






RESEARCH ARTICLE

Ambient precipitation determines the sensitivity of soil respiration to precipitation treatments in a marsh

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Abstract

The effects in field manipulation experiments are strongly influenced by amplified interannual variation in ambient climate as the experimental duration increases. Soil respiration (SR), as an important part of the carbon cycle in terrestrial ecosystems, is sensitive to climate changes such as temperature and precipitation changes. A growing body of evidence has indicated that ambient climate affects the temperature sensitivity of SR, which benchmarks the strength of terrestrial soil carbon–climate feedbacks. However, whether SR sensitivity to precipitation changes is influenced by ambient climate is still not clear. In addition, the mechanism driving the above phenomenon is still poorly understood. Here, a long-term field manipulation experiment with five precipitation treatments (−60%, −40%, +0%, +40%, and +60% of annual precipitation) was conducted in a marsh in the Yellow River Delta, China, which is sensitive to soil drying–wetting cycle caused by precipitation changes. Results showed that SR increased exponentially along the experimental precipitation gradient each year and the sensitivity of SR (standardized by per 100 mm change in precipitation under precipitation treatments) exhibited significant interannual variation from 2016 to 2021. In addition, temperature, net radiation, and ambient precipitation all exhibited dramatic interannual variability; however, only ambient precipitation had a significant negative correlation with SR sensitivity. Moreover, the sensitivity of SR was significantly positively related to the sensitivity of belowground biomass (BGB) across 6 years. Structural equation modeling and regression analysis also showed that precipitation treatments significantly affected SR and its autotrophic and heterotrophic components by altering BGB. Our study demonstrated that ambient precipitation determines the sensitivity of SR to precipitation treatments in marshes. The findings underscore the importance of ambient climate in regulating ecosystem responses in long-term field manipulation experiments.

KEYWORDS

ambient precipitation, field manipulation experiment, marshes, precipitation treatments, sensitivity, soil respiration

1 | INTRODUCTION

The impacts of climate changes on ecosystem carbon cycling have been extensively studied through field observations and manipulation experiments (Chen et al., 2019; Han et al., 2018; Li, Zhou, et al., 2020; Liu et al., 2021; Wang et al., 2021; Zou et al., 2018). Relative to observations, manipulative experiments are very powerful in enabling replication, controlling confounding factors, and studying multiple scenarios simultaneously (Beier et al., 2012; Langley et al., 2018). In general, the previous climate change experiments have typically demonstrated treatment effects by comparison with control conditions (Li, Zhou, et al., 2020; Liu et al., 2018; Zhang et al., 2017). However, the intensified climate changes amplify the intra and interannual variability in ambient climate, and the experiment's effects on ecosystem dynamics may be profoundly altered by ambient climate as the experimental duration increases (Langley et al., 2018; Montgomery et al., 2020; Wang et al., 2021). For instance, ambient climate determines the directional trend of alpine meadow aboveground net primary productivity under the 10-year warming and grazing treatments (Liu et al., 2021). Moreover, some evidence indicated that ambient precipitation is the key factor to regulate the response of the ecosystem carbon cycling to 7-year field warming (Jung et al., 2019; Wang, Song, et al., 2020) and 6-year N-addition treatments (Song et al., 2020).

Soil respiration (SR), mainly composed of soil autotrophic respiration and soil heterotrophic respiration (Yu et al., 2017; Zhang, Li, et al., 2019), is the largest source of carbon flux from the terrestrial ecosystem to the atmosphere (Bond-Lamberty & Allison, 2010; Liu et al., 2016; Wang et al., 2019). And its dynamics will be critically important for the accurate prediction of the potential for carbon sequestration in terrestrial ecosystems (Qu et al., 2019; Zhang, Zhao, et al., 2019). Therefore, in the context of climate change, the sensitivity of SR to environmental changes and its potential regulatory mechanism must be determined to provide an important reference for modeling the terrestrial carbon cycle. A growing body of evidence from field manipulation experiments demonstrated SR is sensitive to changes in temperature (Chen et al., 2022; Li, Leroy, et al., 2021; Wang et al., 2018). Moreover, the sensitivity of SR to temperature changes is a key parameter in benchmarking the intensity of terrestrial soil carbon–climate feedback (Zhao et al., 2019; Zou et al., 2018), which has been widely applied in the evaluation of global carbon cycle models (Harte et al., 2015; Montgomery et al., 2020; Sun et al., 2022).

In addition to changes in temperature, SR is also sensitive to precipitation changes (Deng, Hui, et al., 2017; Du et al., 2020; Yu et al., 2019; Zhang et al., 2015). For example, since the limiting factors of SR may shift between water limitation and soil nutrient and oxygen limitation under precipitation changes in different biomes and treatment years (Liu et al., 2014; Zhao et al., 2016), not only positive (Deng, Aras, et al., 2017; Huang et al., 2015) but also negative (Han et al., 2018; Jiang et al., 2013) responses of SR along the precipitation gradient have been found in previous field precipitation manipulation experiments. The intensified Earth's hydrological cycle under climate changes has resulted in an increase in interannual variability of precipitation over the land surface (Wang et al., 2021; Wilcox et al., 2017).

Furthermore, global climate models forecast continued increases in the magnitude of interannual variation in precipitation (Curtis, 2019; Wang et al., 2021). However, previous field precipitation manipulation experiments ignored the above-mentioned interannual variability in ambient precipitation, the sensitivity of SR to precipitation changes that registered only as a deviation from untreated controls (Du et al., 2020; Liu et al., 2016; Zhang, Li, et al., 2019). As a consequence, the findings based on the above process may potentially pose a challenge to providing accurate information for ecosystem models (Beier et al., 2012; Liu et al., 2021).

