A cross-biome synthesis of soil respiration and its determinants under simulated precipitation changes

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Abstract

Soil respiration (R_s) is the second-largest terrestrial carbon (C) flux. Although R_s has been extensively studied across a broad range of biomes, there is surprisingly little consensus on how the spatiotemporal patterns of R_s will be altered in a warming climate with changing precipitation regimes. Here, we present a global synthesis R_s data from studies that have manipulated precipitation in the field by collating studies from 113 increased precipitation treatments, 91 decreased precipitation treatments, and 14 prolonged drought treatments. Our meta-analysis indicated that when the increased precipitation treatments were normalized to 28% above the ambient level, the soil moisture, R_s, and the temperature sensitivity (Q_{10}) values increased by an average of 17%, 16%, and 6%, respectively, and the soil temperature decreased by −1.3%. The greatest increases in R_s and Q_{10} were observed in arid areas, and the stimulation rates decreased with increases in climate humidity. When the decreased precipitation treatments were normalized to 28% below the ambient level, the soil moisture and R_s values decreased by an average of −14% and −17%, respectively, and the soil temperature and Q_{10} values were not altered. The reductions in soil moisture tended to be greater in more humid areas. Prolonged drought without alterations in the amount of precipitation reduced the soil moisture and R_s by −12% and −6%, respectively, but did not alter Q_{10}. Overall, our synthesis suggests that soil moisture and R_s tend to be more sensitive to increased precipitation in more arid areas and more responsive to decreased precipitation in more humid areas. The responses of R_s and Q_{10} were predominantly driven by precipitation-induced changes in the soil moisture, whereas changes in the soil temperature had limited impacts. Finally, our synthesis of prolonged drought experiments also emphasizes the importance of the timing and frequency of precipitation events on ecosystem C cycles. Given these findings, we urge future studies to focus on manipulating the frequency, intensity, and seasonality of precipitation with an aim to improving our ability to predict and model feedback between R_s and climate change.

Keywords: apparent Q_{10}, aridity index, drought, meta-analysis, precipitation regime, soil moisture, soil temperature, wet

Introduction

Global precipitation regimes have changed and will continue to change as the climate warms (IPCC, 2014). These changes are expected to significantly alter soil respiration (R_s), which is the largest source of carbon (C) flux from terrestrial ecosystems to the atmosphere (Bond-Lamberty & Thomson, 2010; Wu *et al.*, 2011). With the rapidly increasing number of experiments manipulating precipitation across global biomes, our

understanding of how biotic and abiotic factors govern the responses of R_s to diverse precipitation regimes has greatly improved. However, the high spatiotemporal heterogeneity in precipitation and soils contributes to considerable uncertainty in the estimates of global patterns of R_s under future precipitation scenarios. Here, we provide a comprehensive assessment of R_s and its determinants under altered precipitation regimes to help guide predictions on the responses of R_s in a warming world.

Soil moisture and soil temperature are two of the primary abiotic drivers for root and microbial activities. Knowing their potential moderating effects on R_s is

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essential for predicting the responses of R_s to precipitation changes. How R_s is affected by precipitation-induced changes in soil moisture is well studied. In most water-limited ecosystems, changes in R_s are positively correlated with changes in soil moisture; thus, increases in precipitation often increase R_s, whereas decreases can reduce R_s (Knapp *et al.*, 2008; Wu *et al.*, 2011). In high moisture soils, drought treatments can stimulate R_s by improving aeration (Knapp *et al.*, 2008). A number of studies have observed that precipitation-induced moisture changes accompany soil temperature changes. For example, high soil moisture content often enhances plant transpiration, which can cool soil surface, whereas low soil moisture content can reduce transpiration, thus increasing the soil temperature (Lagergren & Lindroth, 2002; Maes & Steppe, 2012). However, few studies have discussed how precipitation-induced temperature changes could obscure the responses of R_s to moisture change (Matias *et al.*, 2012).

Predictions of global R_s rates in response to climate change rely heavily on accurate estimations of R_s sensitivity to temperature. Q_{10} is defined as the change in respiration rate over a 10 °C increase in temperature, and it is one of the most widely used parameters for quantifying temperature sensitivity. However, there is a continued debate on how to select appropriate Q_{10} values when modeling R_s (Davidson & Janssens, 2006; Davidson *et al.*, 2006). For example, the apparent Q_{10} derived from field data can be affected by the inherent temperature sensitivity of R_s and by substrate availability and soil moisture (Davidson & Janssens, 2006). Drought suppresses root and microbe activities; therefore, it can reduce substrate and extracellular enzyme diffusion along water film pathways in soil particles (Davidson & Janssens, 2006). As a result, R_s is often less sensitive to temperature changes in water-limited soils, which leads to a lower apparent Q_{10} value (Suseela *et al.*, 2012). To improve the accuracy of R_s predictions under precipitation changes, a more robust understanding is required on how precipitation regimes alter the apparent Q_{10} in different biomes.

