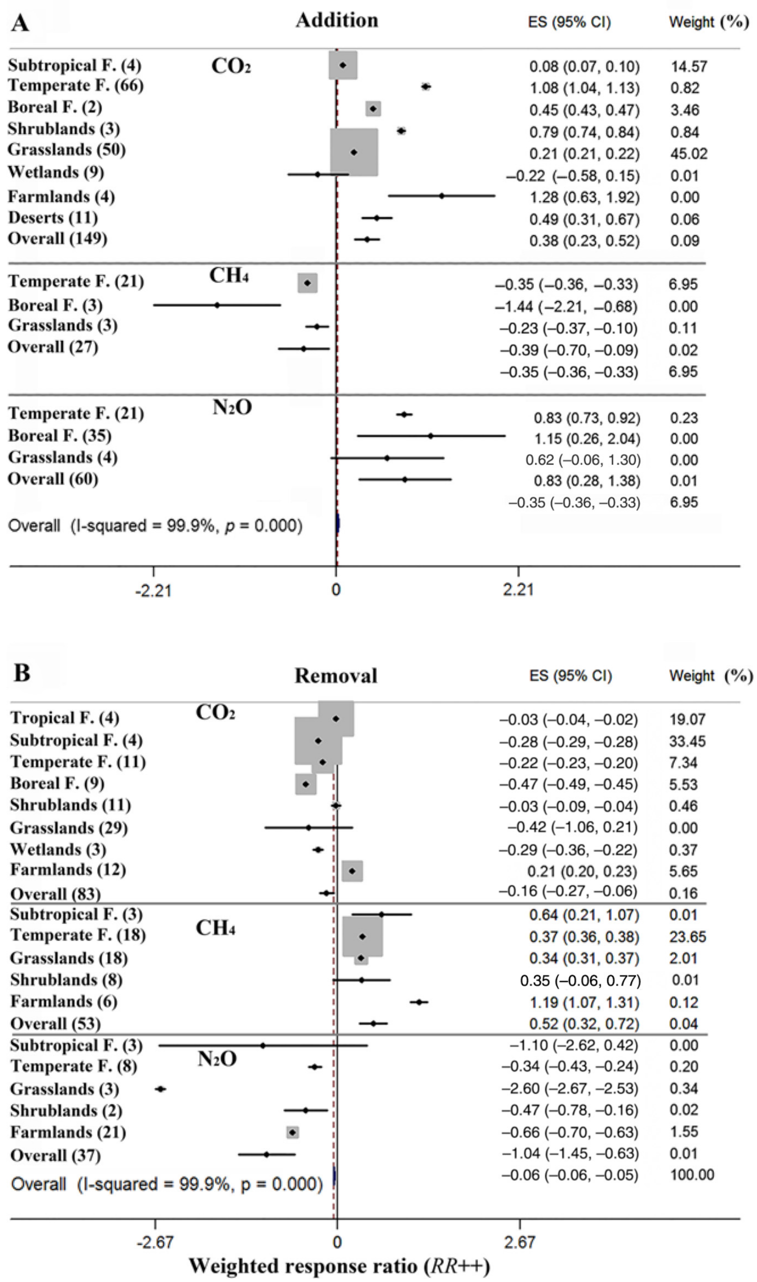
Results

Effects of precipitation increases or decreases on soil CO_2, CH_4, and N_2O fluxes

Averaged across all studies, precipitation increases significantly affected the fluxes of all GHGs (CO_2, CH_4, and N_2O). However, in different ecosystems, the GHG fluxes exhibited various responses to precipitation changes (Fig. 1A; Table 1). Precipitation increases significantly increased the CO_2 emissions from soil in subtropical forests (+17.8%), temperate forests (+195.9%), boreal forests (+56.9%), scrublands (+120.3%), grasslands (+23.9%), and farmlands (+258.3%) but did not significantly alter the CO_2 emissions in wetlands (Fig. 1A). Precipitation increases also significantly increased N_2O emissions in temperate forests (+128.3) and boreal forests (+179.6) but did not significantly affect N_2O emissions in grassland ecosystems (Fig. 1A). However, CH_4 uptake decreased by −29.4% in temperate forests, −76.3% in boreal forests, and −18.5% in grasslands with increased precipitation (Fig. 1A).

