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META-ANALYSIS

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# Precipitation manipulation and terrestrial carbon cycling: The roles of treatment magnitude, experimental duration and local climate

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## Abstract

**Aim:** Precipitation manipulation experiments have shown diverse terrestrial carbon (C) cycling responses when the ecosystem is subjected to different magnitudes of altered precipitation, various experimental durations or heterogeneity in local climate. However, how these factors combine to affect C cycle responses to changes in precipitation remains unclear.

**Location:** Global.

**Time period:** 1990–2019.

**Major taxa studied:** Terrestrial ecosystems.

**Methods:** Using observations from 230 published studies in which precipitation was manipulated and terrestrial C cycling variables were measured, we conducted a global meta-analysis to investigate responses of diverse C cycle processes to altered precipitation, including gross ecosystem productivity, ecosystem respiration, net ecosystem productivity, ecosystem carbon use efficiency, net primary productivity (NPP), aboveground and belowground NPP, aboveground and belowground biomass, shoot-to-root ratio, soil respiration and soil microbial biomass C.

**Results:** We found that C cycling responses were correlated linearly and positively with the magnitude of precipitation treatments. We also detected that the responses of NPP and its aboveground component (ANPP) to altered precipitation weakened with experimental duration. Furthermore, gross ecosystem productivity, ecosystem respiration and net ecosystem productivity showed larger responses to precipitation treatments of greater magnitude over shorter time periods. The response of soil respiration, a key component of the C budget in most terrestrial ecosystems, depended in particular on the local climate. Local temperature and precipitation not only influenced the magnitude of the response of soil respiration to altered precipitation but also affected its sensitivity to the magnitude of the precipitation treatments, with higher sensitivities in the response of soil respiration to treatment magnitude at drier and colder sites.

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Jinsong Wang and Dashuan Tian contributed equally to this work.

**Main conclusions:** Our findings highlight the importance of the interactions between the magnitude of precipitation treatments, their duration and the local climate in the response of ecosystem C cycling to altered precipitation, which is crucial to a better understanding of ecosystem C processes and functioning and projecting them under changing precipitation regimes.

KEYWORDS

carbon cycling, climatic context, experimental duration, precipitation response, synthesis, treatment magnitude

## 1 | INTRODUCTION

Climate change, characterized by increasing atmospheric $CO_2$ and global warming, has been altering precipitation regimes worldwide (Borken et al., 2002; IPCC, 2013; Knapp et al., 2015; Thomey et al., 2011). These changes include increased annual precipitation at high latitudes and decreased annual precipitation in most subtropical regions (Harper et al., 2005). Furthermore, global climate models forecast an increase in the frequency and magnitude of precipitation extremes (Easterling et al., 2000; IPCC, 2013; Tan et al., 2018). These changes in precipitation regimes are expected to affect plant and soil processes (Reichmann et al., 2014; Reichstein et al., 2013), both of which will have a large influence on terrestrial carbon (C) cycling and future climate change (Frank et al., 2015; Heimann & Reichstein, 2008; Wu et al., 2011; Xu et al., 2016).

The effects of altered precipitation on terrestrial C cycling have been examined widely through several precipitation manipulation experiments, covering a broad range of ecosystems (Chen, Yan, et al., 2019; Felton et al., 2019; Li et al., 2019; Zhang, Quan, Ma, Tian, Zhou, et al., 2019). However, findings from individual experiments have been inconsistent, and substantial uncertainty remains regarding how patterns of C cycle processes respond to altered precipitation. These uncertainties are likely to be attributable to: (1) differences in the magnitude of changes in the amount of precipitation (Post & Knapp, 2021); (2) variations in the duration of precipitation manipulation (Felton et al., 2021); and (3) differences in local climate [e.g., mean annual temperature (MAT) and mean annual precipitation (MAP)] (Avolio et al., 2020). A few global syntheses have advanced our understanding of the influences of altered precipitation on C cycle processes, such as soil respiration (Liu et al., 2016), aboveground and belowground net primary productivity (ANPP and BNPP, respectively) (Wilcox et al., 2017), soil C storage, C pools and C fluxes (Song et al., 2019; Wu et al., 2011; Zhou et al., 2016). However, previous studies focused mainly on the effect of the magnitude of altered precipitation, and the influence of experimental duration on C cycling responses has rarely been evaluated (Deng et al., 2021). Moreover, whether or how the magnitude and duration of precipitation treatments affect C cycle processes interactively is largely unclear, although increasing intensity and longer time-scales of altered precipitation (e.g., severe and prolonged drought) are frequent in vast areas of the world (IPCC, 2013).

Regarding the role of changes in precipitation magnitude, one of the central debates is whether the relationships between C cycling responses and the magnitude of altered precipitation are linear or saturating (i.e., strong influence by extreme drought and weak effect by increase in precipitation) (Wilcox et al., 2017). For example, ANPP is correlated linearly with site-level precipitation within the normal range of precipitation variability (Estiarte et al., 2016; Hsu & Adler, 2014; Knapp, Avolio, et al., 2017; Knapp & Smith, 2001; Sala et al., 2012). However, when extremes are included, the response of ANPP to the magnitude of altered precipitation may saturate (Knapp et al., 2017; Luo et al., 2008; Wilcox et al., 2017). But even here, results are equivocal. Felton et al. (2019) reported a linear relationship between ANPP response and changes in amounts of precipitation, even after incorporating precipitation extremes in a mesic grassland. Thus, the general pattern in the relationships between the magnitude of C cycling responses and the magnitude of precipitation treatments remains elusive, but this knowledge gap needs to be resolved to reduce uncertainties in predicting ecosystem responses to future changes in precipitation amounts and extremes (Beier et al., 2012; Knapp et al., 2008).