Due to high primary productivity and low rates of soil organic matter decomposition (Duarte et al., 2013; Han et al., 2018; Mcleod et al., 2011), marshes are considered one of the densest carbon sinks in the biosphere and have great potential to mitigate climate change (Macreadie et al., 2019; Spivak et al., 2019). In addition, in marshes, all of which are in the transition zone between land and water, the ecosystem is strongly affected by the interaction between surface water and groundwater (Cheng et al., 2020; Chu et al., 2021; Zhong et al., 2016). Since the groundwater table in marshes is close to the soil surface, a small amount of precipitation can completely saturate the soil profile (Chu et al., 2018; Han et al., 2018). Moreover, inundated or waterlogged soils are often observed after large precipitation events (Han et al., 2015; Sun et al., 2022). As a result, the soils in marshes exposed to shallow groundwater are sensitive to precipitation changes and may easily induce the drying–wetting cycle of soil, which can regulate ecosystem carbon cycling, such as SR. Given that both soil drought in the dry season and water saturation or flooding in the rainy season in marshes (Han et al., 2015; Hoover et al., 2017; Wei et al., 2021), it is of great significance to investigate whether the sensitivity of SR to long-term precipitation treatments is influenced by ambient precipitation. However, as there have been no *in situ* long-term precipitation manipulation experiments conducted in marshes, the apparent regulation of ambient precipitation on the sensitivity of SR to precipitation treatments in this biome and its underlying mechanisms remains unknown.

To explore how inter-annual variability in ambient precipitation regulates the sensitivity of SR to precipitation treatments, a 6-year (2016–2021) field manipulative experiment with five precipitation treatments (–60%, –40% of annual precipitation, control [annual precipitation], and +40%, +60% of annual precipitation) was conducted in a marsh in the Yellow River Delta, China. The specific objectives that we addressed in this study include (1) how does ambient precipitation regulate the sensitivity of SR to precipitation treatment? (2) what are the pathways of ambient precipitation influencing SR sensitivity to precipitation treatments?

2 | MATERIALS AND METHODS

2.1 | Site description

This study was conducted in the natural marshes (37°45′50″N, 118°59′24″E), which is located in the Yellow River Delta, Shandong, China. The mean annual temperature of this site is 12.9°C with

daily maximum and minimum mean temperatures of 26.7°C in July and -2.8°C in January, respectively. The mean annual precipitation is 606 mm with approximately 74% concentrated from May to September. The soil texture of the experimental site is mainly sandy clay loam, with the soil type gradually varying from flavor-aquic soil to saline soil (Guan et al., 2017; Han et al., 2018). Due to the salinization in the dry season and the long-term flooding in the rainy season of the marshes (Han et al., 2015; Hoover et al., 2017; Wei et al., 2021), the main founding species in this place are flood-tolerant *Phragmites australis* and salt-tolerant *Suaeda salsa*, while other associated species including *Tamarix chinensis*, *Imperata cylindrica*, and *Triarrhena sacchariflora*.

2.2 | Experimental design

Based on the interannual variation in annual precipitation (-41.2% to +54.8%) over the past 54 years (from 1961 to 2014) at the experimental site (Han et al., 2018), the field manipulative precipitation experiment initiated in October 2014 included five precipitation treatments: 60% (P - 6) and 40% (P - 4) precipitation decrease, a control (C), and 40% (P + 4) and 60% (P + 6) precipitation increase. Rather than a nested design based on multiple blocks, this experiment was established using a completely randomized block design on the natural vegetation and soil at the Yellow River Delta Ecological Research Station of the Coastal Wetland, Chinese Academy of Science (<http://hhm.cern.ac.cn/>). In all, 20 plots in total were randomly assigned to the five precipitation treatments, with each treatment being randomly repeated four times (Figure S1; see Li, Han, et al., 2021, for detailed information about the experimental design). Net radiation, air temperature, and ambient precipitation were monitored every 0.5 h using a four-component net radiometer, temperature probe, and tipping bucket rain gauge as described elsewhere (Chu et al., 2019; Han et al., 2015). In addition, the above data were monitored continuously throughout the experimental period and average data every 30 min were stored on a data logger (Em50; Decagon).

2.3 | Soil property and vegetation biomass measurements

Surface (0–10 cm) soil volumetric moisture content (SM), soil temperature (ST), and soil electrical conductivity (EC) in each plot were continuously measured every 15 s using 20 sets of soil three-parameter sensors in the center of each plot (5TE soil three-parameter sensor; Decagon). Three soil parameters data were monitored continuously throughout the experimental period and average data every 30 min were stored on a data logger (Em50; Decagon). In addition, an oven-drying method based on the soil bulk density and soil water content was adopted to standardize the volumetric soil moisture content. In particular, the daily dynamics of volumetric water content was converted into daily dynamics of soil mass water content using the relationship

coefficient between soil mass water content and volumetric water content for each month of the study period.

During the experimental period from 2016 to 2021, aboveground biomass (AGB) was harvested in October by harvesting the aboveground tillers within one-quarter of the 1 × 1 m quadrats in each plot in different places, dried at 65°C for 48 h, and weighed. At the same time, belowground biomass (BGB) was determined by extracting roots from 20 soil samples at a depth of 40 cm and determining the dry mass of root biomass by drying at 65°C to constant weight. Total vegetation biomass (TB) is the sum of AGB and BGB.

