

Global cross-biome patterns of soil respiration responses to individual and interactive effects of nitrogen addition, altered precipitation, and warming

Science of the Total Environment

Ngaba, Mbezele Junior Yannick; Uwiragiye, Yves; Bol, Roland; de Vries, Wim; Jian, Jinshi et al

<https://doi.org/10.1016/j.scitotenv.2022.159808>

This publication is made publicly available in the institutional repository of Wageningen University and Research, under the terms of article 25fa of the Dutch Copyright Act, also known as the Amendment Taverne.

Article 25fa states that the author of a short scientific work funded either wholly or partially by Dutch public funds is entitled to make that work publicly available for no consideration following a reasonable period of time after the work was first published, provided that clear reference is made to the source of the first publication of the work.

This publication is distributed using the principles as determined in the Association of Universities in the Netherlands (VSNU) 'Article 25fa implementation' project. According to these principles research outputs of researchers employed by Dutch Universities that comply with the legal requirements of Article 25fa of the Dutch Copyright Act are distributed online and free of cost or other barriers in institutional repositories. Research outputs are distributed six months after their first online publication in the original published version and with proper attribution to the source of the original publication.

You are permitted to download and use the publication for personal purposes. All rights remain with the author(s) and / or copyright owner(s) of this work. Any use of the publication or parts of it other than authorised under article 25fa of the Dutch Copyright act is prohibited. Wageningen University & Research and the author(s) of this publication shall not be held responsible or liable for any damages resulting from your (re)use of this publication.

For questions regarding the public availability of this publication please contact openaccess.library@wur.nl



Global cross-biome patterns of soil respiration responses to individual and interactive effects of nitrogen addition, altered precipitation, and warming

Mbezele Junior Yannick Ngaba^{a,b,c}, Yves Uwiragiye^{a,b,d}, Roland Bol^{e,f}, Wim de Vries^g, Jinshi Jian^{h,i,j}, Jianbin Zhou^{a,b,*}

^a College of Natural Resources and Environment, Northwest A&F University, Yangling 712100, Shaanxi, China

^b Key Laboratory of Plant Nutrition and the Agri-Environment in Northwest China, Ministry of Agriculture, Yangling 712100, Shaanxi, China

^c Center of Molecular Ecophysiology (CMEP), College of Resources and Environment, Southwest University, Chongqing 400716, China

^d Faculty of Agriculture, Environmental management and Renewable Energy, University of Technology and Arts of Byumba, Rwanda

^e Institute of Bio- and Geosciences, Agrosphere (IBG-3), Forschungszentrum Jülich GmbH, 52425 Jülich, Germany

^f School of Natural Sciences, Environment Centre Wales, Bangor University, Bangor, United Kingdom

^g Alterra, Wageningen University and Research Centre, P.O. Box 47, 6700 AA Wageningen, the Netherlands

^h State Key Laboratory of Soil Erosion and Dryland Farming on the Loess Plateau, Northwest A&F University, Yangling 712100, China

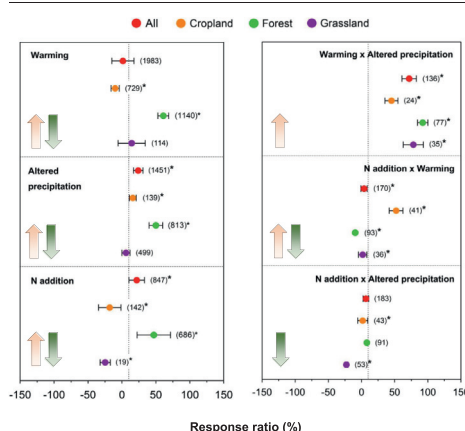
ⁱ Institute of Soil and Water Conservation, Chinese Academy of Sciences & Ministry of Water Resources, 26 Xinong Road, Xianyang 712100, China

^j University of Chinese Academy of Sciences, Beijing 100049, China

HIGHLIGHTS

- Warming x altered precipitation aggravates global warming effects.
- N addition x altered precipitation conditions slow down soil respiration (Rs).
- Globally Rs increased globally up to 1815 mm (precipitation) and 25 °C (temperature).

GRAPHICAL ABSTRACT



ARTICLE INFO

Editor: Elena Paoletti

Keywords:

Soil respiration
Nitrogen addition
Altered precipitation
Warming
Meta-analysis
Drivers

ABSTRACT

Anthropogenic activities have increased atmospheric N, precipitation, and temperature events in terrestrial ecosystems globally, with N deposition increasing by 3- to 5-fold during the previous century. Despite decades of scientific research, no consensus has been achieved on the impact of climate conditions on soil respiration (Rs). Here, we reconstructed 110 published studies across diverse biomes, magnitudes, and driving variables to evaluate how Rs responds to N addition, altered precipitation (both enhanced and reduced precipitation or precipitation changes), and warming. Our findings show that N addition significantly increased Rs by 44 % in forests and decreased it by 19 % and 26 % in croplands and grasslands, respectively ($P < 0.05$). In forests and croplands, altered precipitation significantly increased Rs by 51 % and 17 % (all, $P < 0.05$), respectively, whereas impacts on grassland were insignificant. In comparison, warming stimulated Rs by 62 % in forests but inhibited it by 10 % in croplands (all, $P < 0.05$), whereas impacts on grassland were again insignificant. In addition, across all biomes, the responses of Rs to altered precipitation and

* Corresponding author at: College of Natural Resources and Environment, Northwest A&F University, Yangling 712100, Shaanxi, China.
E-mail address: jbzhou@nwsuaf.edu.cn (J. Zhou).

warming followed a Gaussian response, increasing up to a threshold of 1800 mm and 25 °C, respectively, above which respiration rates decreased with further increases in precipitation and temperature. Our work suggests that the dual interaction of warming \times altered precipitation promotes belowground CO₂ emission, thus enhancing global warming. In general, the interactive effect of N addition \times altered precipitation decreases Rs. Soil moisture was identified as a primary driver of Rs. Given these findings, we recommend future research on warming vs. changed precipitation to better forecast and understand the interaction between Rs and climate change.

1. Introduction

Soil respiration (Rs) is the largest single source of CO₂ and plays a vital role in regulating climatic dynamics in the Earth's system (Luo and Zhou, 2006). It is an essential source of uncertainty in climate projections and C cycle feedback (Huntingford et al., 2013). Soil respiration (Rs) includes both heterotrophic respiration, associated with the decomposition of litter, roots, and soil organic matter, and autotrophic respiration from plant root growth and root biomass maintenance (Metcalf et al., 2011). Major global change drivers, such as climatic factors (temperature and precipitation) and atmospheric N deposition, directly or indirectly affect Rs metabolisms because they control the physiological activities of plants, roots, and soil microorganisms (Luo and Zhou, 2006). However, the response of Rs to these factors is difficult to estimate globally, because the Rs response displays significantly different spatio-temporal dynamics depending on the amount and quality of soil organic matter, temperature, moisture, salinity, pH, and aeration. As a result, global Rs flux dynamics remain poorly constrained (Carey et al., 2016; Pries et al., 2017). Therefore, gaining insight into the regulations of Rs by changes in multiple global controlling drivers, i.e., temperature, precipitation, and N deposition, as a function of site properties (climate and soil properties), is necessary to better predict global C cycling in the future.

The challenging task is to determine how changing global driver factors (N addition, altered precipitation, and warming) would influence Rs patterns in the context of a future worldwide scenario. The widespread N enrichment in the atmosphere and soil has already considerably altered regional and global environments (Luo and Zhou, 2006). Nitrogen input is projected to increase by two to three times between now and the end of this century, further affecting the structure and functioning of terrestrial ecosystems (Gruber and Galloway, 2008). The future climatic warming trend will be even more pronounced owing to the release of CO₂, which has been rising by approximately 1 % per year over the previous decade (Carey et al., 2016; Le Quéré et al., 2020; Pries et al., 2017). This will consequently affect the global ecosystem C and N cycles and lead to an increased N mineralization rate, soil microorganism activities, or plant productivity (Rustad et al., 2001). Consequently, because of more extreme wet and dry periods, precipitation regimes will become more extreme and will inevitably have disproportionately large impacts on the C balance (Smith, 2011; Wu et al., 2011). Hence, a comprehensive study on Rs in response to N enrichment, altered precipitation (both enhanced and reduced precipitation or precipitation changes), warming, and their interactions is urgently needed to understand better the future consequences of global change on the C flux cycle. Therefore, to clarify these controversial and uncertain issues, it is necessary to compile all globally available data of individual biome-scale patterns following specific treatments, their interaction, and their amplitude. The scale and magnitude provide an opportunity to discover more about global Rs in relation to temperature, precipitation, and N addition.