Another critical knowledge gap is whether C cycling responses to altered precipitation vary with experimental duration. Although these responses have been assessed less frequently (Estiarte et al., 2016), the duration of precipitation manipulation should mediate the effects on terrestrial C cycling owing to a lag in treatment effects (Hoover et al., 2016; Yahdjian & Sala, 2006), shifts in species composition (Griffin-Nolan et al., 2019; Smith et al., 2009; Zhang, Quan, Ma, Tian, Hoover, et al., 2019), or the limitation of other resources (e.g., soil nutrients and light). For instance, a decade-long experiment in a temperate grassland showed that increased precipitation initially stimulated ANPP during the first 6 years, but the stimulation diminished in the remaining years owing to enhanced nitrogen (N) losses and consequent N limitation, which constrained plant growth (Ren et al., 2017). However, the opposite was observed in another long-term experiment in grasslands (Knapp et al., 2012). Elsewhere, Luo et al. (2018) found that the drought-induced accumulation of canopy nutrients, mainly driven by species turnover, enhanced grassland resistance to extended drought. Therefore, an understanding of how ecosystem responses shift with the duration of altered precipitation will be vital for assessing and projecting future ecosystem functioning.

Furthermore, previous syntheses might have overlooked the fact that ecosystem C cycling is likely to be affected by a combination of the magnitude and duration of altered precipitation, and that the combination might vary with local climate or differ among ecosystem types. A previous study, albeit limited, showed that grassland ANPP was affected strongly by increased drought intensity over short time-scales, but not over long time-scales (Gao et al., 2019). In contrast, forest ANPP was less responsive to short-term drought but more responsive to long-term drought, predominantly owing to tree mortality (Allen et al., 2010; DeSoto et al., 2020; Reichstein et al., 2013). In dry regions, C cycle processes could be stimulated by increased precipitation owing to the alleviation of water limitation to plant growth and decomposition, whereas wet regions can have small positive responses or even negative responses (Knapp et al., 2008). Therefore, understanding how C cycle processes respond to the magnitude and duration of altered precipitation and heterogeneity in local climate is crucial for forecasting ecosystem responses under future precipitation regimes in global vegetation models (Paschalis et al., 2020).

Here, we conducted a meta-analysis using 1,775 paired observations from global precipitation manipulation experiments to synthesize the effects of changes in precipitation on a diverse array of C cycle processes. The specific questions we addressed using the comprehensive dataset included the following.

1. How do C cycling responses vary with changes in the magnitude of altered precipitation?
2. How do C cycling responses change with the experimental duration of altered precipitation?
3. How do magnitude and duration interact to influence C cycling responses?
4. How do these C cycling responses vary with local climate and differ among terrestrial biomes?

## 2 | MATERIALS AND METHODS

### 2.1 | Data collection

Using ISI Web of Science (www.isiknowledge.com), Google Scholar and China Knowledge Resource Integrated Databases (CNKI; www.cnki.net), we searched for peer-reviewed publications that were published between 1990 and 2019 that had examined the effects of the manipulation of precipitation on terrestrial C cycling. We used the following combination of keywords for our comprehensive search: (climate change OR precipitation OR rainfall OR water OR irrigation OR drought) AND (C fluxes OR gross ecosystem productivity OR net ecosystem productivity OR ecosystem respiration OR soil respiration OR biomass OR production OR allocation OR soil microbial biomass). Primary studies were incorporated only if they met all the following criteria: (1) precipitation was manipulated in the field with paired groups, a control and a precipitation treatment (increased precipitation or decreased precipitation), each of which had at least three replicates; (2) the experiment was conducted in natural terrestrial ecosystems, excluding cropland and laboratory studies, which must have at least one of the selected C cycling variables in both the control and precipitation treatments; (3) experiments must have had consistent environmental conditions in the control and precipitation treatments at the beginning of precipitation manipulation; (4) means, standard deviations or standard errors, and replicates of selected variables in the control and precipitation treatments were reported; (5) C cycling variables were measured during at least one growing season, and the absolute amount or relative change in precipitation and experimental duration (number of years between initiation of the experiment and the measurements) were described clearly; and (6) for multifactorial experiments that included altered precipitation, data from only the control and precipitation treatments were used. If multiple sites or different conditions, such as diverse biomes, multiple years and different magnitudes of changing precipitation were reported in one study, they were treated as independent observations. Using these criteria, we found a total of 1,775 paired observations (1,119 observations for increased and 656 for decreased precipitation treatment) between the control and precipitation treatments from 230 published studies (Supporting Information Data S1; a list of the data sources is given in Supporting Information Appendix S1).

### 2.2 | Variable selection

We selected terrestrial C cycling variables from published studies and grouped these variables into six categories (Supporting Information Table S1): (1) ecosystem C fluxes [gross ecosystem productivity (GEP), ecosystem respiration (ER) and net ecosystem productivity (NEP)], which are typically used to evaluate whether an ecosystem is a C sink or source (Quan et al., 2019); (2) ecosystem C use efficiency (CUE), defined as the ratio of NEP to GEP, which is usually applied to assess the capacity of the ecosystem for C sequestration and is a crucial parameter in ecosystem process models (Chen, Zhang, et al., 2021); (3) net primary productivity (NPP), representing the net C sequestered by plants (i.e., assimilated C minus C released by autotropic respiration) (Roxburgh et al., 2005), which includes ANPP and BNPP; (4) biomass, including aboveground biomass (AGB) and root biomass (BGB); (5) shoot-to-root ratio (S/R), calculated as AGB/BGB or ANPP/BNPP, which is widely used to assess changes in the allocation of C in plant biomass or C allocation in response to climate change (Song et al., 2019); (6) soil respiration (Rs) and soil microbial biomass C (MBC), which are two crucial variables for assessing soil C losses and substrate availability for microbial respiration, respectively.

### 2.3 | Data extraction and compilation

We extracted the means, replicates and standard deviations (if reported) from each study. Data were extracted directly from tables, figures and appendices of the original publications. The graphical data were obtained using Plot Digitizer v.2.6.8 (http://plotdigitizer.sourceforge.net). We also collected experimental conditions, such as the absolute (in millimetres) or relative (percentage) amount of altered precipitation relative to the control and the treatment duration (in years). We converted the reported amount of altered precipitation to a percentage change in precipitation (Wilcox et al., 2017), which represented treatment magnitude ($I$) and allowed for a comparison among studies:

$$I = \frac{A_{\text{treatment}} - A_{control}}{A_{\text{control}}} \times 100\,\%, \tag{1}$$