2.4 | SR measurements

Due to the deep collar being able to exclude about 88%–91% of newly grown roots (Zhang, Li, et al., 2019), the mini-trenching method, which has a comparable partitioning effect with other methods to separate the SR components (Subke et al., 2011), was applied to measure SR and soil heterotrophic respiration. Specifically, a shallow polyvinyl chloride polymer collar (21 cm in diameter and 8 cm in height) was permanently installed into the soil at the center of each plot with 3 cm protruding above the ground level to measure the rate of total SR. Correspondingly, a deep polyvinyl chloride polymer collar (21 cm in diameter and 40 cm in height) was permanently installed to measure the rate of soil heterotrophic respiration. In addition, the rate of soil autotrophic respiration was calculated as the difference between soil heterotrophic respiration and total SR. All living plants inside the collars were carefully clipped from the soil surface to exclude aboveground plant respiration 1 or 2 days prior to the measurements. SR was monitored once every 15 days from 2016 to 2017, once every 10 days in 2018 and 2019 using an LI-8100 infrared gas analyzer (Li-Cor, Inc.) connected to an 8100-103 SR chamber and once every 15 days from 2020 to 2021 using an LI-7810 infrared gas analyzer (Li-Cor, Inc.). And soil heterotrophic respiration has been measured at the same frequency as total SR since 2018. The measurements were collected between 8:00 am and 12:00 pm (local time) for eliminating diurnal variation.

2.5 | Statistical analysis

To determine whether the effects of precipitation treatments on soil factors and biological factors vary from year to year, a two-factor repeated measures analysis of variance (ANOVA) was used to examine the effect of year, precipitation treatments, and their potential interactions on soil properties (SM, ST, and EC), vegetation biomass (AGB, BGB, and TB), and SR. If there was a significant effect ($p < .05$) in the two-way ANOVA, the nonlinear (exponential) regression analyses were applied to evaluate the relationships between annual precipitation and environmental factors and SR under different precipitation treatments from 2016 to 2021 (Li, Han, et al., 2021). The sensitivity of SR to precipitation treatments was calculated for each of the experimental years:

$$SR = SR_0 \times e^{b \times PPT} \quad (1)$$

The coefficient $b \times 100$ values of the relationships were used as the sensitivity of SR to precipitation treatments (i.e., response standardized by per 100mm change in precipitation under precipitation treatments; Batbaatar et al., 2021; Byrne et al., 2016; Huxman et al., 2004). The sensitivities of soil properties (SM, ST, and EC) and vegetation biomass (AGB, BGB, and TB) to precipitation treatments were also calculated using the above method.

To explore the regulation and underlying mechanism of ambient climate on the sensitivity of SR to precipitation treatments, we first used linear regressions to describe the relationship between ambient precipitation, net radiation, and air temperature and the sensitivity of SR to precipitation treatments from 2016 to 2021, respectively. Second, we applied linear models to explore the relationship between variables (soil properties and vegetation biomass) sensitivities and the sensitivity of SR to precipitation treatments from 2016 to 2021. Third, the structural equation model (SEM) of SM, ST, EC, AGB, and BGB under precipitation treatments as predictors for SR was established to examine the direct and indirect effects of driving factors of precipitation treatments on SR over 6 years (AMOS 20.0; Amos Development Co.). The fit of the model was evaluated using the χ^2 -test ($p > .05$), the index of goodness of fit index (GFI $> .90$), and the comparative fit index (CFI $> .90$) to evaluate whether the model was a reasonable explanation of the observed pattern. Lastly and more importantly, the relationships between soil autotrophic respiration and soil heterotrophic respiration and variables (soil properties and

vegetation biomass) in 2019 were developed to explore the internal mechanism of precipitation treatments affecting total SR. In addition, one-factor ANOVA with Tukey honestly significant difference test was conducted to assess the effect of precipitation treatments on SR and its autotrophic and heterogeneous components in 2019. The long-term (1961–2021) trends of precipitation variability (PV) were calculated based on a 30-year moving sum (the number of years included in each PV during a consecutive 30-year period). All statistical analyses with a significance level of 0.05 were performed using SPSS 23.0 (SPSS), and figures were made by Origin version 2021b (OriginLab Inc.).

3 | RESULTS

3.1 | Interannual variations of environmental factors and SR under precipitation treatments

From 2016 to 2021, both precipitation treatments and years had significant effects on SM, ST, EC, AGB, BGB, and TB, but no significant interaction effect was detected in the study for any of the above factors except SM, AGB, and TB (Figure 1a–e; Figure S4; Table 1). During the entire experimental period (2016–2021), not only precipitation treatments and years had significant effects on SR, but the interaction of the two also significantly influenced SR (Table 1). SR among five field precipitation treatments all showed similar dramatic interannual variability across 6 years, with a sudden drop in 2017 and a gradual recovery in the following years (Figure 1f).