Recently, several studies have investigated the responses of Rs to N, water, and warming changes by a meta-analysis of N addition (Janssens et al., 2010; Zhou et al., 2014), altered precipitation (frequency changes) (Du et al., 2020; Liu et al., 2016), and temperature changes (Carey et al., 2016; Rustad et al., 2001; Wang et al., 2014). Although published meta-analyses and case studies have increased our understanding of global Rs response to these factors, several limitations and uncertainties have restricted further progress. We will next expand on these issues. First, previous meta-analyses typically evaluate the response of Rs variables to

a single treatment in different biomes to determine if they stimulate, inhibit, or have a neutral effect on Rs. For example, Zhou et al. (2014) reported that N addition significantly increased the Rs by 12.4 % and 7.8 % in croplands and grasslands, respectively, but decreased it by 1.4 % in forests. Du et al. (2020) found that precipitation change differed significantly between grasslands and forests.

Second, although the quantitative effects of a single treatment have thus been well assessed, few studies consider the interactive effects of (i) N addition \times altered precipitation, (ii) N addition \times warming, (iii) altered precipitation \times warming, and (iv) N addition \times altered precipitation \times warming in different biomes. The only exception is a meta-analysis by Wu et al. (2011), who found that experimental warming and increased precipitation stimulated Rs. Ni et al. (2017) quantified the responses of soil C fluxes and equilibrium to the three single factors and their interactions with warming, whereas Zhou et al. (2016b) determined the responses of Rs and its two components to individual global change factors and the interactive effects of the multiple factors. Third, few meta-analyses have assessed the simultaneous impact of climate factors (mean temperature, precipitation, and N deposition) and soil properties (pH and soil moisture [SM]) on Rs. Responses may deviate owing to the physicochemical properties of soil or changes in the sensitivity of ecosystems to weather conditions (N deposition, mean annual temperature [MAT], and mean annual precipitation [MAP]). According to Zhong et al. (2016), Rs response to N enrichment is correlated with MAT and soil properties.

In this study, we investigated the mechanism by which N addition, altered precipitation, and temperature, separately and in combination, regulate the Rs. We conducted a meta-analysis of worldwide studies using field-based experiments and manipulation spanning different terrestrial ecosystems (forests, croplands, and grasslands) to address these knowledge gaps. Our analysis is unique among Rs studies because we synthesized the largest global dataset to date of Rs, totaling >14,500 observations of Rs response to N addition, altered precipitation, and altered soil temperature (Ts) experiments. The goal was to expand our knowledge regarding the response of Rs to these drivers, both separately and in combination, in different biomes. We investigated: (1) how Rs responds to the change in a single driver (N addition, altered precipitation, and warming) in different biomes; (2) whether there is evidence for interactive effects between N addition \times altered precipitation; N addition \times warming, and warming \times altered precipitation on the response of Rs; and (3) the role of ambient N addition, MAP, MAT, and soil properties in regulating the variation in ambient soil Rs emission. In this study, we used meta-analysis to assess Rs changes in response to single and interacting effects of N addition, altered precipitation, and warming and applied a structural equation model (SEM) to explore how Rs responses are controlled by environmental factors, particularly soil pH, SM, and Ts.

2. Materials and methods

2.1. Data collection and inclusion criteria

Peer-reviewed journal articles (before December 2020) were searched using ISI Web of Science and Google scholar with the following search term combinations: (soil respiration OR ecosystem respiration) AND (nitrogen OR N OR deposition OR addition OR application OR fertiliz* OR fertilizer* OR temperature OR warming OR precipitation OR rain OR rain* change precipitation frequency* OR soil moisture), and references within these articles were also searched. We chose the studies based on the following criteria

to avoid any bias in the choice of publications: (i) experiments were conducted in the field and had at least one pair of data (under control and treatment); (ii) in the studies, the initial environmental conditions and soil properties in the control and treatment plots were the same; (iii) only experiments conducted in terrestrial ecosystems were included; (iv) the means, standard deviations/errors, and sample sizes of variables in the control and treatment groups could be retrieved directly from text or tables or indirectly by digitizing graphs; (v) studies that measured Rs on multiple occasions for at least a full year, to account for seasonal variations and bias caused by a small number of sampling dates; and (vi) studies with more than one magnitude of precipitation, temperature, or N addition manipulation level or more than one vegetation type that were considered as independent treatments. In total, 110 papers regarding Rs studies met these criteria (Table S1) with 226 study sites, including cropland (17), forest (185), and grassland (24) sites (Fig. 1). When different publications included the same data, we recorded the data only once. In this study, we examined how Rs responds to three key environmental factors: N addition, precipitation (water availability/SM), and temperature (Ts). Within this framework, we suggest a set of four broad methods by which Rs can be changed along environmental gradients (Fig. 2).

2.2. Data extraction

Data were extracted from selected papers (Data S1), including Rs, Ts, SM, and soil pH, using data in the text, tables, figures, and appendices of these publications. We extracted the values, the number of replications, and the standard deviation of Rs for each site. When an original study reported results graphically, we used GetData Graph Digitizer v.2.20 (<http://www.getdata-graph-digitizer.com/>) to obtain numerical data.

For comparison and analysis, N addition rates per unit area (for both continuous and single addition experiments) were transformed to the unified unit of kg N ha⁻¹ yr⁻¹. We also extracted environmental factors: MAT, MAP, N deposition, fertilization regimes (addition rates), as well as latitude and longitude as recorded directly in the papers or cited papers. The environmental factors were extracted from the database at <http://www.worldclim.org/> using the location information (e.g., latitude and longitude) in case it was not reported. To test the differences in responses

of Rs to N addition, altered precipitation (= enhanced precipitation and reduced), and warming levels among biome types (cropland, forest, and grassland), we differentiated our analysis by categorizing the drivers into different classes: N deposition (<15, 15–25, and ≥ 25 kg N ha⁻¹ yr⁻¹); MAP (<1500 and ≥ 1500 mm); and MAT (<15 and ≥ 15 °C).

2.3. Data analysis

We evaluated the impacts of environmental conditions on Rs by using (i) meta-analysis to assess Rs changes in response to single and interacting effects of N addition, altered precipitation, and warming in experiments with both a control and treated plot (Section 2.3.1) and (ii) mixed-effect meta-regression analysis and SEMs to assess the relationship between Rs in control plots and environmental conditions (N deposition, MAP, MAT, soil pH, SM, and Ts) as detailed below.

2.3.1. Meta-analysis

The natural log-transformed response ratio was employed to quantify the effects of N addition, altered precipitation, and warming on Rs following the meta-analysis method described by Hedges et al. (1999):

$$RR = \ln \left(\frac{\bar{X}_t}{\bar{X}_c} \right) = \ln (\bar{X}_t) - \ln (\bar{X}_c), \quad (1)$$

where \bar{X}_t and \bar{X}_c were the observed values of treatment and control plots in each study, respectively. The log-ratio compares the relative difference between the treatments and controls. The meta-analyses were performed using the METAWIN software version 2.1 (Sinauer Associates, Inc. Sunderland, MA, USA).

The corresponding sampling variance of the response ratio was estimated as:

$$v = \frac{S_t^2}{n_t \bar{X}_t^2} + \frac{S_c^2}{n_c \bar{X}_c^2} \quad (2)$$

where n_t , n_c , S_t , S_c , \bar{X}_t , and \bar{X}_c are the sample sizes, standard deviations, and mean response values in the experimental and control groups, respectively.

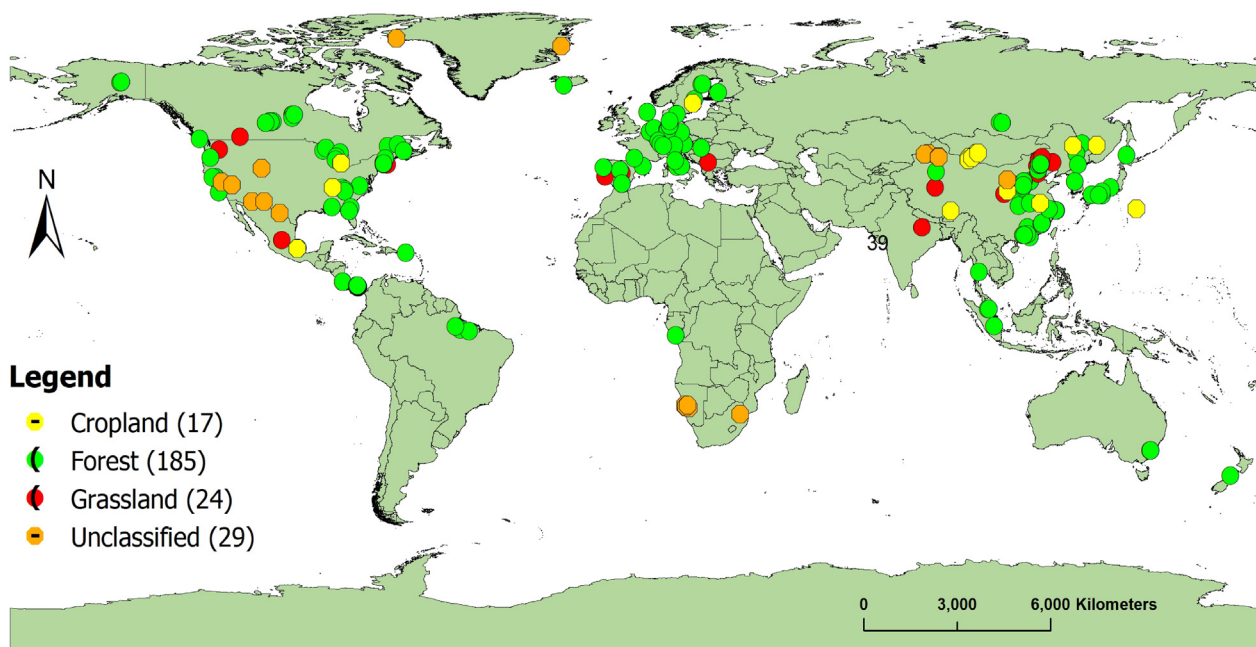


Fig. 1. Global distribution of N addition, precipitation change, and warming experiments selected in this meta-analysis. Numbers in parentheses are the actual number of sites in each biome from 110 papers.