R_s is not only affected by abiotic factors, such as soil moisture and soil temperature, but it can also vary according to the following two biotic processes: autotrophic respiration (R_a), which originates from roots and mycorrhizae activity; and heterotrophic respiration (R_h), which originates from decomposers, such as microbes and soil fauna (Hanson *et al.*, 2000). Because of the different sensitivities of plants and decomposers to water availability, changes in precipitation regimes could have different impacts on R_a and R_h. Labile carbon and most decomposers are concentrated in the surface soil, and a small change in precipitation in this layer could significantly alter the moisture level of the topsoil and induce rapid pulse responses of R_h (Sponseller, 2007; Inglima *et al.*, 2009). However, plants are better at maintaining their water balance through physiological processes, such as adjusting stomatal conductance or taking up water from the deep soil (Jackson *et al.*, 2000; Chaves *et al.*, 2002). Consequently, R_a, which is greatly influenced by plant growth, could be more resistant to mild drought but also less responsive to small increases in precipitation (Sponseller, 2007). However, it is still not clear whether R_a and R_h show different sensitivities to diverse precipitation regimes.

In addition, it is also unclear whether an equivalent increase or decrease in the rate of precipitation would yield similar changes in R_s, and this lack of understanding presents a further challenge for predicting R_s under future climate scenarios. Depending on the region, local climates could become wetter or drier in the future (IPCC, 2014). Previous studies have found that C cycles in grasslands had asymmetrical sensitivities to increases and decreases in precipitation, with greater increases in productivity and the net ecosystem C exchange (NEE) observed in wet years relative to the decreases in these parameters in drought years (Knapp & Smith, 2001; Flanagan *et al.*, 2002). Several precipitation manipulation experiments have examined how R_s responds to the same degree of precipitation change under wet and drought treatments. A study conducted at two arid sites found that R_s was more sensitive to wet treatments than drought treatments (Talmon *et al.*, 2011). In contrast, a study in a subtropical forest found that R_s was more sensitive to the drought treatment relative to the wet manipulations (Jiang *et al.*, 2013). These contradictory findings raise the question of whether changes in R_s can be predicted using the same relationships between climatic drivers and R_s under different precipitation scenarios (Wu *et al.*, 2011; Peng *et al.*, 2013; Vicca *et al.*, 2014).

Ecosystem experiments that manipulate precipitation are crucial for determining the causal relationship between R_s responses and changes in precipitation regimes. Two previous meta-analyses have discussed R_s under precipitation changes. Wu *et al.* (2011) assessed the responses of several major C cycle processes, including R_s, under altered precipitation regimes, and Vicca *et al.* (2014) investigated whether the current relationships between soil moisture and R_s remain valid under altered precipitation regimes. However, these syntheses did not evaluate (1) whether R_s from different biomes responds differently to precipitation changes, (2) whether R_s shows symmetrical/asymmetrical sensitivities to wet and drought treatments, and (3) which (combination of) factors predominantly moderate the responses of R_s to precipitation changes. To address these issues, we combined and compared

published precipitation manipulation experiments across the globe in a meta-analysis to assess and quantify the response of R_s, R_a, R_h, apparent Q_{10}, soil temperature, and soil moisture to precipitation changes.

Materials and methods

Data selection

Precipitation manipulation studies over the period 1994–2014 were initially identified with Web of Science (Thomson Reuters, New York, NY, USA) using a range of search terms and wildcards (outlined in Table S1). Additional searches with the same keywords were conducted on Google Scholar (Google, Mountain View, CA, USA). In total, 868 references were identified with these bibliographic searches, and references were then screened to identify suitable studies based on whether they met the following inclusion/exclusion criteria. Three types of studies that manipulated precipitation in the field were included: wet experiments that increased the precipitation quantity, drought experiments that decreased the precipitation quantity, and prolonged drought experiments that increased the intervals of precipitation but did not alter the precipitation quantity; these studies were referred to as increased precipitation, decreased precipitation, and prolonged drought, respectively. To better represent responses of R_s under natural conditions, we did not include greenhouse studies and laboratory incubation experiments. Soil respiration in most ecosystems presents significant seasonal variations. Therefore, to avoid the potential variability and bias caused by a limited number of sampling dates, we only included studies that repeatedly measured R_s, R_a, and/or R_h for at least one growing season or an entire year. In these cases, we either extracted the annual sum of R_s, R_a, and/or R_h if it was reported, or calculated the mean values for each individual year. In total, 85 studies met these inclusion criteria.