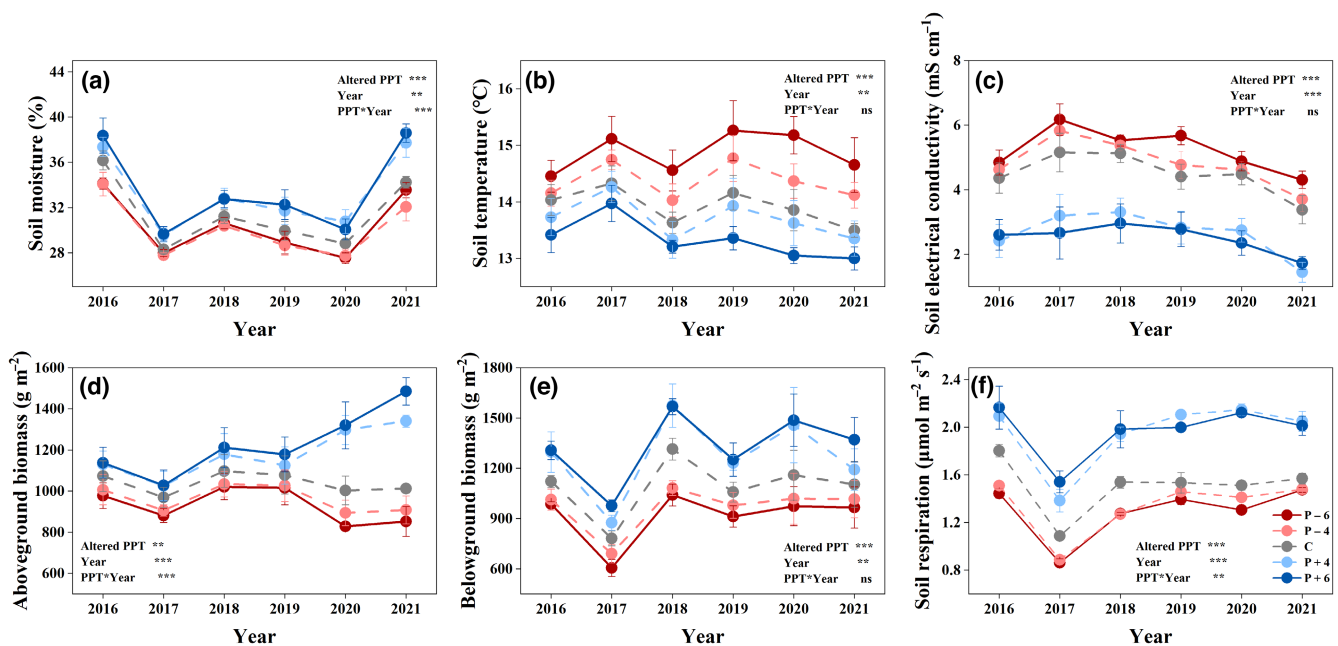


FIGURE 1 Interannual variations of soil moisture (a), soil temperature (b), soil electric conductivity (c), aboveground biomass (d), belowground biomass (e), and soil respiration under different precipitation treatments over 6 years (2016–2021). Results of the two-way analysis of variance were shown in the subplot. “P – 6”, and “P – 4”: 60% and 40% decreases in precipitation, respectively; “C”: ambient precipitation; “P + 4”, and “P + 6”: 40% and 60% increases in precipitation, respectively. PPT, precipitation treatment. Significance levels: * $p < .05$, ** $p < .01$, *** $p < .001$.

TABLE 1 Results of two-factor repeated measures analysis of variance for the effects of year, precipitation treatments, and their interaction on soil moisture (SM), soil temperature (ST), soil electric conductivity (EC), the aboveground biomass (AGB), the belowground biomass (BGB), the total vegetation biomass (TB), and soil respiration (SR) over 6 years (2016–2021) of the study.

Dependent variable	SM (% vol)		ST (°C)		EC (mS cm ⁻¹)		AGB (g m ⁻²)		BGB (g m ⁻²)		TB (g m ⁻²)		SR (μmol m ⁻² s ⁻¹)	
	df	F	df	F	df	F	df	F	df	F	df	F	df	F
Year	3.02	368.07***	5	38.14***	2.82	58.34***	3.02	17.04***	2.04	45.20***	2.30	55.74***	5	227.35***
Precipitation	4	4.39*	4	4.12*	4	9.86***	4	4.02*	4	4.67*	4	115.18***	4	54.10***
Year × precipitation	12.06	4.02***	20	1.17	11.29	1.78	12.08	10.05***	8.14	1.00	9.18	3.23**	20	4.11***

* $p < .05$; ** $p < .01$; *** $p < .001$.

3.2 | Relationship between ambient climate and the sensitivity of SR to precipitation treatments

During the whole experimental period from 2016 to 2021, net radiation and air temperature showed similar temporal variation with the highest value in August and the lowest value in February (Figure S2a,b). And ambient precipitation across the six study years (2016–2021) also exhibited dramatic interannual variability ranging from -21.05% to +20.87% compared with the long-term (1961–2021) annual mean precipitation (605.6 mm; Figure S3).

Our results exhibited that the annual SR showed an exponential increase along the experimental precipitation gradient (all $p < 0.05$) from 2016 to 2021 (Figure 2a). The sensitivity of SR to precipitation treatments varied with years, with the highest sensitivity of SR in 2017 and the lowest in 2021, followed by 2016 (Table S1). In addition, the ambient precipitation exhibited a significantly negative relationship with the sensitivity of SR to precipitation treatments ($R^2 = .90$, $p < 0.01$, Figure 2b). However, both net radiation ($R^2 = .24$, $p = .33$, Figure 2c) and air temperature ($R^2 = .21$, $p = 0.37$, Figure 2d) had no significant relationship with the sensitivity of SR to precipitation treatments across 6 years.