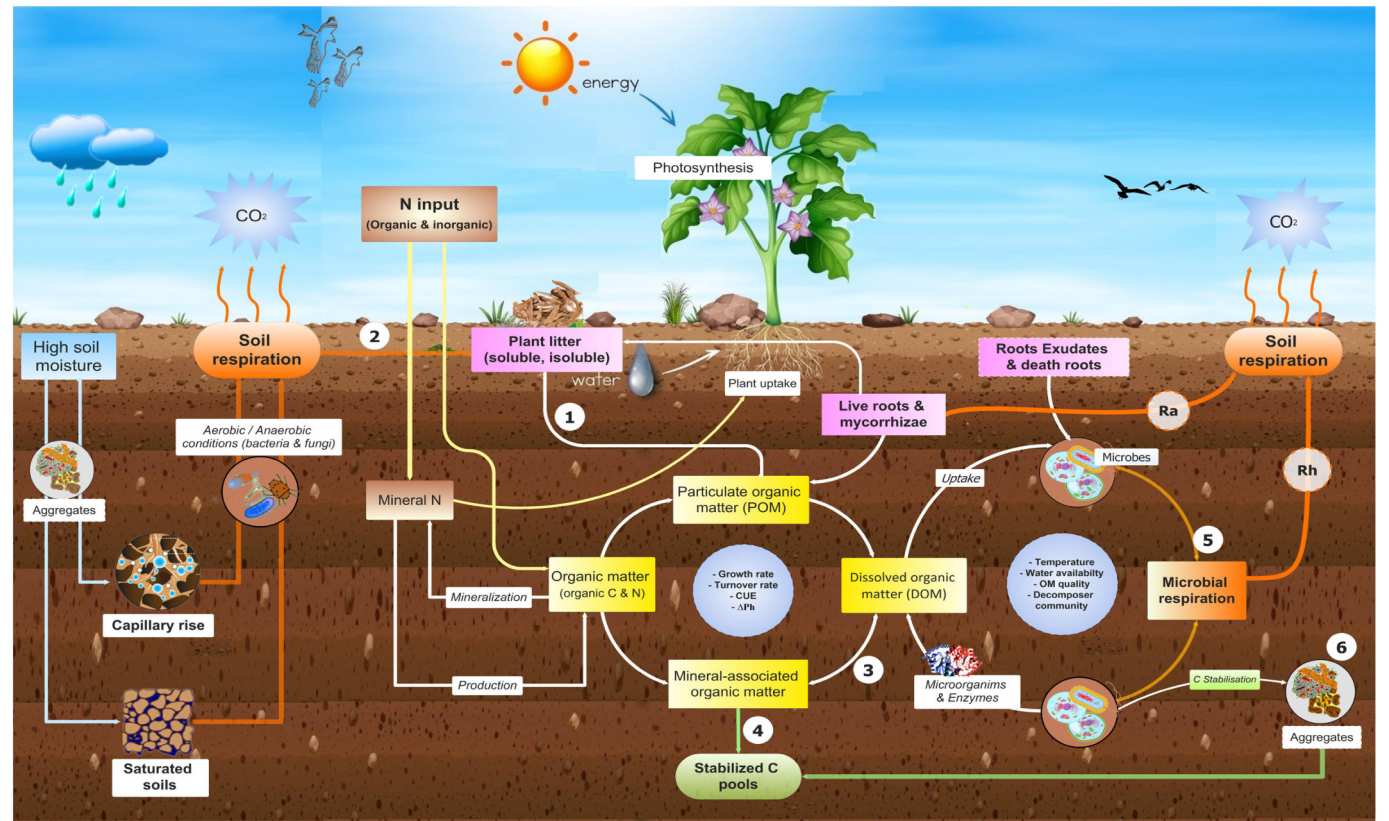


Fig. 2. Conceptual scheme depicting the potential mechanisms underlying soil respiration response to N addition, precipitation, and temperature. In the terrestrial biosphere, including the soil, the sources of C are input by plant litter, root litter and root exudates with photosynthesis being the ultimate driver, while C losses are respiration associated with SOM breakdown by microbes, the balance either resulting in a net gain or loss of C from the global soil C pool to the atmosphere. Carbon inputs from photosynthesis by terrestrial vegetation contribute to the C fixation. However, part of the carbon can be trapped in soil aggregates (a C sink), where it can remain undisturbed for decades or even centuries. Microbial organic matter input factors: organic matter quality, growth rate, turnover, carbon-use efficiency, and pH variation. The main drivers of decomposition: temperature, water availability, organic matter quality, and the decomposer community. 1 = Dissolution; 2 = Decomposition, 3 = Sorption and desorption; 4 = Low carbon availability (C stabilization); 5 = High carbon availability (C destabilization); 6 = Encapsulation in pores macro and microaggregates. OM: organic matter, CUE: carbon use efficiency, Ra = autotrophic soil respiration, Rh = heterotrophic soil respiration.

For literature sources where the standard error (SE) rather than standard deviation (SD) was reported, we recalculated the SD using:

$$SD = SE \times \sqrt{N} \tag{3}$$

where N is the number of replications.

The percentage changes for the variables caused by nutrient addition were calculated as follows:

$$\text{Change (\%)} = (e^{RR} - 1) \times 100\% \tag{4}$$

In addition, linear or logarithmic regression models were used to study the relationships between Rs values in the control plot and environmental

conditions (N deposition, MAP, and MAT) as well as different variables (soil pH, SM, and Ts).

In the evaluation of several analytical models, we used a linear model (Eq. (5)) or Gaussian peak shape function (Eq. (6)) (for all treatments) because it was the best-supported model for most biomes and provided an accurate maximum threshold (N addition, precipitation, and temperature) (Table 1).

$$y = a + bx, \tag{5}$$

$$y = a + \frac{b}{\sqrt{\frac{\pi}{4 \ln 2}}} e^{\frac{-4 \ln 2 (x - c)^2}{d^2}}, \tag{6}$$

Table 1
Regression parameters from linear (a, b) and non-linear (a, b, c, and d) models of soil respiration as function of N deposition, MAP and MAT. Rs ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$), MAP (mm), and MAT ($^{\circ}\text{C}$) are soil respiration, mean annual precipitation, and mean annual temperature at 10 cm depth, respectively.

Function	N deposition		Function	MAP		MAT
	Linear			Gaussian		Gaussian
Equation	$y = (2.53203) + (-0.0174817) \times x$		Equation	$y = a + b / (d \cdot \sqrt{\pi / (4 \cdot \ln(2))}) \cdot \exp(-4 \cdot \ln(2) \cdot (x - c)^2 / d^2)$		$y = a + b \cdot \exp(-0.5 \cdot ((x - c) / d)^2)$
Pearson's r	0.503		Reduced Chi-Sqr	9.91181		10.2694
Adj. R-Square (R^2)	0.334		Adj. R-Square	0.11258		0.09309
Intercept (a)	2.53 ± 0.26		a	-23.04242 ± 56.1332		-1.43413 ± 1.18838
Slope (b)	-0.017 ± 0.004		b	$203,965.10868 \pm 636,048.69353$		14.85888 ± 2.42742
			c	1815.58626 ± 59.93424		17.32882 ± 0.61289
			d	$6909.10011 \pm 7580.99825$		5.83901 ± 1.153
P	<0.05		-	<0.05		<0.05

c = threshold

where y represents soil respiration ($\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$) and x represents N deposition ($\text{kg N ha}^{-1} \text{ y}^{-1}$), or MAP (mm), or MAT ($^{\circ}\text{C}$). The efficiency of this model was validated using an interactive analysis of the linear and polynomial models (Eqs. (5) and (6)). The two curves overlapped at two locations, with the upper point corresponding to the established threshold.

2.3.2. Mixed-effect meta-regression analysis and SEM

In addition to Rs changes in response to N addition, altered precipitation, and warming, based on experimental data, we also evaluated the impacts of environmental conditions on Rs in control plots, using mixed-effect meta-regression analysis and SEMs. We used mixed-effect meta-regression analysis to assess the impact of N deposition, MAP, and MAT, Ts, and soil pH using the “glmulti” package in R version 4.1. The importance of each predictor was expressed as the sum of Akaike weights for models that included this factor. A cutoff of 0.8 was set to differentiate between important and unimportant predictors.