where $A_{\text{treatment}}$ is the amount of precipitation for the treatment, and $A_{\text{control}}$ is the amount of precipitation for the control. We also collected background environmental variables from the original publications that included latitude and longitude (in degrees), ecosystem type, MAT (in degrees Celsius) and MAP (in millimetres per year). For those data observations in which MAT or MAP was missing, we searched for these values in other publication sources using the name of the site, state and country, or we contacted the study authors. The database contained a broad range of ecosystems, including forests, deserts, shrublands, savannas, grasslands, tundra and wetlands. The coarse definition of forests in the literature can provide limited information for comparing the differences in C cycling responses to manipulation of precipitation among forest biomes. For studies that did not specify the type of forest biome, we classified the forest biome as boreal, temperate/subtropical or tropical as described in a previous study (Yuan & Chen, 2015). Specifically, forests located between 23.5° S and 23.5° N were classified as tropical forests and those distributed between 46 and 66° N were classified as boreal forests; temperate/subtropical forests were those between the tropical and boreal latitudes. Likewise, grasslands were subdivided into tropical and temperate grasslands. Thus, the dataset was classified into 10 biomes: boreal forest, temperate forest, tropical forest, desert, shrubland, savanna, temperate grassland, tropical grassland, tundra and wetland (Figure 1).

## 2.4 | Data analysis

All statistical analyses were performed using R v.3.5.2 (R Core Team, 2018). Initially, we used a linear mixed-effects model to inspect the responses of C cycling variables to precipitation treatment (increased or decreased precipitation):

$$\ln RR = \beta_0 + \beta_1 \times \text{treatment} + \pi_{\text{study}} + \varepsilon, \tag{2}$$

where $\beta_0$ and $\beta_1$ are estimated coefficients; $\pi_{\text{study}}$ is the random effect of "study", which accounts for the autocorrelation among observations within each study; $\varepsilon$ is the sampling error; and ln*RR* is the effect size of altered precipitation on C cycle processes from each observation following Hedges et al. (1999):

$$\ln RR = \ln \overline{X}_{\text{treatment}} - \ln \overline{X}_{\text{control}}, \tag{3}$$

where $\overline{X}_{\text{treatment}}$ and $\overline{X}_{\text{control}}$ are the mean values of a given C cycling variable under the treatment and control group, respectively. ln*RR* has been applied widely in previous meta-analyses (Chen et al., 2021; Peng & Chen, 2021) owing to its ease of interpretation. For example, a positive ln*RR* indicates that increased precipitation stimulated C cycling, whereas a negative ln*RR* indicates that increased precipitation inhibited C cycling.In the meta-analysis, it is also important to weight individual observations to estimate the effect size. Previous studies suggested that weighting based on sampling variance might assign extreme importance to only a few individual observations, and subsequently,

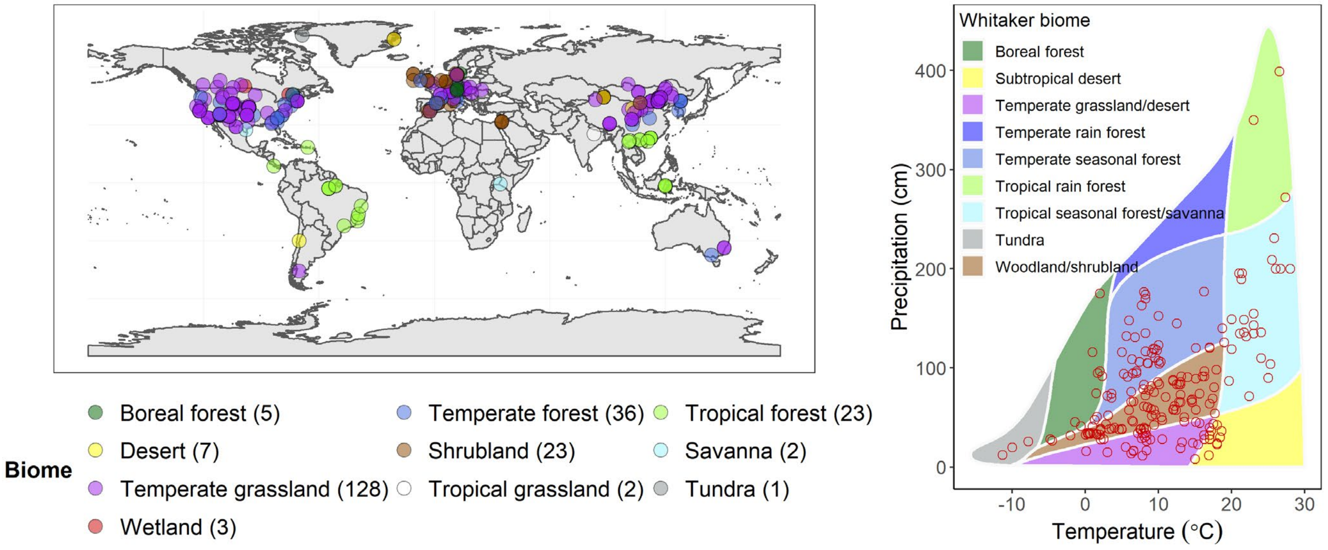


**FIGURE 1** A map of the geographical distribution and local climate of the study sites used in this meta-analysis. Circles represent study sites, and the different colours indicate various biomes. The number of studies is shown in parentheses for each biome type [Colour figure can be viewed at wileyonlinelibrary.com]

average ln*RR* could be determined by a small number of studies (Ma & Chen, 2016). Thus, we used the number of replicates for weighting as recommended in previous studies (Chen et al., 2019; Ma et al., 2020):

$$W_r = \left(N_{\text{control}} \times N_{\text{treatment}}\right) / \left(N_{\text{control}} + N_{\text{treatment}}\right), \quad (4)$$

where $W_r$ is the weight associated with each ln*RR* observation, and $N_{\text{control}}$ and $N_{\text{treatment}}$ are the numbers of replicates in the control and treatment group, respectively.

Next, we applied a mixed-effects weighted-estimation model to test whether the responses of individual C cycling variables to precipitation treatments differed from zero. The mixed-effects models were fitted with restricted maximum likelihood using the *lme4* package, with $W_r$ as the weight for each corresponding ln*RR* observation (Bates et al., 2015). The Shapiro–Wilk test was applied to check the normality of all models, and the fitted coefficients were bootstrapped by 1,000 iterations when the normality assumption was violated, using the *boot* package (Chen, Chen, et al., 2021). The weighted effect size and its 95% confidence interval (CI) were calculated for each individual C cycling variable. For ease of interpretation, ln*RR* and its corresponding CI were transformed back to percentage change as $(e^{\ln RR} - 1) \times 100\%$. If the 95% CI of weighted ln*RR* did not overlap zero ($\alpha = .05$), the effects of precipitation manipulation on C cycling were considered significant.