The effects of decreased precipitation on the fluxes of GHGs (CO_2, CH_4, and N_2O) were different from the effects of increased precipitation. Across all ecosystems, decreased precipitation significantly decreased N_2O emissions (−64.7%) and CO_2 fluxes (−8.6%) and significantly increased CH_4 uptake (+32.4%) (Fig. 1B). The CO_2 fluxes displayed a negative response to decreased precipitation in tropical forests (−3.2%), subtropical forests (−24.6%), temperate forests (−19.5%), boreal forests (−37.3%), and wetlands (−15.2%), a positive response in farmlands (+23.9%) and no change in scrublands and grasslands (Fig. 1B). Decreased precipitation significantly increased CH_4 uptake in subtropical forests (+154.6%), temperate forests (+44.5%), grasslands (+40.4%), and farmlands (+228.3%) but did not significantly affect CH_4 uptake in scrublands. In addition, the effects of decreased precipitation on N_2O fluxes were significant in temperate forests (−24.3%), scrublands (−38.4%), grasslands (−92.6%), and farmlands (−48.5%) but were not significant in subtropical forests.

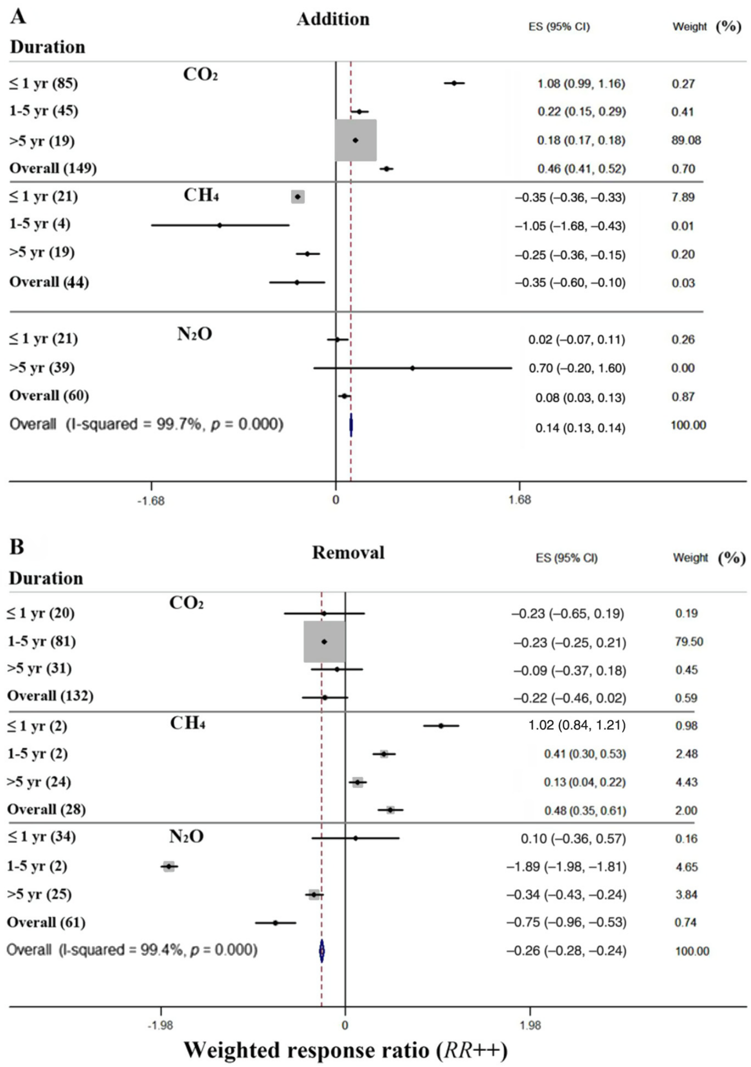
Fig. 1. Effects of (A) precipitation addition and (B) precipitation removal on soil CO_2 fluxes, CH_4 uptake, and N_2O emissions for all ecosystems, tropical forests, subtropical forest, temperate forests, boreal forests, grasslands, shrublands, farmlands, wetlands, and deserts. The black circles with error bars indicate the weighted response ratios (RR_{++}) with 95% bootstrap CIs across all sampling methods. The vertical line is drawn at $RR_{++} = 0$. The sample size for each variable is shown in parentheses. Tropical F. represents tropical forests; Subtropical F. represents subtropical forests; Temperate F. represents temperate forests; Boreal F. represents boreal forests. The smaller the CIs, the larger the gray squares. The vertical dashed red line signifies the total effect line of all parameters in each picture.