3.3 | Pathways of ambient precipitation influencing the sensitivity of SR to precipitation treatments

When exploring the pathways of ambient precipitation influencing the sensitivity of SR to precipitation treatments, we found that among all soil factors and biological factors (Figure 3; Figure S5), the sensitivity of SR was only significantly positively related to the sensitivity of BGB to precipitation treatments across the six study years (2016–2021; $R^2 = .87$, $p < .01$, Figure 3e).

The SEM analysis showed that precipitation manipulation affected SM directly, then the altered SM regulated SR through direct and indirect pathways (EC, AGB, and BGB) over the 6 years. Finally, the variation of SR across 6 years was predominantly determined by SM, EC, and BGB, which were explained in the model by 47%, 36%, and 36%, respectively (Figure 4a). Furthermore, based on linear regression analysis of the autotrophic and heterotrophic components of SR and BGB under different precipitation treatments in 2019, our results found that the BGB was significantly positively related to the soil autotrophic respiration ($R^2 = .70$, $p < .01$; Figure 4b) and soil heterotrophic respiration ($R^2 = .60$, $p < .01$; Figure 4c), respectively.

4 | DISCUSSION

4.1 | Effect of ambient precipitation on SR sensitivity to precipitation treatments

In this study, through quantifying the sensitivity as changes in SR per 100 mm unit of precipitation (Figure 2a), we examined how ambient

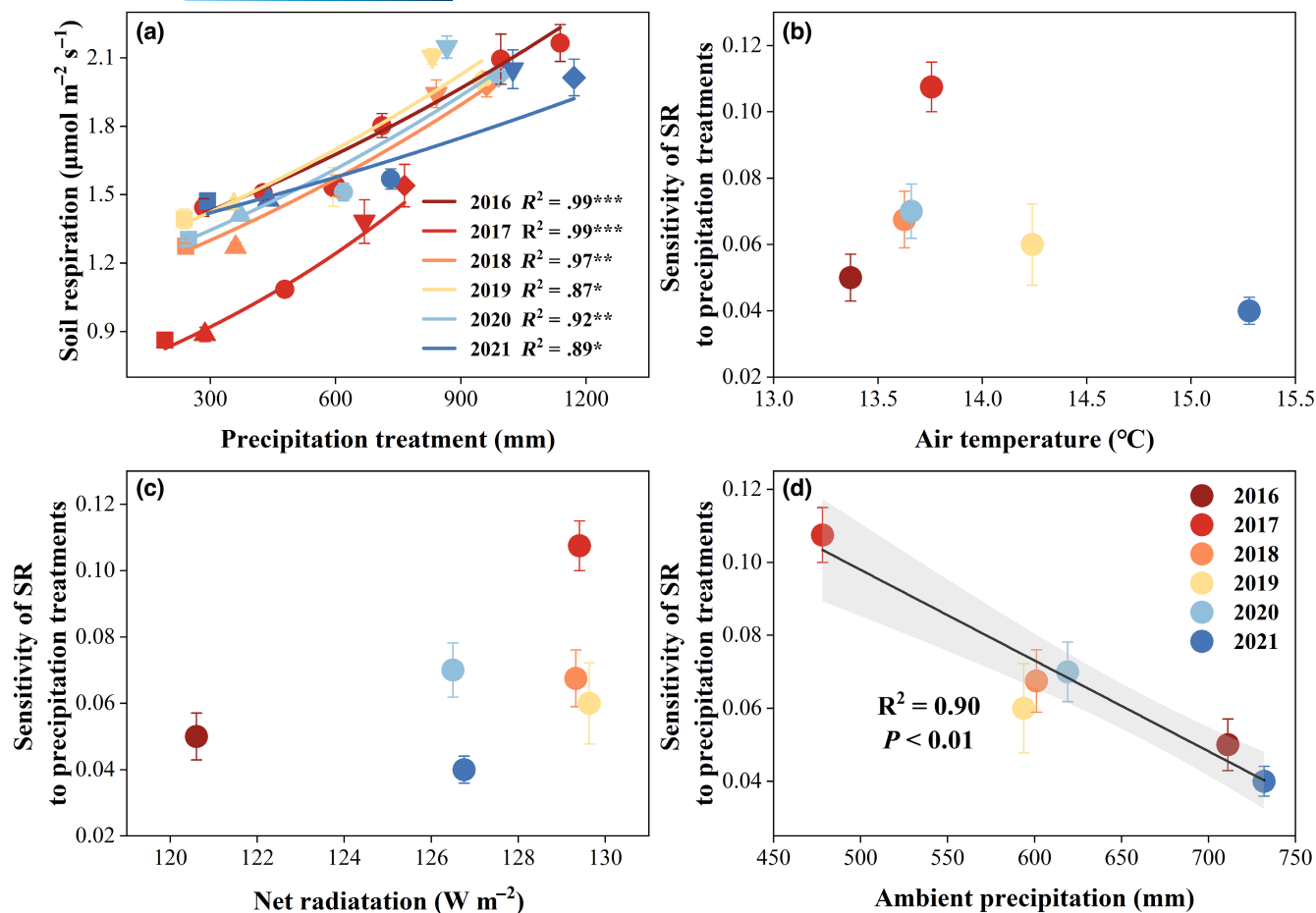


FIGURE 2 Exponential regression between soil respiration (SR) and annual precipitation under different precipitation treatments (a) and the relationship between the sensitivity of SR to precipitation treatments and ambient precipitation (b), net radiation (c), and air temperature (c) across 6 years (2016–2021). The black and dotted lines indicate linear regression. Dashed lines indicate 95% confidence intervals of the regression. Different shapes indicate precipitation treatments, and the square and regular triangle represent the 60% and 40% decreases in precipitation, respectively, the circle represents ambient precipitation, and the inverted triangle and diamond represent 40% and 60% increases in precipitation, respectively. *** $p < .001$, ** $p < .01$, * $p < .05$.