In addition, we used SEMs to analyze the relationships among Rs in control plots and N deposition, MAP, MAT, Ts, SM, and soil pH following different path models. A path model was developed based on the theoretical knowledge of major environmental factors regulating the variations in Rs during N enrichment, altered precipitation, and warming. Structural equation model testing was performed using the “Lavaan” package in R. We evaluated the conceptual model by goodness-of-fit statistics [p -value (χ^2) > 0.05, comparative fit index = 0.99, and Tucker–Lewis index = 0.91] and Akaike Information Criterion (AIC). A χ^2/df value between 0 and 2 indicated that the model is acceptable.

3. Results

3.1. Soil respiration responses to individual effects of N addition, water treatment, and warming in different biomes

Overall, the average response of Rs to N addition significantly increased the response of Rs in forests by 44 % (24 %; 73 %) but reduced it in croplands by –19 % (–34 %; –1 %), and grasslands by –25 % (–32 %; –17 %) ($P < 0.05$, for all biomes; Fig. 3a). Regarding altered precipitation treatment, the response of Rs was stimulated in forests (by 51 % [40 %; 60 %]) and croplands (by 17 % [11 %; 21 %]) ($P < 0.05$, for all biomes; Fig. 3a), but there were no significant effects on grasslands (6 % [1 %; 12 %]) (Fig. 3a). Furthermore, the response of Rs to warming increased by 62 % (53 %; 69 %) in forests, 14 % (–5 %; 35 %) in grasslands but decreased by –10 % (–16 %; –4 %) ($P < 0.05$; Fig. 3a). The response of Rs to N addition, water treatments, and warming differed considerably across treatments, biomes, and magnitude (Fig. S1, S2, and S3).

3.2. Soil respiration response to interactive effects of N addition, water treatment, and warming in different biomes (cropland, forest, and grassland)

The interaction between warming \times altered precipitation had a significant and positive impact on Rs in all biomes. Forests (by 92 % [85 %; 100 %]), grasslands (by 78 % [62 %; 93 %]), and croplands (by 45 % [36 %; 55 %]) were the most affected ($P < 0.05$; Fig. 3b). In contrast, the interaction between N addition \times warming only enhanced the response of Rs in croplands by 52 % (42 %; 63 %) and inhibited Rs in forests by –9 % (–11 %; –10 %) and grasslands by –23 % (–25 %; –20 %) ($P < 0.05$, for all biomes; Fig. 3b). In contrast, the interaction between N

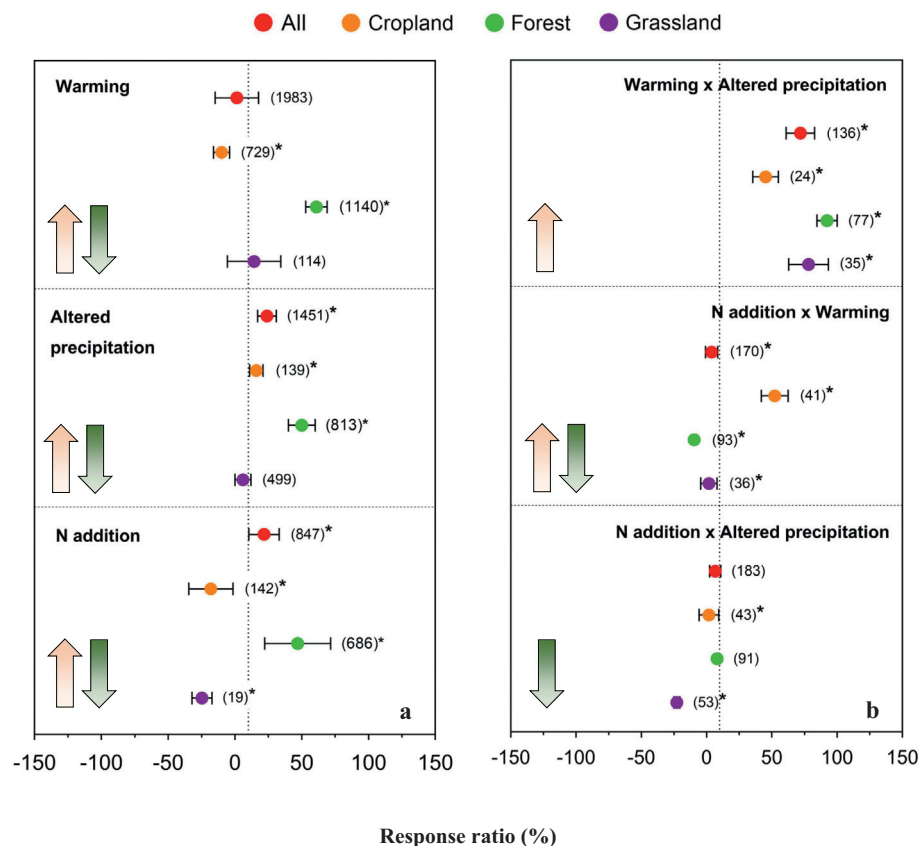


Fig. 3. Response ratios of soil respiration (Rs) to single factor (N addition, altered precipitation, and warming) (a) and their interactive interaction (N addition \times precipitation; N addition \times warming, and altered precipitation \times warming) (b) across biomes (cropland, forest, and grassland). Error bars represent 95 % confidence intervals (CIs), random effect model. The numbers in the brackets represent sample sizes. *Represents significant responses ($P < 0.05$) that are recognized if the 95 % CI does not overlap with zero. Red in the arrow means negative effect, and green means positive effect. The dashed lines represent 10 %.

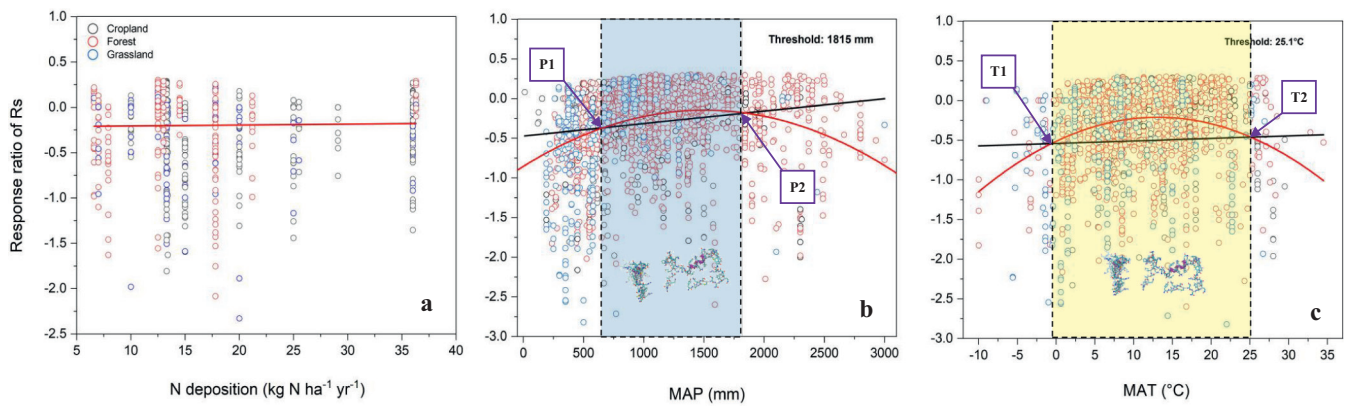


Fig. 4. Relationship between the response ratio of soil respiration and (a) N deposition, (b) mean annual precipitation (MAP), and (c) mean annual temperature (MAT) in control plots across all biomes. The *P* values represent the statistical significance between the magnitudes as determined using independent sample *t*-test. The yellow and blue area represents the microbial acclimation period during increasing precipitation and temperature respectively. Dashed horizontal lines show the threshold for MAP or MAT and the grey color represent the precipitation or temperature rates above the threshold at which soil respiration decreases. The yellow and blue area represents where the response of *R_s* increases. P1 and T1 = the levels at which temperature and precipitation stopped to rise linearly. P1 (MAP: 640 mm; *R_s* = 2.7 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$); T1 (MAT: 25.1 °C; *R_s* = 2.5 $\mu\text{mol CO}_2 \text{ m}^{-2} \text{ s}^{-1}$).

addition \times altered precipitation had no positive effects on any biome. Our findings indicated a slight increase of *R_s* response in forests by 8 % (7 %; 9 %) and in croplands by 1.8 % (− 6 %; 9 %) but a significant reduction in grasslands by 1.7 % (− 4 %; 8 %) ($P < 0.05$; Fig. 3b).

3.3. Effect of environmental factors on *R_s*

Because the amount of N deposition, precipitation, and temperature differed significantly among biomes, the relationships between *R_s* were analyzed in each type of biome (Fig. 4). Furthermore, our meta-analysis showed an increase or decrease in *R_s* after a precipitation threshold of 1815 mm (Fig. 4b). In addition, the best-fitted regression model with a positive linear relationship between *R_s* and MAT was obtained above the temperature threshold of 25.1 °C (Fig. 4c). These relationships of climate factors and N deposition with pH, SM, and Ts are illustrated in Fig. S4.