Factors influencing the responses of CO_2 fluxes, CH_4 uptake, and N_2O emissions to increased or decreased precipitation

Changes in precipitation intensity and experimental duration influenced the direction and magnitude of CO_2 flux, CH_4 uptake, and N_2O emission responses to precipitation increases or decreases (Table 1). The duration of increased precipitation affected the GHG emissions (Fig. 2A). For precipitation increases, short- (≤1 yr), medium- (1–5 yr), and long-term (>5 yr) experiments caused strong and statistically significant increases in CO_2 fluxes and CH_4 uptake, whereas short- (≤1 yr) and long-term (>5 yr) experiment durations did not significantly affect the soil N_2O fluxes (Fig. 2A). Decreases in

Fig. 2. Effect of (A) precipitation addition duration and (B) precipitation removal duration on soil CO_2 fluxes, CH_4 uptake, and N_2O emissions. The black circles with error bars indicate the weighted response ratios (RR_{++}) with 95% bootstrap CIs across all sampling methods. The vertical solid line is drawn at $RR_{++} = 0$. The sample size for each variable is shown in parentheses. The smaller the CIs, the larger the gray squares. The vertical dashed line signifies the total effect line of all parameters in each picture.



precipitation significantly reduced CO_2 fluxes in medium-term experiments, but fluxes were unaffected by precipitation decreases in both short- and long-term experiments. Decreased precipitation reduced CH_4 uptake in short-term studies but had a lesser effect in long-term studies (Fig. 2B). However, different durations, in increased precipitation treatments, did not significantly affect CO_2 fluxes, CH_4 uptake, and N_2O emissions (Table 2). In decreased precipitation treatments, different durations had different effects on CO_2 fluxes and N_2O emissions (Table 3). In addition to experiment duration, the relative changes in precipitation intensity in the manipulative experiments also had significant effects on CO_2 fluxes and N_2O emissions when precipitation increased (Table 2) and had significant effects on CH_4 uptake and N_2O emissions when precipitation decreased (Table 3). Nevertheless, in the scenarios where precipitation increased, all intensity treatments significantly increased CO_2 fluxes. With the exception of the low-intensity precipitation addition (<30%), increased precipitation intensity decreased CH_4 fluxes, whereas only moderate- and high-intensity precipitation increases significantly increased N_2O emissions (Fig. 3A). Moreover, in decreased precipitation scenarios, low and moderate precipitation intensities significantly decreased CO_2 fluxes, all intensities significantly increased CH_4 uptake, and low and moderate precipitation intensities significantly decreased N_2O emissions (Fig. 3B).

In addition, increased precipitation significantly decreased soil total C, fungal abundance number, soil microbial biomass C : soil microbial biomass N ratio, root biomass, and root:shoot ratio, and significantly increased soil total N, soil total P, soil NH_4-N concentration, soil temperature, soil microbial biomass C, soil

Table 2. Effects of precipitation addition on between-group heterogeneity (Q_b) of soil greenhouse gas fluxes (CO_2 flux, CH_4 uptake, and N_2O emission).

	CO_2 flux		CH_4 uptake		N_2O emission	
Categories	Q_b	*P* value	Q_b	*P* value	Q_b	*P* value
Ecosystem type	25.63	<0.0001***	0.03	0.8656	4.21	0.0424*
Precipitation variation	31.47	<0.0001***	0.88	0.3483	4.97	0.0258*
Treatment duration	0.59	0.4433	0.01	0.9980	2.04	0.1535

Note: Ecosystem types include subtropical forests, temperate forests, boreal forests, grasslands, shrublands, farmlands, deserts, and wetlands. Precipitation variations include <30% precipitation addition, 30%–50% precipitation addition, and >50% precipitation addition. Treatment durations include short-term treatments (<1 yr), medium-term treatments (>1 yr, <5 yr), and long-term treatments (>5 yr). *, **, and *** indicate significance at $p < 0.05$, $p < 0.001$, and $p < 0.0001$, respectively.

Table 3. Effects of precipitation removal on between-group heterogeneity (Q_b) of soil greenhouse gas fluxes (CO_2 flux, CH_4 uptake, and N_2O emission).