To answer our first question, as in a previous study (Zhou et al., 2016), we pooled increased and decreased precipitation to examine whether the ln*RR*–*I* relationship ($\ln RR = \beta_0 + \beta_1 \times I + \pi_{\text{study}} + \varepsilon$) was linear or saturating by comparing the Akaike information criterion (AIC) values of linear (*I*) and ln-transformed (ln*I*) models, as proposed by Wilcox et al. (2017). The linear models (*I*) had lower AICs or similar AICs (e.g., BGB) compared with the saturated models (ln*I*) based on AIC selection (Changes in AICs < 2) (Supporting Information Table S2).

To answer our second and third questions, mixed-effects models were performed to inspect whether ln*RR* varied with *I* and *D* and their interactions with the following model structure:

$$\ln RR = \beta_0 + \beta_1 \times I + \beta_2 \times D + \beta_3 \times I \times D + \pi_{\text{study}} + \varepsilon. \quad (5)$$

Four of the C cycling variables showed significantly lower AIC values in the ln-linear models (ln*D*) than in the linear models (*D*) based on the AIC selection (Supporting Information Table S3). Hence, the models with ln*D* were used as parsimonious models for C cycle processes. Furthermore, the continuous predictors (*I* and *D*) in Equation 5 were scaled (*z* transformation; the observation minus the mean and divided by one standard deviation) to facilitate the comparison among C cycling variables that had different values of *I* and *D*. As such, $\beta_1$ and $\beta_2$ represent the standardized effects of *I* and *D* on C cycling variables, respectively (Cohen et al., 2013).

To answer our fourth question, we explored whether ln*RR* varied with environmental conditions by adding individual predictors (i.e., MAT, MAP and biomes) and their respective interactions with *I* and *D* in Equation 5. The environmental variables were modelled individually because simultaneous modelling of these predictors would result in strong multicollinearity (Zuur et al., 2010). To prevent overfitting (Johnson & Omland, 2004), we selected the most parsimonious model among all possible models with the condition to retain *I*, because it was the key aspect of altered precipitation to be tested. The model selection was performed using the "*dredge*" function of the *MuMIn* package (Barton, 2018).

## 3 | RESULTS

### 3.1 | Overview of the dataset

The observations we amassed were collected mainly in North America, Europe and Asia (Figure 1). The studies that fitted our criteria were located between 45.7° S and 76.5° N, with MAT ranging from −11.3 to 28°C and MAP from 81 to 3,990 mm (Supporting Information Table S4). The magnitude of precipitation treatments ranged from −100 to 268%, the treatment duration ranged from 1 to 15 years, and the observations were taken from different biome types (Supporting Information Table S5).

### 3.2 | General effects of altered precipitation on terrestrial carbon cycling

On average, increased precipitation stimulated C cycling processes across all studies, whereas decreased precipitation suppressed them (Figure 2). Compared with the control, increased precipitation significantly enhanced GEP, ER and NEP by 16% ($n = 56$), 17% ($n = 54$) and 16% ($n = 50$), respectively ($p < .05$). In contrast, decreased precipitation significantly reduced GEP, ER and NEP by 22% ($n = 28$), 17% ($n = 29$) and 28% ($n = 27$), respectively ($p < .05$). Increased precipitation had no significant effect on CUE ($n = 50$, $p > .05$), but CUE was reduced by 6% with decreased precipitation ($n = 28$, $p < .05$).

NPP was on average 19% higher with increased precipitation ($n = 68$, $p < .05$), but NPP was 9% lower with decreased precipitation ($n = 30$, $p < .05$) relative to the control (Figure 2). Both increased and decreased precipitation affected ANPP and AGB more strongly than BNPP and BGB. On average, ANPP and BNPP were 26% ($n = 229$, $p < .05$) and 9% ($n = 85$, $p < .05$) higher than the control, respectively, with increased precipitation, but were 19% ($n = 174$, $p < .05$) and 7% ($n = 36$, $p > .05$) lower, respectively, with decreased precipitation. On average, AGB was 34% ($n = 91$, $p < .05$) higher with increased precipitation and 29% ($n = 40$, $p < .05$) lower with decreased precipitation relative to the control. BGB was on average 12% ($n = 76$, $p < .05$) higher than the control with increased precipitation but was not significantly different from the control with decreased precipitation ($n = 29$, $p > .05$).

Compared with the control, shoot-to-root ratios were 20% higher with increased precipitation ($n = 107$, $p < .05$), whereas the ratios were 12% lower with decreased precipitation ($n = 41$, $p < .05$; Figure 2). Increased precipitation enhanced Rs and MBC relative to the control