3.4. Relationships between *R_s* and abiotic factors

An SEM analysis of the cause-and-effect relationships between *R_s* and abiotic factors indicated that the effect of Ts on *R_s* was inhibited by MAP, soil pH, and SM but was stimulated by N deposition, MAT, and Ts (Fig. 5). Fig. S5 shows the response ratios of soil properties to N addition, altered precipitation, and warming. The statistical analysis on the standardized total effects (direct plus indirect effects) showed that SM (0.91; $P < 0.01$) had a direct impact and was the most dominant driver of *R_s* (Fig. S6a). Moreover, the model-averaged analysis revealed that SM and Ts have the greatest control in predicting the global *R_s* pathway (Fig. S6b). In addition, N deposition and the soil pH \times SM interaction had a significant and indirect effect on *R_s*, and only SM had a direct effect on *R_s* (Table S2).

4. Discussion

4.1. Effect of biomes on the response of *R_s* to individual treatments

4.1.1. Soil respiration response to N enrichment across biomes

Although the growth of forests is not much affected by exogenous N, our results showed that the response of *R_s* to N addition was significantly positive only in the forest ecosystems (Fig. 3) because the basal respiration of C-rich soil is generally higher than that of C-poor soils. This discrepancy in response among biomes is probably owing to a dense woody plant structure dominated by trees, shrubs, and herbaceous species of plants. It implies that nutrient release was not proportional to C release during mineralization in different treatments because of plant productivity and photosynthesis stimulation. For instance, C assimilated by plants is translocated to plant

organs and is used as a building material for storage, structural biomass, or as the substrate for respiration. As a result, an increase in N availability may increase the need for plants to invest C in N-absorbing mycorrhizal fungi with fine roots. This could cause a shift in C allocation toward aboveground tissue production (Rustad et al., 2001; Xu and Wan, 2008).

Nevertheless, the N status (N-sufficient or N-rich environments) and duration might also significantly influence the response of *R_s*. For instance, *R_s* is closely associated with nutrient processes, such as organic matter production, mineralization, and decomposition (Fig. 2). According to Luo and Zhou (2006), N addition can exacerbate conditions of “N saturation,” resulting in N leaching and runoff and little change in *R_s*. Furthermore, our results showed that the response of *R_s* is highly pronounced in the short-term (Fig. S7) and low-level across biomes, suggesting that the current and near-future N enrichment rates may not induce the emission of a large amount of soil CO_2 into the atmosphere in the global forest ecosystem. For example, the highest response of *R_s* rates occurred in forests <3 years old, which is in line with the findings of a previous study (Zhang et al., 2014).

4.1.2. Soil respiration response to altered precipitation in different biomes

Our findings suggest that the response of *R_s* to altered precipitation significantly differed among ecosystem types, with a positive response in forests and croplands (Fig. 3), probably owing to the available soil water content. We observed an increase in the response of *R_s* with the increase in precipitation (Fig. S8), indicating that high soil water content promotes *R_s* emission. This finding highlights the crucial role of soil water availability in regulating soil and microbial respiratory processes, microbial biomass, and climate change responses (Liu et al., 2009). However, the observed change in the response of *R_s* to altered precipitation may partly be a transient response because SM might limit *R_s* at extreme values (Tingey et al., 2006), which is in line with our result. Fig. 4b shows that this trend occurred at precipitation rates below a threshold (1815 mm). Several threshold values in precipitation have been reported to affect *R_s* patterns in different ecosystems (Table 2) (Liu et al., 2009). However, the threshold values are often site-specific (Xu et al., 2004) and can be very different depending on the ecosystem types because of limiting factors (e.g., nutrients, water, and solar radiation uptake by plants and microbes).

In contrast, the response of *R_s* to altered precipitation was significantly lower in grasslands than in other biomes (Fig. 3), probably because it is a water-limited ecosystem or because of its low soil water-holding capacity. According to Emmett et al. (2004), SM can become a controlling factor only at very high or at deficient moisture levels. Consequently, an increase in SM may suppress plant biomass and productivity, soil and microbial activities and result in an overall decrease in *R_s* (Liu et al., 2009; Wu et al.,

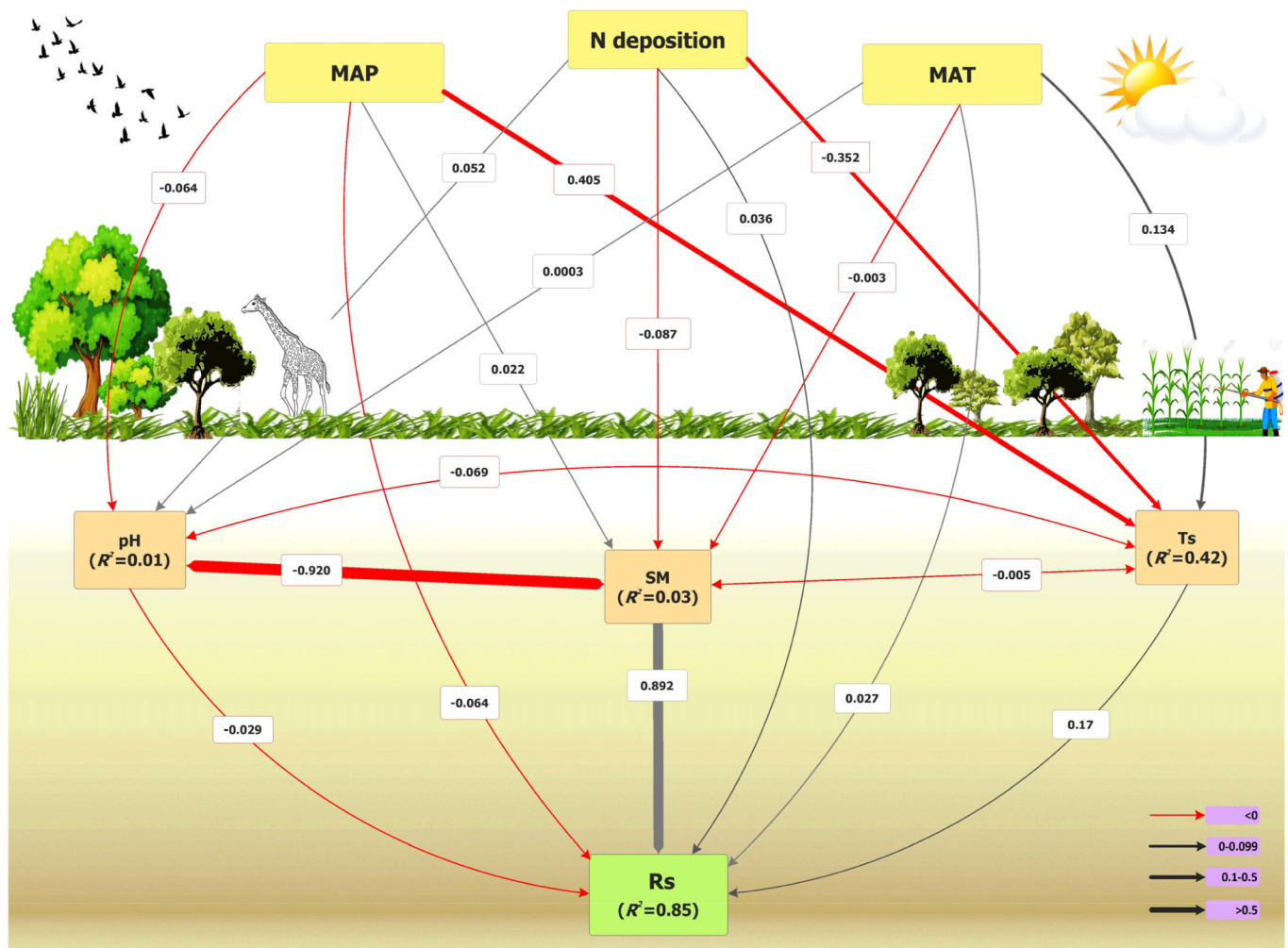


Fig. 5. Structural equation model (SEM) evaluating the direct and indirect effects of controlling drivers on soil respiration (Rs) in control plots following MAP, N deposition, and MAT at the global scale ($n = 66$). SEM reveals the influences of soil moisture (SM), soil temperature (Ts), soil pH, mean annual precipitation (MAP), mean annual temperature (MAT) and nitrogen (N) deposition. Black and red lines indicate positive and negative relationships, respectively. Line thickness represents the magnitude of the strength of the relationship. Numbers adjacent to arrows are standardized path coefficients, indicating the effect size of the relationship. The proportion of variance explained appears alongside the response variable in the model. Goodness-of-fit statistics for the model are shown below the model. The black arrows indicate significant positive relationships, whereas the red arrows indicate significant negative relationships, where the significance level was set at $\alpha = 0.05$. Numbers beside the arrows are standardized coefficients. R^2 refers to the variation degree of the variable interpreted by all paths from the combination of the fixed and random effects.