	CO_2 flux		CH_4 uptake		N_2O emission	
Categories	Q_b	*P* value	Q_b	*P* value	Q_b	*P* value
Ecosystem type	2.69	0.1010	3.93	0.0474*	1.87	0.1717
Precipitation variation	0.03	0.8573	12.22	<0.0005**	5.03	0.0249*
Treatment duration	7.82	0.0052*	22.39	<0.0001***	1.41	0.2350

Note: Ecosystem types include subtropical forests, temperate forests, boreal forests, grasslands, shrublands, farmlands, deserts, and wetlands. Precipitation variations include <30% precipitation removal, 30%–50% precipitation removal, and >50% precipitation removal. Treatment durations include short-term treatments (<1 yr), medium-term treatments (>1 yr, <5 yr), and long-term treatments (>5 yr). *, **, and *** indicate significance at $p < 0.05$, $p < 0.001$, and $p < 0.0001$, respectively.

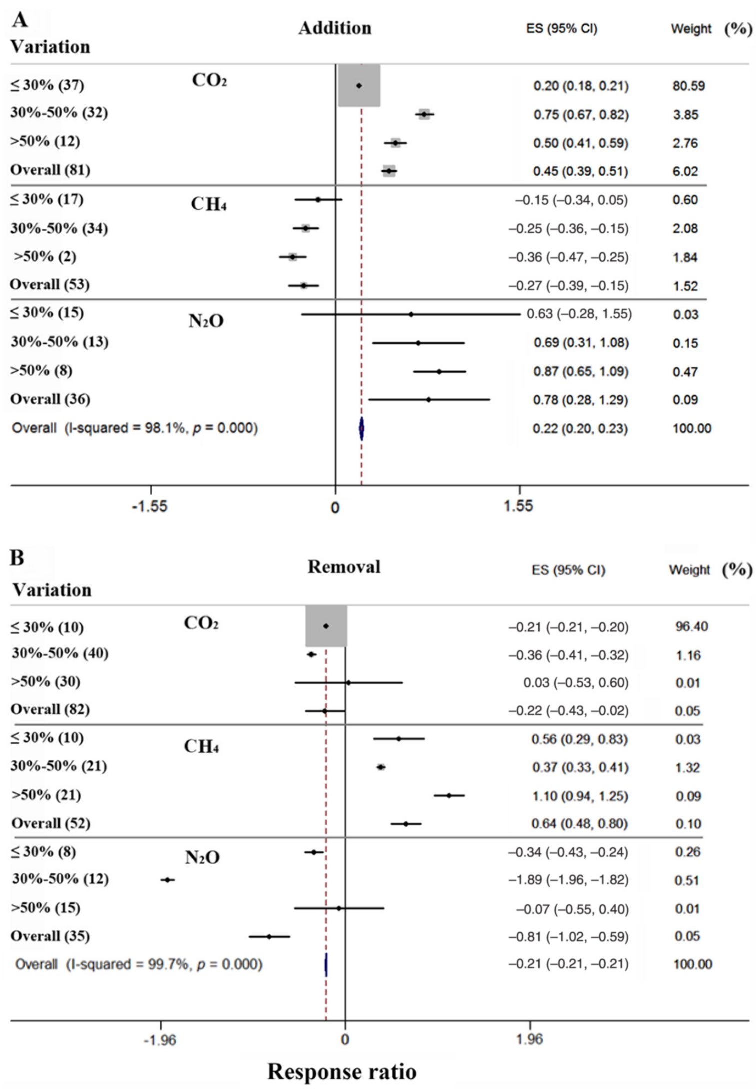
microbial biomass N, litter biomass, shoot biomass, and aboveground net primary productivity (Fig. 4A). Decreased precipitation significantly increased fine root C concentration, root:shoot ratio, and fine root C:N ratio and significantly decreased soil pH, soil microbial biomass C : soil microbial biomass N ratio, fungi:bacteria ratio, fine root N concentration, shoot biomass, litter biomass, root biomass, and aboveground net primary productivity (Fig. 4B). However, increased or decreased precipitation did not significantly affect the other parameters, that is, soil total N, soil total C : total N ratio, soil total P, dissolved organic C, and dissolved organic N.