Control and treatment means ($\bar{X}$), standard deviation (SD, or surrogates), and sample sizes (N) of R_s, R_a, or R_h, the apparent Q_{10}, soil temperature, soil moisture, and precipitation manipulation level were extracted from each study when possible. When the data were graphically presented, the figures were digitized to extract the numerical values using Engauge Digitizer (Free Software Foundation, Inc., Boston, MI, USA). All of the study sites were classified into biome types according to the modified terrestrial ecoregions defined by the World Wildlife Fund. Other ancillary site information, such as the latitude, longitude, elevation, and mean annual temperature (MAT) and precipitation (MAP) were also extracted. For individual studies that did not report the MAT or MAP for their site, these values were determined by the site locations using Climatic Research Unit Climatology version 2.0 dataset (CRU CL 2.0, New *et al.*, 2002). Several studies manipulated multiple levels of precipitation in the same experiment, used different plant communities, or manipulated other factors, such as elevating the CO_2, elevating the temperature or adding N. The results from different precipitation manipulation levels, plant communities, or treatments were treated as independent measurements (Lajeunesse, 2010).

Effect size calculation and meta-regression

We performed a meta-analysis and meta-regression to assess the responses of R_s, R_a, R_h, Q_{10}, soil temperature, and soil moisture to precipitation treatments. Only studies that reported variances were included in the analysis (Table S3). The effects of the precipitation treatments were quantified using the natural log of the response ratio (RR), which effect sizes are calculated as:

$$\mathrm{RR} = \ln(\bar{X}_T / \bar{X}_C), \qquad (1)$$

with a variance of:

$$\mathrm{var(RR)} = \mathrm{SD}_T^2 / (N_T \bar{X}_T^2) + \mathrm{SD}_C^2 / (N_C \bar{X}_C^2), \qquad (2)$$

and where $\bar{X}_C$, SD_C, and N_C represent the mean, standard deviation, and sample size of the (C)ontrol group, respectively; and $\bar{X}_T$, SD_T, and N_T represent the mean, standard deviation, and sample size of the (T)reatment group, respectively (Hedges *et al.*, 1999). For all of the meta-analyses and meta-regressions, we used inverse-variance weighted regressions and random-effects models to pool and compare the RRs. Our random-effects analyses used a REML approach for estimating the between-study variance of each regression model, and non-zero effects were assessed with 95% confidential intervals (CI). All of the meta-analyses and meta-regressions were performed in R using the *metafor* package (Viechtbauer, 2010). The pooled effects were back-transformed to unlogged RRs to estimate the percentage change due to precipitation manipulations.

For studies that reported R_s values for more than 2 years, the temporal change in the RR was assessed for each individual study (Fig. S1). Most studies did not present a significant temporal pattern except for one increased precipitation study that found that the RR increased with treatment duration (Liu *et al.*, 2009) and one decreased precipitation study that found that the RR decreased with treatment duration (Lellei-Kovács *et al.*, 2008). The temporal pattern for the entire dataset was also assessed, and significant temporal trends were not observed in the increased precipitation, decreased precipitation, or prolonged drought experiments (Fig. S2). Therefore, we used the overall mean across the entire experimental period to quantify the precipitation effects.

Approximately one-fourth of the studies in our dataset manipulated precipitation across the entire year (N = 24), and the remainder only manipulated precipitation during the growing season (N = 58). To standardize the precipitation treatment levels across the studies, all of the manipulation levels were converted into a percentage of the annual precipitation (Table S2), and when the annual precipitation was not reported, the MAP was used as a substitute. Overall, the increased precipitation treatments ranged from 10% to 300% of the MAP, with a median of 25%, and the decreased precipitation treatments ranged from −7.5% to −100% of the MAP, with a median of −30% (Table S2, Fig. S3a, b). All of the studies were pooled together to determine the absolute values of their manipulation levels, and the median was 28% of the MAP for the whole dataset (Fig. S3c).