2011), but this only occurs when precipitation change is extreme (Du et al., 2020) or if the initial SM content was high (Li et al., 2008). Moreover, the difference in soil water-holding capacity and infiltration within ecosystems can optimize plant production and favor aerobic or anaerobic conditions. Likewise, high soil water availability will promote water-saturated soils and favor anaerobic conditions, which will inhibit Rs.

4.1.3. Soil respiration response to warming in different biomes

In agreement with our study, previous studies have reported that warming increased Rs (Mertens et al., 2001; Wu et al., 2011). Following warming events, many potential mechanisms could have contributed to the enhancement of Rs: the high activity rate of microbes and roots (Bergner et al., 2004; Sardans et al., 2008), an increase in C input from plant production (Luo et al., 2009; Welker et al., 1999), or microbial and root acclimation (Arft et al., 1999; Zogg et al., 1997). However, soil warming tests frequently enhance Rs in the early stages, followed by a slowing of respiration until a certain temperature magnitude is reached (Table 2) (Melillo et al., 2017). This trend is supported by Fig. 3c, which shows an increase, and then, a dramatic decrease in Rs rates with a temperature threshold of 25.1 °C (T2).

The short-lived increase in the response of Rs below the threshold has been suggested to be because of the depletion of the labile soil C pool (Melillo et al., 2002), the oxidation of most labile soil C compounds (Rustad et al., 2001) or the adverse effect of warming on microbial C use efficiency (Frey et al., 2001). We hypothesized that the stage between T1 (MAT: -0.1 °C) and the temperature threshold (T2) (MAT: 25.1 °C) (Fig. 4c) corresponds to the time needed for soil decomposers (i.e., bacteria, fungi, protists, and metazoans) or microbial community composition and functional structure (Guo et al., 2020) to acclimate to warming, which leads to slowed soil C decomposition, and thus, Rs. This finding suggests that high temperatures may reduce Rs by limiting the ability of microbes to break down organic materials.

4.2. Interaction effects of dual combination treatments on Rs response

4.2.1. Interaction between altered warming \times precipitation

In this study, we found that the interaction of warming \times altered precipitation increased Rs rates (Fig. 3). However, these Rs responses may differ depending on the specific environmental conditions, microbial communities (Lellei-Kovács et al., 2011), threshold values (Table 2), or the effect of

Table 2

Drivers thresholds in meta-analysis and experimental studies with respect to single and multifactor responses in different ecosystems.

Drivers	References	Function	Ecosystems	Threshold	Trend	Implication
N input	Zhong et al. (2016)	Parabolic relationship	Boreal, temperate tropical forests, croplands, wetlands, deserts and grasslands	50 kg ha ⁻¹ yr ⁻¹	Increase and decrease	<ul style="list-style-type: none"> - N enrichment is not significantly related to global Rs - The response of Rs to future N enrichment should be predicted separately for each biome.
Precipitation	Wei et al. (2010)	Responded non-linearly	Naturally-regenerated forests EBF, ENF and MF	813 mm	Increase and decrease	<ul style="list-style-type: none"> - Regression method used matter (e.g., piecewise-regression model, linear regression might lead to different responses)
	Raich and Schlesinger (1992)	Linearly	Terrestrial and wetland	1800, 1113 and 813 mm	Increase and decrease	
	This study	Linearly	Terrestrial and wetland	100 mm	Frequency	
Temperature	Carey et al. (2016)	Log-quadratic	Forests, croplands, grasslands Boreal forest and northern scrubland biomes	1815 mm ~ 25 °C	Increase and decrease	<ul style="list-style-type: none"> - Acclimation of soil communities to warmer conditions is likely to have greater consequences for soil C dynamics - N enrichment can promote the growth of herbaceous plants - Rs to warming is highly heterogeneous - Root growth and root C content are two key factors of Rs - Ecosystem turnover rate may increase (i.e., C residence decrease)
	, Zhou et al. (2014)	Parabolic relationship	Desert Forests, croplands, grasslands, wetlands deserts	55 °C 15 °C	Increase and decrease	
	Parker et al. (1983), O'connell (1990)	Asymptote fitted curves	Deserts, forests	41 °C	Increase and decrease	
	Kesik et al. (2006)	Parabolic relationship	Croplands	4–32 °C	Increase and decrease	
	This study	Hypernomial	Forests, croplands, grasslands	25 °C	Increase and decrease	
		Hypernomial	Forests, croplands, grasslands	25 °C	Increase and decrease	

Deciduous broadleaf forest (DBF), evergreen needleleaf forest (ENF) and needle and broadleaf mixed forest (MF).

one variable on the range of the other variable. For example, a previous study reported that interaction of high temperatures with low water availability might limit the increase in Rs but this response might be more sensitive to temperature under high moisture content (10 to 25 %) than under low moisture conditions (below 7.5 % volumetrically) (Carlyle and Than, 1988). Such conditions might increase the water use efficiency of plant species to cope with water stress, producing more energy and cutting down on water costs. For example, Lellei-Kovács et al. (2011) suggested clear thresholds for SM controls on Rs, which would limit moisture limitation for soil biological activity to 4.0 vol%.

Another aspect to consider is treatment frequency, which can be described as the alternation or succession of wet and dry episodes (e.g., rewetting effect and Birch effect) or the C type (labile or recalcitrant C) being used by the microbial community. When dry soils rewet, the respiration rate increases rapidly owing to the immediate availability of nutrients for microbial activity (Lee et al., 2004; Orchard and Cook, 1983). This occurs when liquid contact is re-established with a solid surface whose starting temperature is higher than the maximum temperature at which the surface can be wet. Furthermore, Frey et al. (2013) indicated that chronically warmer soils have lower amounts of readily available C and that the C utilized by the microbial population is likely more recalcitrant. Hence, the warming × altered precipitation effect on Rs stimulated the priming effect mechanism, by limiting the capacity of any ecosystem to stabilize C in depth and resulting in soil C loss.

4.2.2. Interaction between N addition × warming

This study showed that the interactive effect of N addition × warming enhances Rs with the temperature effect dominating over the effect of N addition. This is most likely because warming affects Rs directly but also indirectly though enhanced N availability. Previous studies have shown that Rs is influenced mainly by Ts (Zhou et al., 2007) and substrate supply (Bahn et al., 2008), but both are correlated as chronic soil warming enhances decomposition, thereby increasing soil N availability (N mineralization) (Frey et al., 2014). Any change in N inputs or Ts may affect Rs by influencing the temperature sensitivity of Rs or by altering the belowground C supply (e.g., belowground biomass and litter inputs) (Mo et al., 2008; Xu and Wan, 2008). The increase in Rs in response to N addition × warming (Fig. 3) observed in the present study supports this idea. According to Contosta et al. (2011) soil processes might be perturbed much more strongly by an increase in Ts than by that in N addition. They observed, for example, an increase of 14 % in Rs in the N addition plot, whereas the Rs in the warming plots increased by 44 %. Furthermore, we found that

both N addition × warming had a strong and positive effect on the soil pH (Fig. 5). Taken together, these observations indicate that warming stimulates the effect of N addition by increasing N mineralization. Similarly, previous studies in temperate regions have reported that warming stimulates net N mineralization (Melillo et al., 2011) by reducing the competition of microbes in relative N-limited temperate forests (Liu et al., 2017). However, a combination of long-term and altered seasons with simultaneous warming and N addition experiments and modeling studies are required to address future seasonal changes in soil C and N budgets (Zhang et al., 2014).

4.2.3. Interaction between N addition × altered precipitation

A considerable amount of evidence reviewed in this study highlighted a decrease in Rs owing to the interactive effect of N addition × altered precipitation (Fig. 3). Water availability is well known to be a critical determinant of nutrient uptake for plants because it controls nutrient transport and microbial activity may influence the transformation of N (Kübert et al., 2019). The literature supports this argument. For example, Song et al. (2020) found that the response of Rs was negatively correlated to N addition in wet years owing to the decrease in heterotrophic respiration via the increase in soil microbial biomass and that activity induced by increased precipitation was, to some extent, suppressed by N addition, thus causing a decline in heterotrophic respiration (Treseder, 2008; Zhou et al., 2016a). The decreased soil pH could partly contribute to the adverse effects of N addition on Rs, resulting in a decline in microbial biomass and activity (Li et al., 2018). Nevertheless, Yue et al. (2018) indicated that the interactive responses of Rs could vary depending on precipitation or N addition rate. They reported that the response of Rs was reduced with increasing N deposition and precipitation on account of the inhibitor effect of available soil N content when SM is sufficient and microbial activity is high. Hence, N addition × altered precipitation would exert severe C-limitation and inhibitory effects on bacterial growth and activity (Song et al., 2020). This finding indicates the critical role played by the N addition rate in modifying the stimulating effects of soil water availability on Rs at the global scale. In contrast, Yan et al. (2010) found that N addition increased the Rs in the wet year but decreased Rs in a dry year in a temperate steppe in northern China. In a temperate region of northeast China, Chen et al. (2017) also found that N addition in average rainfall years was mainly owing to increased autotrophic respiration. Interactive responses of Rs to fertilizer application and water addition resulted in increased Rs (Wang et al., 2013). A meta-analysis of precipitation and N enrichment interactive experiments showed highly significant positive effects on Rs (Zhou et al., 2016a).