Discussion

Differential effects of increased and decreased precipitation on soil GHG fluxes

Based on the meta-analysis of experimental manipulations, we found that increased precipitation significantly increased CO_2 fluxes in most of the global terrestrial ecosystems (mainly focusing on forests and grasslands because they constituted a relatively large amount of data; Fig. 1A). Soil moisture is a critical environmental control as it directly and indirectly affects soil CO_2 flux (Huang et al. 2015; Yuste et al. 2017). Precipitation-induced changes in soil water availability simultaneously cause shifts in the soil environments, roots, and microbe activities, which might affect CO_2 production and diffusion rates from soil (Burton et al. 2004; Yuste et al. 2017). Several potential mechanisms have been proposed to explain the precipitation-induced enhancements in CO_2 fluxes: (1) increased precipitation alleviates the water limitations of soil microbes and consequently increases heterotrophic respiration and soil C release (Huang et al. 2015); (2) increased precipitation can disrupt soil aggregates and lead to increased substrate supplies and then indirectly increase soil C release (Smith et al. 2017); (3) increased precipitation may increase soil respiration indirectly by increasing plant photosynthesis and causing physical changes in the soil environment (Högberg et al. 2001); or (4) increased precipitation would increase soil CO_2 flux indirectly through increasing the temperature sensitivity of respiration (McCulley et al. 2007). In this meta-analysis, we found that increased precipitation significantly decreased root biomass and the root:shoot ratio (Fig. 4A), indicating that increased precipitation may relieve water stress in plants and shift C allocation from belowground to aboveground tissues, which is not consistent with the third mechanism mentioned above. However, increased precipitation was found to

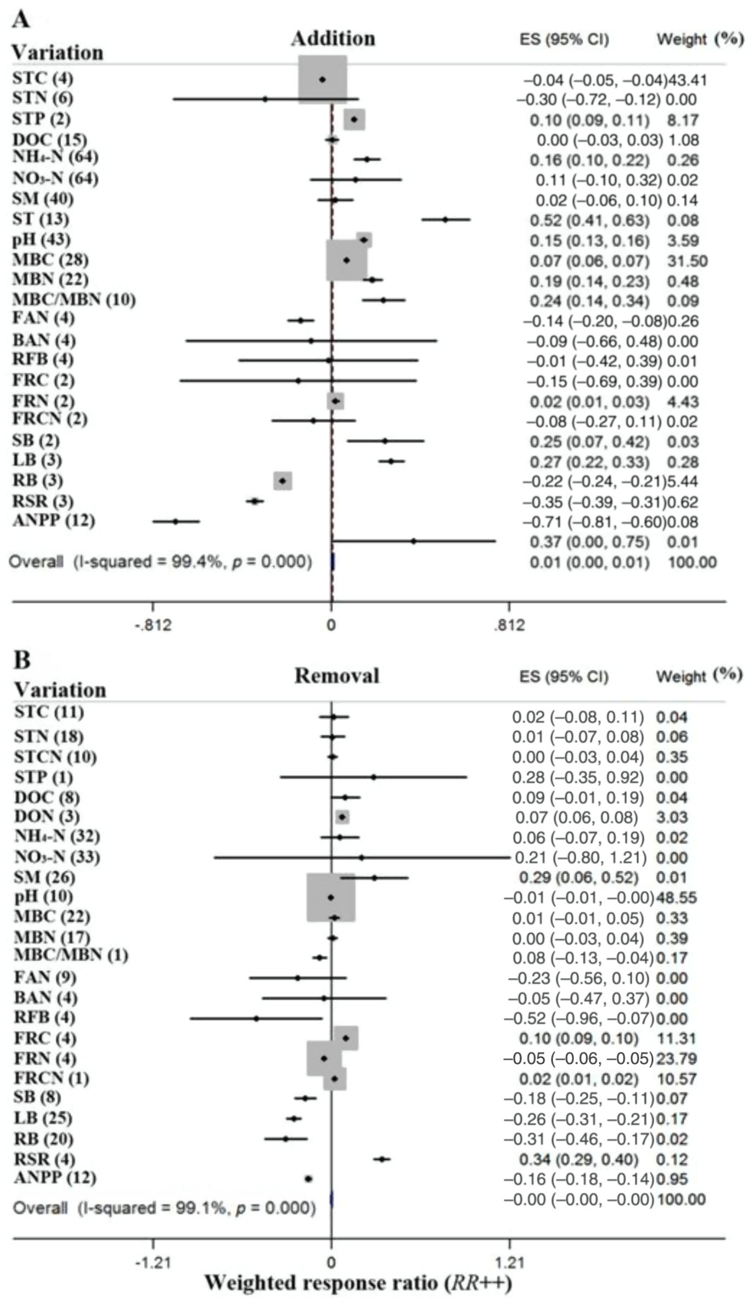
Fig. 3. Effect of (A) precipitation addition variation and (B) precipitation removal variation on soil CO_2 fluxes, CH_4 uptake, and N_2O emissions. The black circles with error bars indicate the weighted response ratios (RR_{++}) with 95% bootstrap CIs across all sampling methods. The vertical solid line is drawn at $RR_{++} = 0$. The sample size for each variable is shown in parentheses. The smaller the CIs, the larger the gray squares. The vertical dashed line signifies the total effect line of all parameters in each picture.