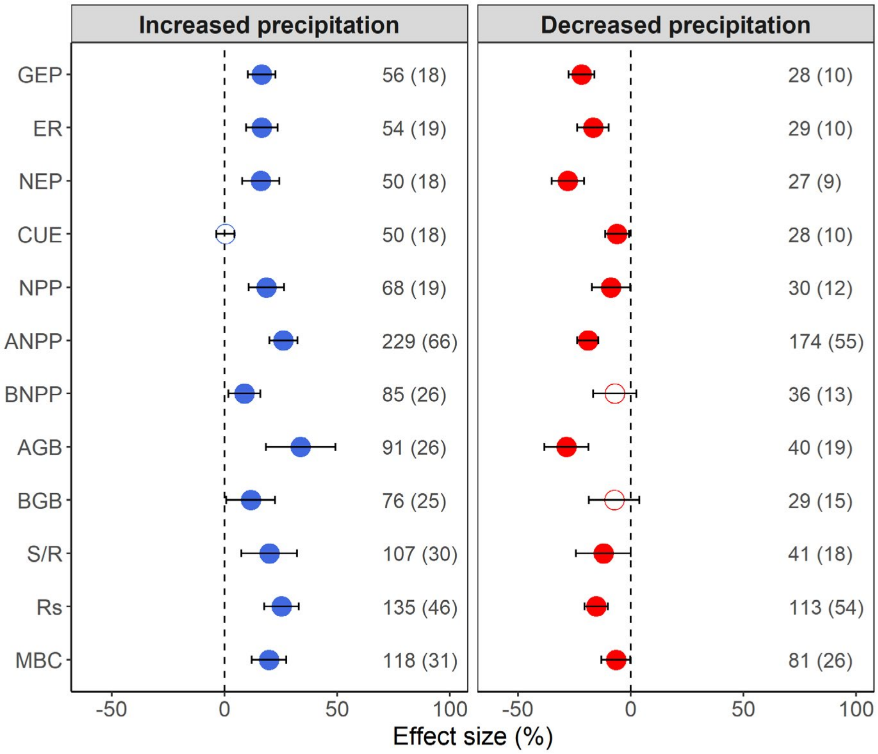


**FIGURE 2** Responses of terrestrial carbon cycling variables to precipitation treatments. Values are weighted effect sizes and their 95% confidence intervals. Values represent the strength of the effect of altered precipitation on carbon cycling variables relative to the control. Numbers indicate the number of data observations, and the numbers in parentheses are the numbers of studies. Blue and red represent carbon cycling responses to increased precipitation and decreased precipitation treatments, respectively. Filled circles indicate significant altered precipitation effects, and open circles represent insignificant effects. AGB = aboveground biomass; ANPP = aboveground net primary productivity; BGB = belowground biomass; BNPP = belowground net primary productivity; CUE = carbon use efficiency; ER = ecosystem respiration; GEP = gross ecosystem productivity; MBC = soil microbial biomass carbon; NEP = net ecosystem productivity; NPP = net primary productivity; Rs = soil respiration; S/R = the ratio of aboveground to belowground biomass/productivity [Colour figure can be viewed at wileyonlinelibrary.com]

by an average of 25% ($n = 135$, $p < .05$) and 20% ($n = 118$, $p < .05$), respectively, whereas decreased precipitation reduced them by an average of 15% ($n = 113$, $p < .05$) and 7% ($n = 81$, $p < .05$), respectively.

### 3.3 | Carbon cycling responses in relationship to treatment magnitude and duration

The responses of C cycle processes were related linearly to the magnitude of altered precipitation (Supporting Information Figure S1; Table S2), with significantly positive relationships between each C cycling response except CUE and treatment magnitude (Figure 3). Moreover, the response sensitivity to treatment magnitude was greater for aboveground processes (e.g., ANPP and AGB) than belowground processes (e.g., BNPP and BGB). The effect sizes for NPP and ANPP decreased significantly as treatment duration increased (Figure 3).

We also found a significant interaction between treatment magnitude and duration in regulating the responses of ecosystem C fluxes (i.e., GEP, ER and NEP; $p < .001$, $p < .001$ and $p = .004$, respectively) to altered precipitation (Supporting Information Table S6). Specifically, the effect sizes for GEP, ER and NEP weakened over time with increased treatment magnitude (Figure 4).

### 3.4 | Carbon cycling responses in relationship to local climate

The effect sizes for Rs and MBC declined significantly with MAT (Figure 5; Supporting Information Table S7). In addition, the effect size for Rs decreased significantly with MAP. We also found a significant interaction between treatment magnitude and MAT ($p = .008$) or MAP ($p = .001$) in regulating the Rs response, which was more strongly influenced in colder and drier climates with increasing treatment magnitude (Figure 6). The responses of other C cycling variables did not change with MAT or MAP (Supporting Information Table S7). Moreover, the effects of altered precipitation on C cycling did not differ significantly among biomes (Supporting Information Figure S2; Table S7).

## 4 | DISCUSSION

In our meta-analysis, we found linear relationships between the magnitude of C cycling responses and the magnitude of altered precipitation. We revealed responses of plant productivity (i.e., NPP and ANPP) to altered precipitation to be more apparent over shorter

**FIGURE 3** Effects of the treatment magnitude and duration of precipitation manipulation on terrestrial carbon cycling processes. Treatment magnitude is the magnitude of the altered precipitation expressed as a percentage relative to the control, and duration is the experimental duration in years; values (estimated $\beta_1$ and $\beta_2$ in Equation 5, respectively) are the mean and 95% confidence intervals. Filled circles indicate significant altered precipitation effects, and open circles represent insignificant effects. Abbreviations are defined in the legend to Figure 2 [Colour figure can be viewed at wileyonlinelibrary.com]