precipitation regulated the impact of field precipitation treatments on the carbon cycle of marsh ecosystems. Our study found that there was an inconsistent directional trend (i.e., a negative relationship) between the sensitivity of SR to precipitation treatments and ambient precipitation based on a 6-year field precipitation manipulation experiment. And similar results also have been found in some multi-year field manipulation experiments (Batbaatar et al., 2021; Jung et al., 2019; Song et al., 2020; Wang, Song, et al., 2020). For example, the interannual variation of precipitation in the growing season was positively correlated with the metric standardized change percentages of growing-season SR relative to warming in the Tibetan alpine grassland (Wang, Song, et al., 2020). Similarly, PV has dominated the response of SR and soil heterotrophic respiration to nitrogen addition in a temperate forest plantation (Song et al., 2020).

Our results showed clear evidence that ambient precipitation determines the sensitivity of SR to precipitation treatments in the marsh, which might have strong implications for long-term field manipulation experiments under intensified ambient climate (Dangal et al., 2017; Korth et al., 2015). The importance of ambient climate

in long-term field manipulation experiments highlighted by our study was consistent with the conclusions of previous studies that ambient climate plays a crucial role in regulating ecosystem functions (community stability and ecosystem carbon cycle; Chen et al., 2017; Jung et al., 2019; Liu et al., 2021). For instance, field warming experiments not only underpredict plant phenological responses to climate change (Wolkovich et al., 2012), but also shows similar but faster changes in vegetation community composition compared to that in ambient plots (Harte et al., 2015).

4.2 | Mechanisms of ambient precipitation determining SR sensitivity to precipitation treatments

Our study illustrated that the sensitivity of SR showed a significant positive relationship with the sensitivity of BGB to precipitation treatments during the entire experimental period (Figure 3e), demonstrating that the changes in BGB under precipitation treatments dominate the response of SR to altered precipitation. This could

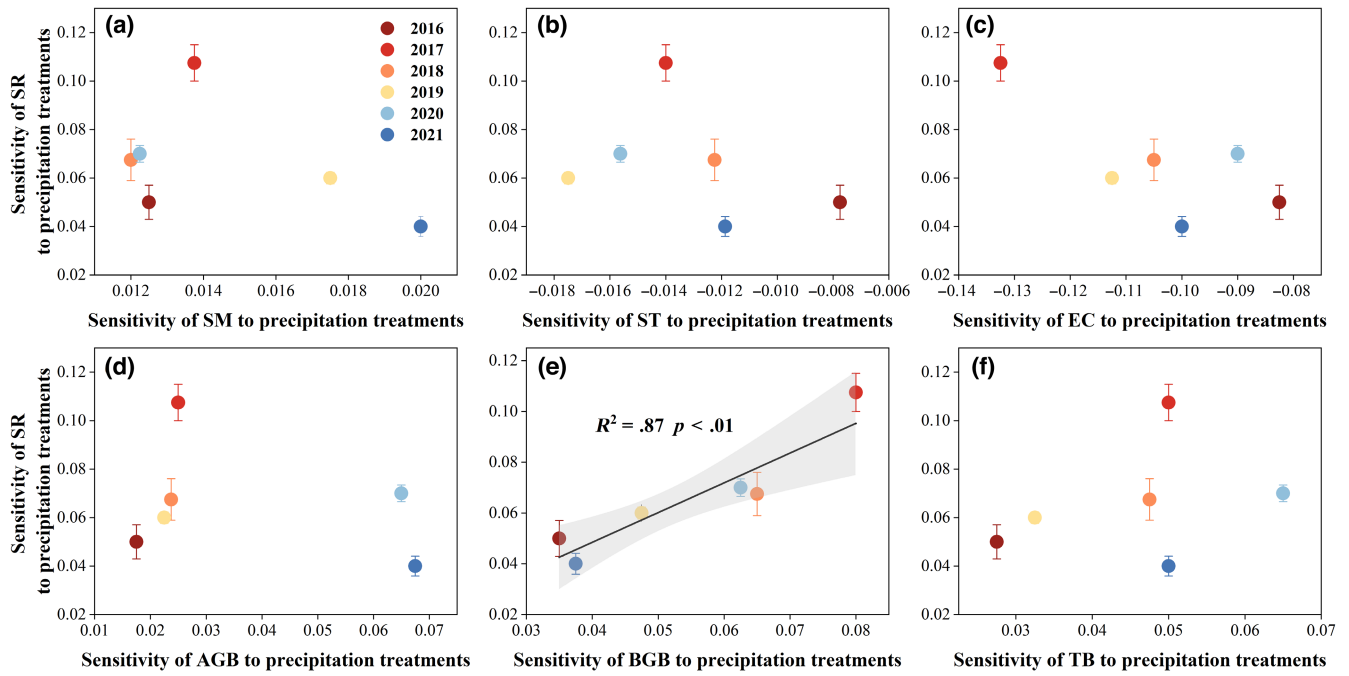
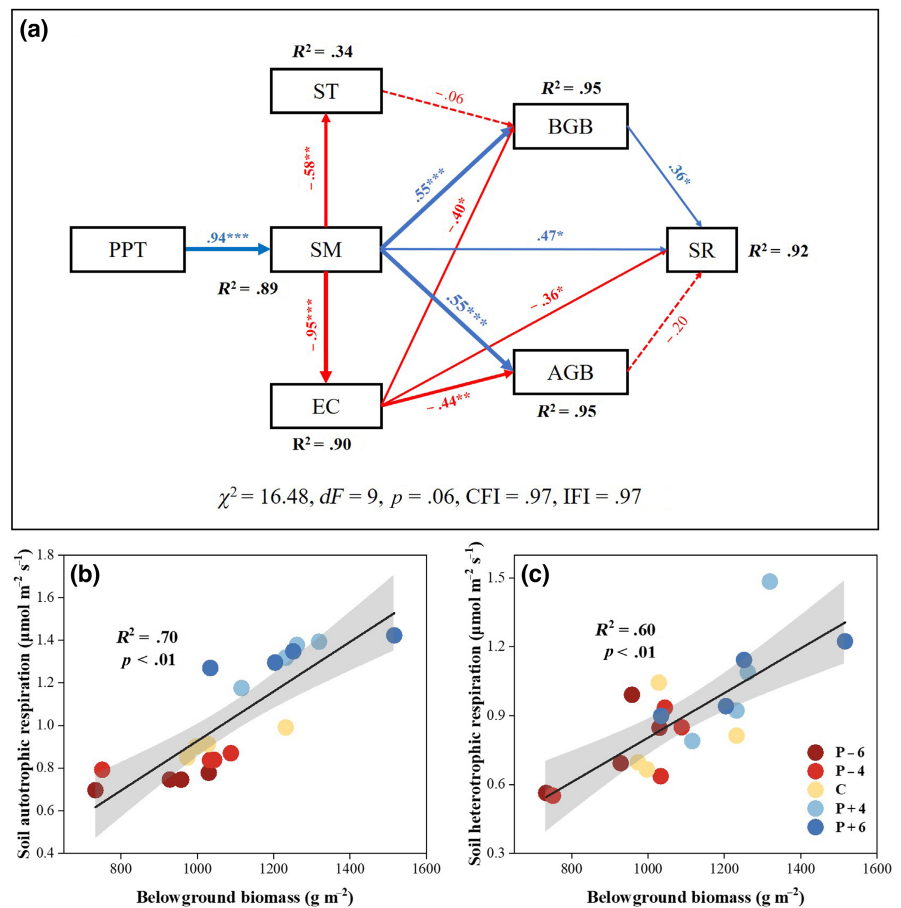