significantly increase soil microbial biomass in this meta-analysis (Fig. 4A), which was consistent with first mechanism mentioned above. Thus, under increased precipitation, increases in CO_2 flux may be mainly due to the increases in microbial biomass. We also synthesized the effects of decreased precipitation on soil CO_2 flux and found that decreased precipitation and increased precipitation induced opposite effects on soil CO_2 flux. Decreased precipitation may reduce nutrient availability because of the water limitations on soil microbial processes (Chapin and Matson 2011), thus resulting in the decrease in CO_2 flux and an increase of soil organic C and N in the meta-analysis (Fig. 4B). Furthermore, decreased precipitation reduced the root biomass (Fig. 4B; Meier and Leuschner 2008), which may have led to lower CO_2 fluxes. To sum up, the responses of soil CO_2 flux to increased or decreased precipitation are driven mostly by soil biological responses to altered water availability, which is partly consistent with our first hypothesis.

The N_2O emissions were also significantly increased by increased precipitation and significantly decreased by precipitation decreases (Fig. 1). There are many pathways for N_2O production in soils including nitrification and denitrification (Wrage et al. 2001), and these processes occur under aerobic and anaerobic soil conditions, respectively. Increased precipitation increases soil moisture and slows O_2 diffusion rates from the atmosphere into the soil while promoting the decomposition of residual organic matter that allows the release of organic and inorganic substances into the soil, which enhances the supply of N and C substrates for denitrification

Fig. 4. Effects of (A) precipitation addition variation and (B) precipitation removal variation on soil physical and chemical properties, soil microorganisms, and fine root morphologies. STC represents soil total C; STN represents soil total N; STCN represents ratio of soil total C : total N; STP represents soil total P; DOC represents dissolved organic C; DON represents dissolved organic N; NH_4-N represents soil NH_4-N; NO_3-N represents soil NO_3-N; SM represents soil moisture; ST represents soil temperature; MBC represents soil microbial biomass C; MBN represents soil microbial biomass N; MBC/MBN represents ratio of soil microbial biomass C : soil microbial biomass N; FAN represents fungal abundance number; BAN represents bacterial abundance number; RFB represents ratio of fungi to bacteria; FRC represents fine root C concentration; FRN represents fine root N concentration; FRCN represents fine root C:N; SB represents shoot biomass; LB represents litter biomass; RB represents root biomass; RSR represents root:shoot ratio; ANPP represents aboveground net primary productivity. The black circles with error bars indicate the weighted response ratios (RR_{++}) with 95% bootstrap CIs across all sampling methods. The vertical solid line is drawn at $RR_{++} = 0$. The sample size for each variable is shown in parentheses. The smaller the CIs, the larger the gray squares. The vertical dashed line signifies the total effect line of all parameters in each picture.



(Chen et al. 2013). Therefore, increases in precipitation may promote N_2O emissions from denitrification by increasing soil N and C availability (Chen et al. 2013). In contrast, decreased precipitation promotes soil aeration, resulting in unfavourable conditions for N_2O production by denitrification (Homyak et al. 2017). Other have found that although soil O_2 increased due to precipitation decreases, no substantial increases in N_2O emissions were detected from nitrification (Homyak et al. 2017). The reason for this result may be that low soil moisture decreases the soil substrate supply for nitrifying microorganisms, and increased soil organic N may support this conclusion (Fig. 4B). Therefore, it is possible that this effect led to the reductions in N_2O emissions (Hartmann and Niklaus 2012; Homyak et al. 2017). In addition, nitrifiers are very slow-growing, and make small contributions to N_2O emissions when active overall (Stark and Firestone 1995). Therefore, reducing soil moisture may decrease N_2O emissions, and even if the nitrifiers are still active, very little N_2O from their activity may be produced (Stark and Firestone 1995; Wu et al. 2017).