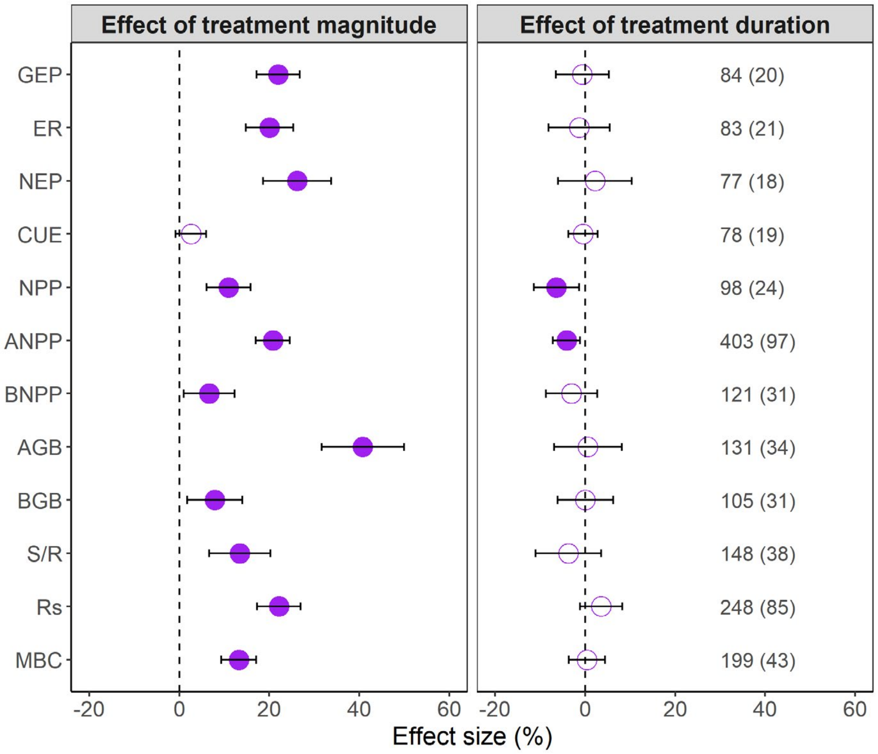
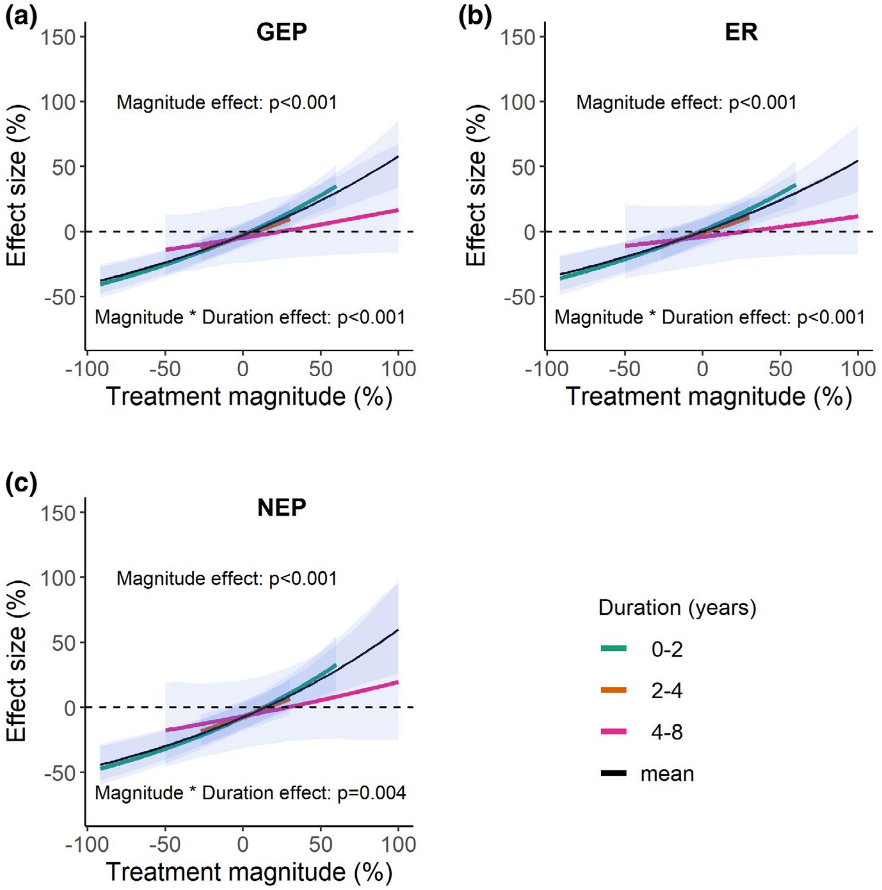


**FIGURE 4** Effects of altered precipitation on ecosystem carbon fluxes in relationship to the combination of treatment magnitude and duration. (a) The interactive effects of treatment magnitude and duration on gross ecosystem productivity (GEP). (b) The interactive effects of treatment magnitude and duration on ecosystem respiration (ER). (c) The interactive effects of treatment magnitude and duration on net ecosystem productivity (NEP). Treatment magnitude is the magnitude of altered precipitation expressed as a percentage relative to the control, and duration is the experimental duration in years. Lines were fitted from duration-dependent regressions with bootstrapped 95% confidence intervals in shading. The level of significance (*p*) is presented for each term tested [Colour figure can be viewed at wileyonlinelibrary.com]



time-scales. We also discovered that the responses of ecosystem C fluxes (i.e., GEP, ER and NEP) varied with the combination of treatment magnitude and duration, with larger responses to greater treatment magnitude at shorter time-scales. Local climate regulated the magnitude of the soil respiration response to precipitation treatments and influenced its sensitivity to changes in precipitation

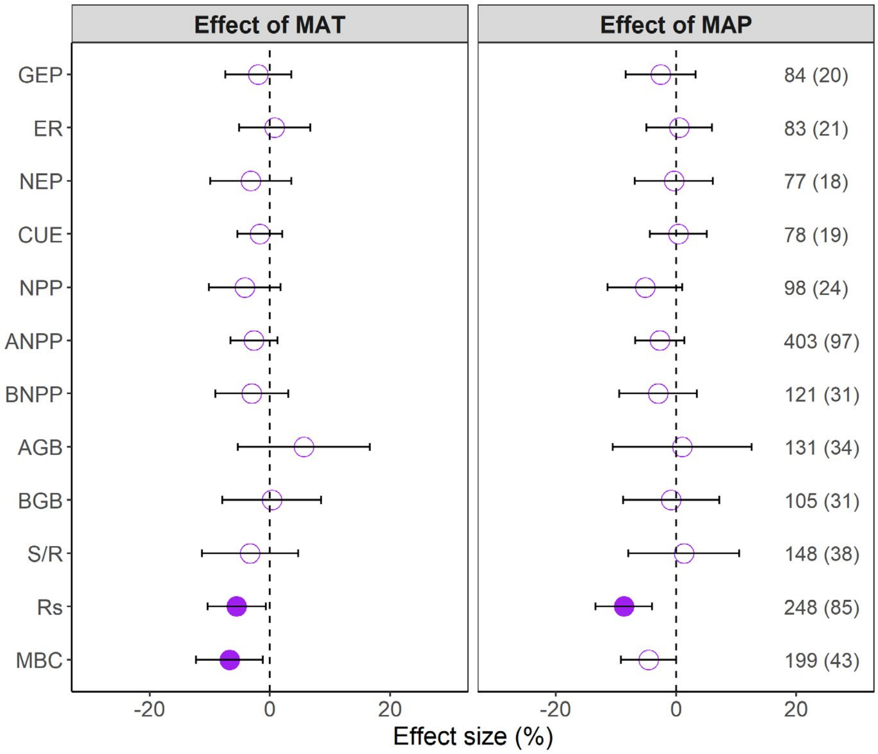


**FIGURE 5** Effects of local climate [mean annual temperature (MAT) and mean annual precipitation (MAP)] on terrestrial carbon cycling responses to altered precipitation. Values are means and 95% confidence intervals. Filled circles indicate significant altered precipitation effects, and open circles represent insignificant effects. Abbreviations are defined in the legend to Figure 2 [Colour figure can be viewed at wileyonlinelibrary.com]

magnitude. Our findings show the significant changes in terrestrial C cycling in response to altered precipitation and suggest that C cycling responses are dependent on the interplay of the magnitude of precipitation treatments, the experimental duration and the heterogeneity of the local climate.