4.3. Effects of climate factors and soil properties on Rs efflux

The SEM analysis demonstrated that SM and Ts were the key factors regulating Rs. As an available nutrient for plant growth, the increase in soil N availability and temperature directly had significant and positive effects on Rs, whereas SEM showed an adverse effect of water availability and soil pH on Rs variations (Fig. 5). However, changes in precipitation were positively correlated with changes in SM, and changes in SM also had a positive correlation with Rs. The results can be interpreted as follows: the proportional change in soil properties induced by MAP was more significant than that by N enrichment and MAT, consistent with findings of Chen et al. (2017). This assumption is supported by the high mean average of Rs responses and the contrasting effects of different treatments on SM (Figs. S1 and S2). Several studies have observed that precipitation-induced moisture changes accompany Ts changes; as a result of this, SM is more important than Ts in regulating Rs (Emmett et al., 2004; Knapp et al., 2008).

The model-averaged analysis indicates that Rs rates were well predicted by combining SM and Ts (Fig. S6) ($P < 0.05$). These results indicated that Rs depends mainly on variations in SM and Ts in global climate change. For example, Ts and SM are widely considered to be two critical factors in controlling Rs processes (Yue et al., 2018). Similar conditions have been observed in several field experiments (Liu et al., 2016; Matías et al., 2012). The present study reveals that the positive effects of MAP are much stronger than the adverse effects of increasing temperature on SM, whereas the inhibitor effect of water is suppressed by MAT. Consequently, MAP had an indirect and positive effect on Rs and acted as a critical factor regulating Rs globally.

5. Conclusions

Our findings show that the impacts of major global change drivers, i.e., N addition, altered precipitation, and warming, on Rs vary with biome. All three drivers significantly increased Rs in forests by approximately 50 %. However, N addition decreased Rs in croplands and grasslands, whereas altered precipitation and warming increased and decreased Rs in croplands, respectively, and the impacts on grassland were insignificant. Across all biomes, the responses of Rs to altered precipitation and warming followed a Gaussian response, increasing up to a threshold of 1800 mm and 25 °C, respectively, above which respiration rates decreased with a further increase in precipitation and temperature. Our work suggests that the dual interaction of warming \times altered precipitation promotes belowground CO₂ emission, thus enhancing global warming. In general, the interactive effect of N addition \times altered precipitation decreases soil respiration. Soil moisture was identified as a primary driver of Rs. Given these findings, we recommend future research on warming vs. changed precipitation to better forecast and understand the interaction between Rs and climate change.

CRediT authorship contribution statement

Mbezele Junior Yannick Ngaba: Conceptualization, Methodology, Visualization, Data curation, Writing – original draft, Investigation. **Yves Uwiragiye:** Visualization, Data curation, Investigation. **Roland Bol:** Supervision, Writing – review & editing. **Wim de Vries:** Supervision, Writing – review & editing. **Jinshi Jian:** Supervision, Writing – review & editing. **Jianbin Zhou:** Funding acquisition, Supervision, Writing – review & editing.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare no competing financial interests.

Acknowledgments

National Natural Science Foundation of China (No. 41671295), National Key Research & Development Program of China (No. 2017YFD0200106), 111 Project (No. B12007).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2022.159808>.

References

- Arft, A., Walker, M., Gurevitch, J., Alatalo, J., Bret-Harte, M., Dale, M., et al., 1999. Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecol. Monogr.* 69, 491–511.
- Bahn, M., Rodeghiero, M., Anderson-Dunn, M., Dore, S., Gimeno, C., Drösler, M., et al., 2008. Soil respiration in European grasslands in relation to climate and assimilate supply. *Ecosystems* 11, 1352–1367.
- Bergner, B., Johnstone, J., Treseder, K.K., 2004. Experimental warming and burn severity alter soil CO₂ flux and soil functional groups in a recently burned boreal forest. *Glob. Chang. Biol.* 10, 1996–2004.
- Carey, J.C., Tang, J., Templer, P.H., Kroeger, K.D., Crowther, T.W., Burton, A.J., et al., 2016. Temperature response of soil respiration largely unaltered with experimental warming. *Proceedings of the National Academy of Sciences* 113, 13797–13802.
- Chen, T., Huang, Q., Liu, M., Li, M., La, Q., Deng, S., et al., 2017. Decreasing net primary productivity in response to urbanization in Liaoning Province, China. *Sustainability* 9, 162.
- Contosta, A.R., Frey, S.D., Cooper, A.B., 2011. Seasonal dynamics of soil respiration and N mineralization in chronically warmed and fertilized soils. *Ecosphere* 2, 1–21.
- Du, Y., Wang, Y.P., Su, F., Jiang, J., Wang, C., Yu, M., et al., 2020. The response of soil respiration to precipitation change is asymmetric and differs between grasslands and forests. *Glob. Chang. Biol.* 26, 6015–6024.
- Emmett, B.A., Beier, C., Estiarte, M., Tietema, A., Kristensen, H., Williams, D., et al., 2004. The response of soil processes to climate change: results from manipulation studies of shrublands across an environmental gradient. *Ecosystems* 7, 625–637.
- Frey, S., Gupta, V., Elliott, E., Paustian, K., 2001. Protozoan grazing affects estimates of carbon utilization efficiency of the soil microbial community. *Soil Biol. Biochem.* 33, 1759–1768.
- Frey, S.D., Lee, J., Melillo, J.M., Six, J., 2013. The temperature response of soil microbial efficiency and its feedback to climate. *Nat. Clim. Chang.* 3, 395–398.
- Frey, S.D., Ollinger, S., Ke, Nadelhoffer, Bowden, R., Brzostek, E., Burton, A., et al., 2014. Chronic nitrogen additions suppress decomposition and sequester soil carbon in temperate forests. *Biogeochemistry* 121, 305–316.
- Gruber, N., Galloway, J.N., 2008. An earth-system perspective of the global nitrogen cycle. *Nature* 451, 293–296.
- Guo, X., Gao, Q., Yuan, M., Wang, G., Zhou, X., Feng, J., et al., 2020. Gene-informed decomposition model predicts lower soil carbon loss due to persistent microbial adaptation to warming. *Nat. Commun.* 11, 1–12.
- Hedges, L.V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* 80, 1150–1156.
- Huntingford, C., Zelazowski, P., Galbraith, D., Mercado, L.M., Sitch, S., Fisher, R., et al., 2013. Simulated resilience of tropical rainforests to CO₂-induced climate change. *Nat. Geosci.* 6, 268–273.
- Janssens, I., Dieleman, W., Luyssaert, S., Subke, J.-A., Reichstein, M., Ceulemans, R., et al., 2010. Reduction of forest soil respiration in response to nitrogen deposition. *Nat. Geosci.* 3, 315–322.
- Jt, Carlyle, Than, U.B., 1988. Abiotic controls of soil respiration beneath an eighteen-year-old pinus radiata stand in South-Eastern Australia. *The J. Ecol.* 654–662.
- Kesik, M., Blagodatsky, S., Papen, H., Butterbach-Bahl, K., 2006. Effect of pH, temperature and substrate on N₂O, NO and CO₂ production by *Alcaligenes faecalis* p. J. *Appl. Microbiol.* 101, 655–667.
- Knapp, A.K., Beier, C., Briske, D.D., Classen, A.T., Luo, Y., Reichstein, M., et al., 2008. Consequences of more extreme precipitation regimes for terrestrial ecosystems. *Bioscience* 58, 811–821.
- Kübert, A., Götz, M., Kuester, E., Piayda, A., Werner, C., Rothfuss, Y., et al., 2019. Nitrogen loading enhances stress impact of drought on a semi-natural temperate grassland. *Front. Plant Sci.* 1051.
- Le Quéré, C., Jackson, R.B., Jones, M.W., Smith, A.J., Abernethy, S., Andrew, R.M., et al., 2020. Temporary reduction in daily global CO₂ emissions during the COVID-19 forced confinement. *Nat. Clim. Chang.* 10, 647–653.
- Lee, X., Wu, H.J., Sigler, J., Oishi, C., Siccamo, T., 2004. Rapid and transient response of soil respiration to rain. *Glob. Chang. Biol.* 10, 1017–1026.
- Lellei-Kovács, E., Kovács-Láng, E., Botta-Dukát, Z., Kalapos, T., Emmett, B., Beier, C., 2011. Thresholds and interactive effects of soil moisture on the temperature response of soil respiration. *Eur. J. Soil Biol.* 47, 247–255.
- Li, H.-j., Yan, J.-x., Yue, X.-f., Wang, M.-b., 2008. Significance of soil temperature and moisture for soil respiration in a Chinese mountain area. *Agric. For. Meteorol.* 148, 490–503.
- Li, J., Huang, Y., Xu, F., Wu, L., Chen, D., Bai, Y., 2018. Responses of growing-season soil respiration to water and nitrogen addition as affected by grazing intensity. *Funct. Ecol.* 32, 1890–1901.
- Liu, L., Wang, X., Lajeunesse, M.J., Miao, G., Piao, S., Wan, S., et al., 2016. A cross-biome synthesis of soil respiration and its determinants under simulated precipitation changes. *Glob. Chang. Biol.* 22, 1394–1405.