Similar to soil CO_2 fluxes and N_2O emissions, soil CH_4 uptake is also regulated by changes in precipitation. In this study, precipitation increases tended to decrease CH_4 uptake, whereas precipitation decreases tended to increase CH_4 uptake (Fig. 1). The rate of soil CH_4 uptake is determined by the balance of its production and oxidation in the soil, resulting from anaerobic methanogenesis and aerobic/anaerobic methanotrophy (Chen et al. 2014). Increases in soil moisture caused by increased precipitation decreases CH_4 uptake (increases CH_4 emissions) by decreasing CH_4 and O_2 diffusion (Hartmann et al. 2011). Conversely, CH_4 uptake increased in an aerobic environment with decreased precipitation due to limited methanogen activity (Fenner and Freeman 2011; Martins et al. 2017). However, previous studies have suggested that the effects of soil moisture on CH_4 uptake vary. For example, for soils in arid or semiarid regions, increased soil moisture may stimulate CH_4 uptake when the activity of the soil microbial community is water-limited (Steenwerth et al. 2005; Chen et al. 2013). But Thomas et al. (2018) found that increased soil moisture led to less CH_4 uptake, which was mainly due to seasonal precipitation changes in semiarid grassland. In general, the relationship of soil moisture and CH_4 uptake can be described by a parabola (reflecting the physiological optimum), where soil CH_4 uptake is highest at optimum soil moisture levels because CH_4 uptake at very low soil moisture levels is limited by biological activity, and CH_4 uptake at higher soil moisture levels is limited by the diffusion of CH_4 and O_2 through the soil profile (Del Grosso et al. 2000). Therefore, the effect of precipitation change on CH_4 flux is regulated by the background value of soil moisture.

Factors affecting responses of GHG fluxes to increased or decreased precipitation

Changes in precipitation intensity and duration have been demonstrated to influence soil GHG fluxes (Peng et al. 2013; Wu et al. 2015; Vidon et al. 2016). In this study, different precipitation intensities and durations were found to have different effects on soil GHG fluxes (Figs. 2, 3), which is consistent with our third hypothesis. Soil CO_2 flux generally increased with increased precipitation intensity and reached maximum values when soil moisture was at the intermediate level; however, CO_2 flux decreased when precipitation intensity continued to increase, indirectly suggesting that soil organisms have maximum physiological responses at an optimum water-filled pore space (Fig. 2A; Cable et al. 2008). Moreover, Deng et al. (2011) also suggested that soil CO_2 flux generally increased following low precipitation intensities, and the magnitude of soil CO_2 flux gradually declined with increasing precipitation intensity. These previous findings are consistent with our results, as soil CO_2 flux was highest when there was an increase in intermediate precipitation intensity (30%–50% increase in natural precipitation) compared with low precipitation intensity (<30% increase in natural precipitation) and high precipitation intensity (>50% increase in natural precipitation). A trade-off between enhanced soil moisture and decreased soil gas diffusion coupled with soil substrate supply may explain the phenomenon of the optimum precipitation intensity (Deng et al. 2011). However, decreased precipitation intensity did not significantly affect soil CO_2 fluxes, which may be caused by the acclimations of plant communities and soil microbes. For decreased precipitation to cause drought conditions, it would have to be sustained for long enough periods. We speculate, if this condition is sustained long enough to induce drought, plant communities and soil microbes will switch their functioning to adapt to the drier conditions, which may lead to no change in soil CO_2 fluxes. In this meta-analysis, decreased precipitation was shown to have no significant effect on microbial biomass (Fig. 4B), which may partially support the suggested mechanism above.

The CH_4 uptake rate decreased with increased precipitation intensity, but this decrease was not significant. Previous studies provided evidence that increased precipitation intensity may not only increase CH_4 uptake but also reduce CH_4 uptake (Blankinship et al. 2010), which may be due to the local climate. For example, precipitation increases may promote CH_4 uptake at a relatively dry site but decrease CH_4 uptake at a relatively wet site (Blankinship et al. 2010). We speculate that if a region is extremely dry, the CH_4 absorption rate may increase with the increase of precipitation intensity within a certain range. Thus, on a global scale, the increased precipitation intensity may not affect the total CH_4 uptake. However, decreases in precipitation intensity were found to significantly increase CH_4 uptake in this meta-analysis. This result may be because both the soil gas diffusion rate and soil O_2 concentration increased with decreasing precipitation intensity, which inhibited the activity of methanogens (methanogens are anoxic archaea) and increased the activity of methanotrophs (methanotrophs can operate under different oxygen conditions), thus resulting in increased CH_4 uptake rates (Hiltbrunner et al. 2012; Aronson et al. 2013). The

CH_4 uptake rates may increase with decreasing precipitation intensity within a certain range. However, previous studies have suggested that CH_4 uptake in extreme drought conditions is limited by physiological stress in soil microbes (Del Grosso et al. 2000). At this stage, most experimental manipulations did not reach extreme drought scenarios, so the decrease in precipitation intensity significantly increased CH_4 absorption.