### 4.1 | Carbon cycling responses are correlated linearly with treatment magnitude

Responses of aboveground and belowground C cycle processes showed positive and linear correlations with the magnitude of altered precipitation, which is consistent with previous meta-analyses (Liu et al., 2016; Zhou et al., 2016). Non-hydric ecosystems are often subject to water limitation, especially during growing seasons. The enhancement of soil water availability with increased precipitation could stimulate plant growth and microbial activity, litter decomposition and microbial decomposition of soil organic matter, and vice versa with decreased precipitation (Zhou et al., 2016), resulting in a linear relationship between C cycling responses and changes in precipitation magnitude. These linear relationships could have resulted from the normal range of treatment magnitude in most precipitation experiments world-wide.

It has also been suggested that responses of other C cycle processes might deviate from linear relationships with the magnitude of altered precipitation when precipitation extremes are incorporated (Luo et al., 2017). Unfortunately, many studies did not perform multiple levels of precipitation treatments to assess the effects of extreme treatment magnitude on C cycling responses. Therefore, we recommend that more extreme precipitation treatments and multiple levels of treatments should be conducted in the future to assess whether these linear relationships hold true in extreme conditions.

We also found greater response sensitivities for aboveground than belowground C processes, which agrees with the findings of previous global meta-analysis syntheses (Song et al., 2019; Wu et al., 2011; Zhou et al., 2016). The greater response sensitivity of aboveground than belowground C cycling could be attributed to the shift in C allocation from root to shoot (Wilcox et al., 2015); that is, plants tend to allocate more carbohydrates aboveground in wet conditions to favour light capture and prioritize C allocation to roots in dry conditions to facilitate belowground resource acquisition (Farrior et al., 2015; Hertel et al., 2013). Moreover, the root turnover rate is usually slow in dry conditions (Wang et al., 2019). Both these factors could contribute to the lower sensitivity of belowground C processes to altered precipitation.

### 4.2 | Carbon cycling responses weaken over longer time-scales

We found responses of plant productivity (i.e., NPP and ANPP) in short-term experiments to be less pronounced over longer time-scales (Figure 3). This finding implies that previous reports on the short-term responses in plant productivity should be regarded with caution, because long-term responses will ultimately determine the feedbacks of ecosystems to climate change. There are two main mechanisms that can explain the diminishing effect of altered precipitation on plant productivity over long time-scales. First, as the

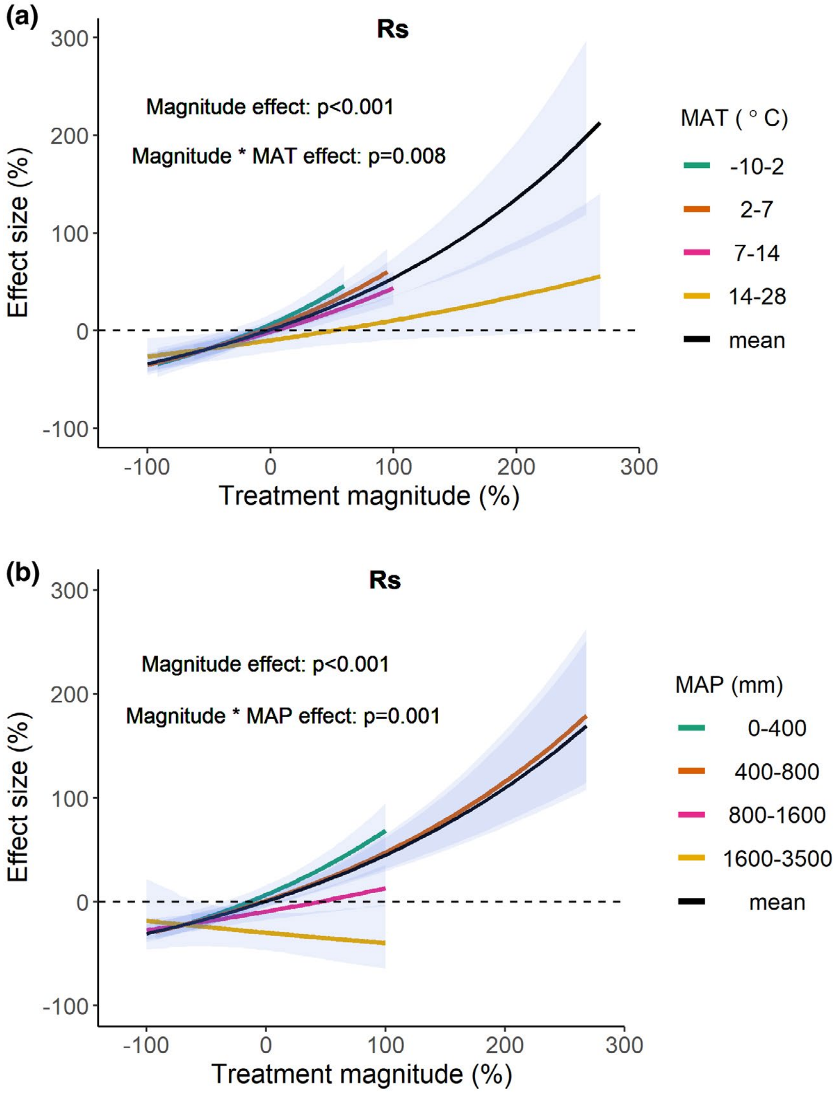


**FIGURE 6** Effects of altered precipitation on soil respiration in relationship to the combination of treatment magnitude and local climate. (a) The interactive effects of treatment magnitude and mean annual temperature (MAT) on soil respiration. (b) The interactive effects of treatment magnitude and mean annual precipitation (MAP) on soil respiration. Treatment magnitude is the magnitude of altered precipitation expressed as a percentage relative to the control. Lines were fitted from MAT- or MAP-dependent regressions, with bootstrapped 95% confidence intervals indicated by shading. The level of significance (*p*) is presented for each term tested [Colour figure can be viewed at wileyonlinelibrary.com]

experimental period lengthens, other resources, such as light and soil nutrients, might limit plant growth in response to altered precipitation (Huxman et al., 2004). Second, changes in plant functional composition might strengthen ecosystem resistance to long-term alterations of precipitation (Griffin-Nolan et al., 2019).