- Liu, W., Zhang, Z., Wan, S., 2009. Predominant role of water in regulating soil and microbial respiration and their responses to climate change in a semiarid grassland. *Glob. Chang. Biol.* 15, 184–195.
- Liu, X., Yang, Z., Lin, C., Giardina, C.P., Xiong, D., Lin, W., et al., 2017. Will nitrogen deposition mitigate warming-increased soil respiration in a young subtropical plantation? *Agric. For. Meteorol.* 246, 78–85.
- Luo, Y., Zhou, X., 2006. Soil respiration and the Environment.
- Luo, Y., Sherry, R., Zhou, X., Wan, S., 2009. Terrestrial carbon-cycle feedback to climate warming: experimental evidence on plant regulation and impacts of biofuel feedstock harvest. *GCB Bioenergy* 1, 62–74.
- Matías, L., Castro, J., Zamora, R., 2012. Effect of simulated climate change on soil respiration in a Mediterranean-type ecosystem: rainfall and habitat type are more important than temperature or the soil carbon pool. *Ecosystems* 15, 299–310.
- Melillo, J., Steudler, P., Aber, J., Newkirk, K., Lux, H., Bowles, F., et al., 2002. Soil warming and carbon-cycle feedbacks to the climate system. *Science* 298, 2173–2176.
- Melillo, J.M., Butler, S., Johnson, J., Mohan, J., Steudler, P., Lux, H., et al., 2011. Soil warming, carbon–nitrogen interactions, and forest carbon budgets. *Proc. Natl. Acad. Sci.* 108, 9508–9512.
- Melillo, J.M., Frey, S.D., DeAngelis, K.M., Werner, W.J., Bernard, M.J., Bowles, F.P., et al., 2017. Long-term pattern and magnitude of soil carbon feedback to the climate system in a warming world. *Science* 358, 101–105.
- Mertens, S., Nijs, I., Heuer, M., Kockelbergh, F., Beyens, L., Kerckvoorde, A.V., et al., 2001. Influence of high temperature on end-of-season tundra CO₂ exchange. *Ecosystems* 4, 226–236.
- Metcalfe, D.B., Fisher, R., Wardle, D.A., 2011. Plant communities as drivers of soil respiration: pathways, mechanisms, and significance for global change. *Biogeosciences* 8, 2047–2061.
- Mo, J., Zhang, W., Zhu, W., Gundersen, P., Fang, Y., Li, D., et al., 2008. Nitrogen addition reduces soil respiration in a mature tropical forest in southern China. *Glob. Chang. Biol.* 14, 403–412.
- Ni, X., Yang, W., Qi, Z., Liao, S., Xu, Z., Tan, B., et al., 2017. Simple additive simulation overestimates real influence: altered nitrogen and rainfall modulate the effect of warming on soil carbon fluxes. *Glob. Chang. Biol.* 23, 3371–3381.
- O'connell, A., 1990. Microbial decomposition (respiration) of litter in eucalypt forests of South-Western Australia: an empirical model based on laboratory incubations. *Soil Biol. Biochem.* 22, 153–160.
- Orchard, V.A., Cook, F., 1983. Relationship between soil respiration and soil moisture. *Soil Biol. Biochem.* 15, 447–453.
- Parker, L., Miller, J., Steinberger, Y., Whitford, W., 1983. Soil respiration in a chihuahuan desert rangeland. *Soil Biol. Biochem.* 15, 303–309.
- Pries, C.E.H., Castanha, C., Porras, R., Torn, M., 2017. The whole-soil carbon flux in response to warming. *Science* 355, 1420–1423.
- Raich, J.W., Schlesinger, W.H., 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. *Tellus B* 44, 81–99.
- Rustad, L., Campbell, J., Marion, G., Norby, R., Mitchell, M., Hartley, A., et al., 2001. A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia* 126, 543–562.
- Sardans, J., Peñuelas, J., Estiarte, M., Prieto, P., 2008. Warming and drought alter C and N concentration, allocation and accumulation in a Mediterranean shrubland. *Glob. Chang. Biol.* 14, 2304–2316.
- Smith, M.D., 2011. An ecological perspective on extreme climatic events: a synthetic definition and framework to guide future research. *J. Ecol.* 99, 656–663.
- Song, H., Yan, T., Wang, J., Sun, Z., 2020. Precipitation variability drives the reduction of total soil respiration and heterotrophic respiration in response to nitrogen addition in a temperate forest plantation. *Biol. Fertil. Soils* 56, 273–279.
- Tingey, D., Lee, E., Waschmann, R., Johnson, M., Rygielwicz, P., 2006. Does soil CO₂ efflux acclimatize to elevated temperature and CO₂ during long-term treatment of Douglas-fir seedlings? *New Phytol.* 170, 107–118.
- Treseder, K.K., 2008. Nitrogen additions and microbial biomass: a meta-analysis of ecosystem studies. *Ecol. Lett.* 11, 1111–1120.
- Wang, X., Zhao, X., Li, Y., Zuo, X., Cui, D., Qu, H., et al., 2013. Responses of soil respiration to simulated precipitation and nitrogen, phosphorus additions in horqin Sandy land of northeastern China. *Fresenius Environ. Bull.* 22, 12.
- Wang, X., Liu, L., Piao, S., Janssens, I.A., Tang, J., Liu, W., et al., 2014. Soil respiration under climate warming: differential response of heterotrophic and autotrophic respiration. *Glob. Chang. Biol.* 20, 3229–3237.
- Wei, W., Weile, C., Shaopeng, W., 2010. Forest soil respiration and its heterotrophic and autotrophic components: global patterns and responses to temperature and precipitation. *Soil Biol. Biochem.* 42, 1236–1244.
- Welker, J., Brown, K., Fahnestock, J., 1999. CO₂ flux in arctic and alpine dry tundra: comparative field responses under ambient and experimentally warmed conditions. *Arct. Antarct. Alp. Res.* 31, 272–277.
- Wu, Z., Dijkstra, P., Koch, G.W., Peñuelas, J., Hungate, B.A., 2011. Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Glob. Chang. Biol.* 17, 927–942.
- Xu, L., Baldocchi, D.D., Tang, J., 2004. How soil moisture, rain pulses, and growth alter the response of ecosystem respiration to temperature. *Glob. Biogeochem. Cycles* 18.
- Xu, W., Wan, S., 2008. Water- and plant-mediated responses of soil respiration to topography, fire, and nitrogen fertilization in a semiarid grassland in northern China. *Soil Biol. Biochem.* 40, 679–687.
- Yan, L., Chen, S., Huang, J., Lin, G., 2010. Differential responses of auto- and heterotrophic soil respiration to water and nitrogen addition in a semiarid temperate steppe. *Glob. Chang. Biol.* 16, 2345–2357.
- Yue, P., Cui, X., Gong, Y., Li, K., Goulding, K., Liu, X., 2018. Impact of elevated precipitation, nitrogen deposition and warming on soil respiration in a temperate desert. *Biogeosciences* 15, 2007–2019.
- Zhang, C., Niu, D., Hall, S.J., Wen, H., Li, X., Fu, H., et al., 2014. Effects of simulated nitrogen deposition on soil respiration components and their temperature sensitivities in a semi-arid grassland. *Soil Biol. Biochem.* 75, 113–123.
- Zhong, Y., Yan, W., Shangguan, Z., 2016. The effects of nitrogen enrichment on soil CO₂ fluxes depending on temperature and soil properties. *Glob. Ecol. Biogeogr.* 25, 475–488.
- Zhou, J., Fu, B., Gao, G., Lü, Y., Liu, Y., Lü, N., et al., 2016a. Effects of precipitation and restoration vegetation on soil erosion in a semi-arid environment in the loess plateau. *China. Catena* 137, 1–11.
- Zhou, L., Zhou, X., Zhang, B., Lu, M., Luo, Y., Liu, L., et al., 2014. Different responses of soil respiration and its components to nitrogen addition among biomes: a meta-analysis. *Glob. Chang. Biol.* 20, 2332–2343.
- Zhou, L., Zhou, X., Shao, J., Nie, Y., He, Y., Jiang, L., et al., 2016b. Interactive effects of global change factors on soil respiration and its components: a meta-analysis. *Glob. Chang. Biol.* 22, 3157–3169.
- Zhou, X., Wan, S., Luo, Y., 2007. Source components and interannual variability of soil CO₂ efflux under experimental warming and clipping in a grassland ecosystem. *Glob. Chang. Biol.* 13, 761–775.
- Zogg, G.P., Zak, D.R., Ringelberg, D.B., White, D.C., MacDonald, N.W., Pregitzer, K.S., 1997. Compositional and functional shifts in microbial communities due to soil warming. *Soil Sci. Soc. Am. J.* 61, 475–481.