Soil N_2O emissions increased with increasing precipitation intensity. Soil N_2O is the intermediate product or by-product of soil nitrification and denitrification, and increases in precipitation intensity can decrease soil O_2 concentrations and limit nitrification; however, the redox potential can drop low enough within microsites to enable the release of comparably large amounts of N_2O from denitrification (Chen et al. 2013). Overall, different degrees of precipitation intensity decreases had different effects on soil GHG emissions due to differences in background value of soil moisture and land use categories.

In addition to precipitation intensity, experiment duration may also affect the responses of GHG fluxes to precipitation changes because time is crucial for biotic acclimation after a disturbance (Dale et al. 2001). Our results showed that soil GHG fluxes were more sensitive to short-term manipulations (≤1 yr) than long-term manipulations (>5 yr). Soil GHG fluxes can be highly variable in soils with short-term drying or wetting than in soils with long-term drying or wetting (Wang et al. 2015). The acclimation or adaptation of plants and microbes to increased or decreased precipitation may largely contribute to the lack of differences observed for soil GHG fluxes over long-term experimental durations. Both plants and microbes may develop multiple mechanisms to maintain physiological activity under increased or decreased soil water conditions. For example, increased precipitation could relieve water shortages in a soil and then microbial activity might be more limited by nutrient availability (Huxman et al. 2004). Over longer durations of increased precipitation, the positive responses to precipitation may dampen and become less responsive (Wang et al. 2015; Zhou et al. 2016). Moreover, Wang et al. (2015) also suggested that the insignificant changes in soil GHG fluxes in long-term experiments of precipitation increases may be explained by the greater losses of dissolved organic C, which could energetically limit microbial activity. However, future studies should consider the differences between long- and short-term experimental durations, which may be easily used to develop and improve land surface models.

Limitations and future experiments

Our results from a meta-analysis of 84 individual studies provide some insights as to how soil GHGs fluxes respond to altered precipitation patterns (intensity and duration). Change in precipitation affected GHGs differently in the different land use categories. Due to the nature of a meta-analysis, some land uses are underrepresented on a global scale. Our dataset is biased towards temperate ecosystems, especially for CH_4 and N_2O.

The N_2O and CH_4 addition and removal of precipitation datasets lack studies with mid-range (1–5 yr) studies in duration. More data are required within this experimental duration to better understand the impacts of precipitation changes over this time; this duration may help explain how episodic changes to climate, such as droughts or excessive precipitation impact GHG emissions.

Limited information about soil biochemical properties from the existing studies limited our mechanistic understanding of soil GHG fluxes response to precipitation change. Such biological and chemical properties were not often included in the selected datasets, and few datasets were available over the various time frames considered in this study. However, these factors exhibit strong regulatory effects on soil GHG emissions, and their coupling with how GHG emissions may change with altered precipitation may help explain why there are differences (or similarities) between land uses, as well as offer insights into ecosystem resilience. However, across precipitation experiments, different measurement methods, different time intervals and frequencies, made it difficult to compare the responses of GHGs fluxes to changes in precipitation. Future studies should follow a common metric that carefully characterizes the actual treatment in the design of manipulative experiments to make their results more comparable, which may be more meaningful for future meta-analyses.

Conclusion

Changes in precipitation regimes will affect soil GHG fluxes in terrestrial ecosystems. At a global scale, our meta-analysis found that increased precipitation led to higher soil moisture and increased soil CO_2 and N_2O emissions and reduced CH_4 uptake. Decreased precipitation reduced soil CO_2 and N_2O emissions and increased soil CH_4 uptake. The land use categories to assess increased precipitation on CO_2 dynamics were more diverse (eight land uses), and there were more observations available compared with N_2O and CH_4 (three land uses each). The CH_4 data used for the increased precipitation dataset are heavily biased towards temperate forests, and the N_2O data used for the increased precipitation dataset are heavily biased towards temperate and boreal forests. The CO_2, CH_4, and N_2O fluxes exhibited heterogeneous responses to precipitation manipulation depending on the ecosystem type, experimental durations, and relative changes in precipitation intensity. Many physical, biological, and chemical factors act collectively to determine the response of terrestrial GHGs to precipitation intensity and duration. These regulatory factors may help inform soil GHG flux models to better predict the effects of altered precipitation on soil GHG fluxes across a global scale.

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