To our knowledge, this significant temporal variation in the response of plant productivity to altered precipitation has not been reported in previous syntheses or meta-analyses (e.g., Estiarte et al., 2016; Wu et al., 2011; Zhou et al., 2016). Considering that most precipitation experiments were conducted for < 4 years (Supporting Information Figure S3), conclusions should be drawn carefully for these short-term experiments because they might overestimate precipitation-induced changes in C cycling. The lack of long-term data might also bias the observed responses of other C cycle processes that had weak relationships with experimental duration. Thus, more long-term precipitation manipulation experiments are necessary to verify our findings in order to assess the consequences of longer durations on C cycling accurately.

Furthermore, we found that with increased magnitude of precipitation treatments, the magnitude of the response of ecosystem C fluxes (e.g., GEP, ER and NEP) was larger in short-term studies than in long-term studies (Figure 4). This finding suggested that the magnitude and duration of precipitation treatments could influence ecosystem C fluxes interactively. We are aware that this pattern has not been observed in previous manipulation experiments or global syntheses. Larger responses of ecosystem C fluxes with greater treatment magnitude at shorter time-scales could be attributable mainly to the rapid shifts in C flux responses (e.g., hours or days) to changes in precipitation magnitudes, whereas the response of the C pool (e.g., soil organic C pool), which is characterized by a slow C turnover rate, might be apparent at decadal time periods. Given that the feedbacks of terrestrial ecosystems to the global C cycle are ultimately contingent upon long-term responses, the lower sensitivities of ecosystem C fluxes to the magnitude of precipitation treatments over a longer time-scale will pose a challenge in forecasting ecosystem net C sink or source in scenarios of precipitation regime shifts.

### 4.3 | Carbon cycling responses depend on local climate

Although local climate exhibited no effects on the responses of most C cycle processes, we found that the effect size for Rs decreased significantly with ambient temperature and precipitation (Figure 5). The negative correlation between MAP and Rs response suggested a greater magnitude of Rs response to increased precipitation in arid and semi-arid regions or to decreased precipitation in humid areas.

Here, we emphasize that the local climate not only affected the magnitude of Rs response to altered precipitation, but also influenced its sensitivity to treatment magnitude (i.e., significant treatment magnitude × MAT or MAP), which has rarely been explored in previous studies. We found a greater sensitivity of Rs responsiveness with increasing treatment magnitude at colder and drier sites. Partly supporting our findings, a recent global synthesis demonstrated that the sensitivity of Rs to the amount of altered precipitation was greater at drier sites, but this pattern is possible only with increased precipitation rather than decreased precipitation (Song et al., 2019). The stronger sensitivity of Rs to the treatment magnitude in drier areas might support the saturating model (i.e., larger responses to extreme drought and smaller responses to increased precipitation), which is used to depict NPP–precipitation relationships (Knapp, Ciais, et al., 2017). Specifically, at humid sites where water is not a limiting factor, water addition might induce anaerobic soil conditions and restrain microbial activities (Sotta et al., 2007), consequently reducing Rs. Hence, with increasing water supply, the sensitivity of Rs to increased precipitation will be weaker in more humid conditions than in arid conditions, with a potential to saturate in extremely wet conditions. Alternatively, in arid and semi-arid areas, plant and microbial activities are largely constrained by soil water availability. If we decrease the water supply further in dry areas, in order to mimic an extreme drought, the rate of Rs change in response to decreasing precipitation would be fast (Du et al., 2020), and the ecosystem would be likely to collapse. Overall, our findings highlight the dual role of local climate in regulating the magnitude of the response of Rs to altered precipitation and its sensitivity to treatment magnitude.

### 4.4 | Conclusions

The interplay of altered precipitation magnitude, duration and local climate in determining terrestrial C cycling has rarely been considered in previous global syntheses or meta-analyses. Our study found that the responses of ecosystem C fluxes were dependent upon the interaction between the magnitude and duration of precipitation treatments, which implies the complexity of changing precipitation regimes in regulating whether ecosystems are net sinks or sources of C. We also found that local climate affected the magnitude of the soil respiration response to altered precipitation and modified its sensitivity to treatment magnitude, suggesting the importance of climatic conditions in modulating the rate of soil C losses in response to the precipitation magnitude. Overall, our findings highlight that the impacts of altered precipitation on terrestrial C cycling depend on the magnitude of precipitation treatments, experimental duration and local climate, and on their interactions.

Based on our meta-analysis, we identified limitations and suggestions for future studies. In the present study, we discerned the importance of the duration of treatment on plant productivity responses, but there a comprehensive understanding of the consequences of altered precipitation at longer time-scales is still lacking because the experimental periods were rather short (< 4 years) for most of the C cycling processes. Thus, more long-term field data are needed to assess accurately how altered precipitation influences C cycling processes in the long term (> 10 years). In the meta-analysis, most precipitation experiments have been conducted in temperate grasslands and forests, and we lack a more balanced representation of other biomes, such as deserts, wetlands, tundra and savanna. This hampers our ability to identify the significant differences among biomes more broadly. Therefore, more study sites in these regions should be advocated for future experiments. Furthermore, altered precipitation could affect terrestrial C cycling jointly with multiple climate change factors; hence, multifactorial experiments will be greatly appreciated for studying ecosystem responses in future.

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## CONFLICT OF INTEREST

The authors declare no competing interests.

## AUTHOR CONTRIBUTIONS

J.W. and S.N. conceived the ideas, designed the study and wrote the first draft of manuscript. J.W. and D.T. collected and analysed the data. All authors contributed critically to the writing through multiple rounds of revisions.

## DATA AVAILABILITY STATEMENT

Data supporting the results and R codes are available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.dr7sqv9z6).

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the Supporting Information section.

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