FIGURE 3 Relationship between the sensitivity of soil respiration (SR) and the sensitivity of soil moisture (SM) (a), soil temperature (ST) (b), soil electric conductivity (EC) (c), aboveground biomass (AGB) (d), belowground biomass (BGB) (e), and total vegetation biomass (TB) (f) to precipitation treatments across 6 years (2016–2021).

FIGURE 4 Structural equation model analysis was performed to evaluate the effects of precipitation treatment (PPT) on soil respiration (SR) through various factors from 2016 to 2021, and the relationship between belowground biomass (BGB) and soil autotrophic respiration (b), and soil heterotrophic respiration (c) under precipitation treatments in 2019, respectively. Blue and red arrows (a) indicate significant positive and negative relationships, respectively. The dotted lines (a) refer to insignificant relationships ($p > 0.05$). Numbers on arrows (a) represent standardized path coefficients, and the width of arrows (a) is proportional to the strength of the path coefficients. R^2 values (a) represent the proportion of variance explained for each variable, respectively. *** $p < .001$, ** $p < .01$, * $p < .05$. AGB, aboveground biomass; EC, soil electric conductivity; SM, soil moisture; ST, soil temperature.



be explained by the organic substrate dependence of the sensitivity of SR to precipitation treatments, which was also supported by the positive relationship between BGB and SR under precipitation treatments in SEM (Figure 4a). This observation is in accordance with results from previous studies showing that roots exert a strong influence on the sensitivity of SR to precipitation in field manipulation experiments (Li, Pendall, et al., 2020; Miao et al., 2017; Zhou et al., 2018). For example, a meta-analysis showed that the response of root biomass to precipitation treatments positively influenced the sensitivity of SR and its components to precipitation treatments in grasslands, while in forest ecosystems the sensitivity of total and autotrophic SR to precipitation treatments was also influenced by root biomass (Du et al., 2020).

Based on the significant positive relationship between BGB and soil autotrophic respiration and soil heterotrophic respiration under different precipitation treatments, respectively (Figure 4b,c), several potential mechanisms working independently or in combination may explain the climate-dependent of SR sensitivity to altered precipitation. First, in consideration of the tight linkage between the activities of plant roots and soil autotrophic respiration (Wang, Huang, et al., 2020; Zhang, Cadotte, et al., 2019), changes in plant BGB under precipitation treatments may lead to altered soil autotrophic respiration. Therefore, the sensitivity of BGB to precipitation treatments may, in turn, affect the sensitivity of soil autotrophic respiration to altered precipitation. Second, the root exudates and litters generally influence soil heterotrophic respiration by providing substrates for soil microorganisms (Cui et al., 2019; Deng, Aras, et al., 2017; Miao et al., 2017). In addition, previous precipitation manipulation treatments reported that enhanced root exudates as precipitation increases promoted soil microorganism activities (Huang et al., 2015; Zhang & Xi, 2021). Therefore, the variation of the substrate's quantity induced by BGB may influence the sensitivity of soil heterotrophic respiration to precipitation changes. Third, studies have shown that the variation of soil nutrient content has an important potential influence on soil microbial community composition (Zechmeister-Boltenstern et al., 2015; Zhou et al., 2018). For example, previous studies have showed that variation in soil nutrient content induced by plant roots under precipitation changes may shift the microbial communities from being bacteria to fungi dominated (Chen et al., 2016; Zhou et al., 2018). Therefore, BGB sensitivity may affect the sensitivity of soil heterotrophic respiration to precipitation treatments by changing soil microbial community structure (Prommer et al., 2019; Zhou et al., 2016). Remarkably, our study indicated that the BGB showed a significant positive relationship with SM but a significant negative relationship with EC during the whole experimental period (2016–2021; Figure 4a; Figure S7). It is worth pointing out that such regulation of soil water and salt conditions could significantly influence the BGB sensitivity with an increasing possibility of changing the sensitivity of SR to precipitation treatments. This finding is also supported by other precipitation manipulation experiments that antecedent SM and EC are substantial for plant growth and microbial activity response to precipitation (Forni et al., 2016; Parihar et al., 2015; Wang, Huang, et al., 2020; Zhou et al., 2018).

4.3 | Implications for long-term field manipulation experiments under intensified ambient climate

Based on the increase in the interannual variability of ambient precipitation over the past 61 years (1961–2021), the results of the significant negative correlation between the sensitivity of SR to precipitation treatment and ambient precipitation observed in this study suggest that amplified interannual variation in ambient precipitation in future may modulate the sensitivity of SR to climate changes (Figure 5). In addition, the magnitude of soil carbon stability feedback to climate changes depends on the sensitivity of soil carbon emission to climate gradient (Sun et al., 2019; Zhang, Li, et al., 2019; Zhang, Zhao, et al., 2019). Therefore, ignoring the regulatory role of ambient precipitation changes on ecosystem responses in field manipulation experiments may reduce the accuracy of soil carbon pool stability assessments.

The strong dependence of the sensitivity of SR on ambient climate highlighted in our study suggests that ambient climate variability may be a key factor in the variability of the results from field manipulation experiments (Langley et al., 2018; Wang et al., 2021). As a consequence, strict focus on treatment effect sizes and overlooking background changes (warming or flooding) in long-term field

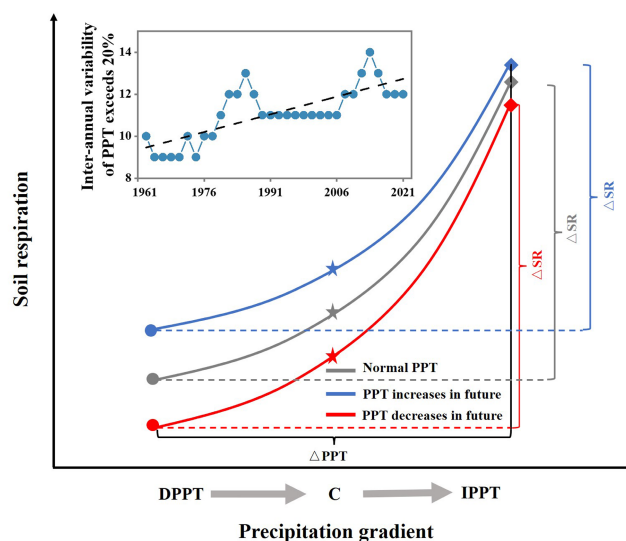


FIGURE 5 The conceptual model predicts the change in soil respiration (Δ SR) along the precipitation (Δ PPT) gradient in the future. The black line shows the variation of SR along the precipitation gradient under normal ambient precipitation in the future. The red line predicts the variation of SR along the precipitation gradient under decreased ambient precipitation in the future, and the blue line predicts the variation of SR along the precipitation gradient under increased ambient precipitation in the future. The insert showed the long-term trend (1961–2021) of annual precipitation variability (PVs > 20%) defined according to historical precipitation distribution. The long-term trends of precipitation variability are calculated based on a 30-year moving sum (the number of years included in each PV during a consecutive 30-year period). DPPT, decreased precipitation; IPPT, increased precipitation.

manipulation climate experiments may not completely provide the relevant information about ecosystem response to climate changes (Al-Yaari et al., 2020; Beier et al., 2012; Wilcox et al., 2015). In addition, it is worth noting that previous models of ecosystem responses to climate change rely on the results of field manipulation experiments (Garcia-Palacios et al., 2018; Harte et al., 2015). Thus, our findings have potential implications for modeling ecosystem C cycling, for providing an additional reference for the ecosystem models that rely only on experimental effects to accurately predict soil carbon fluxes in the future (Langley et al., 2018; Montgomery et al., 2020).

5 | CONCLUSION

Using a 6-year field precipitation manipulation experiment, we found that ambient precipitation was negatively correlated with the sensitivity of SR to precipitation treatment, and the sensitivity of BGB and SR to precipitation treatment were consistent under different ambient precipitation. Our study revealed that interannual variability in ambient precipitation played an important role in modulating the sensitivity of SR to altered precipitation. Our study provided a new comprehensive perspective related to precipitation treatments and the interannual variability of ambient precipitation and their potential impacts on soil carbon emission. The findings highlight that incorporating the effects of ambient climate into the SR-precipitation relationship becomes necessary for an accurate prediction of soil carbon flux as the interannual variability in precipitation is likely to increase in the future.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available at <https://zenodo.org/record/7487999>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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