To compare the responses of R_s, R_a, R_h, and Q_{10} among the evaluated studies and test whether the values presented

symmetric sensitivity to an equivalent increase and decrease of precipitation, we normalized the RR under the increased precipitation studies to 28% above the ambient MAP and the decreased precipitation studies to −28% below the ambient MAP. Our meta-regression indicated that across all sites and biomes, the R_s, R_a, R_h, and Q_{10} values showed linear responses to precipitation manipulation levels (Fig. 1). Therefore, we used the following linear transformation to normalize the measurements under the different treatment/manipulation levels to ~28% of the MAP:

$$\bar{X}_{NT} = \bar{X}_C + \frac{(\bar{X}_T - \bar{X}_C)}{P} \times (\sim 28), \qquad (3)$$

where $\bar{X}_{NT}$ is the normalized value under 28% of the MAP; $\bar{X}_T$ and $\bar{X}_C$ represent the mean of the treatment and control groups, respectively; and P is the precipitation manipulation level expressed as a proportion of the local annual precipitation, with positive values indicating the increased precipitation treatments and negative values indicating the decreased precipitation treatments. The mean natural log effect size of the normalized variable was calculated according to $RR_{norm} = \ln(\bar{X}_{NT}/\bar{X}_C)$ ($\bar{X}_{NT}$ was also used to calculate the variances of RR_{norm}), and the meta-analysis results were back-transformed.

Between-group heterogeneity tests (Q_B tests) were used to assess whether different ecosystem types showed different responses to precipitation change, with a significant Q_B indicating that the groups differed. We also used heterogeneity tests to explore the potential methodological moderators of the soil respiration experiments. For example, we compared the responses of R_s between experiments that manipulated precipitation only during growing season and experiments that manipulated precipitation across the entire year. We also compared the three major methods used to measure soil respiration, including dynamic chamber methods that use an infrared gas analyzer or other CO_2 measurement instruments, static chamber methods that use gas chromatography, and finally static chamber methods using alkali absorption; and four different approaches were used to partition R_a and R_h, including trenching, root extraction, clipping, and isotopic labeling.

Publication bias in the studies where variances were reported was evaluated by funnel plots and Egger regressions (Jennions et al., 2013). Funnel plots are scatterplots of the treatment effect size against their standard errors, and in the absence of publication bias, the studies should be distributed symmetrically in a 'funnel' shape around a mean effect size. The potential asymmetry of the funnel plot was assessed by Egger's regression (Jennions et al., 2013). A sensitivity analysis was further performed using the trim and fill method, which calculates the number of missing studies related to publication bias and estimates their effect size and standard error (Jennions et al., 2013). Publication bias was adjusted by adding the missing studies to the analysis.

The interactions between precipitation changes and other global change factors were assessed following Dieleman et al. (2012). Briefly, for the experiments that manipulated precipitation and other factors simultaneously, a paired meta-analysis was conducted by comparing whether the 95% CI for the RR

of each single factor significantly differed from that of the combined treatment. Partial regression analyses were conducted to assess the relative importance of the changes in soil temperature and soil moisture to the responses of R_s.

The De Martonne aridity index (de Martonne, 1926) was calculated as follows for each site:

$$\text{Aridity index} = \text{MAP}/(\text{MAT} + 10) \qquad (4)$$

Here, lower aridity index values correspond to more arid climate conditions and higher aridity index values correspond to more humid climate conditions. A meta-regression was used to explore how the normalized responses of soil moisture, R_s and Q_{10} change along climate gradients. The study sites were further binned by 20 arid index intervals. For each variable in each aridity index bin, the pooled RR_{norm} under the increased and decrease precipitation treatments were assessed, and the 95% CI of $\exp[RR_{norm}] - 1$ was calculated. If the absolute values of the two ranges did not overlap with each other, we defined the response as an asymmetrical sensitivity.

Results

Overview of the dataset, publication bias, and methodological effects

Collectively, 218 effect sizes were derived from 85 soil respiration studies, including 113 from increased precipitation experiments, 91 from decreased precipitation experiments, and 14 from prolonged drought manipulations. The geographical range of these studies spanned from 37.42 S to 78.88 N (Fig. S4, Table S2), the MAT ranged from −18.1 to 28.0 °C, and the MAP ranged from 109 to 3990 mm. Furthermore, our meta-analysis spanned 12 biomes, including tropical savanna, tropical and subtropical forest, temperate shrubland, temperate forest, temperate grassland, Mediterranean, boreal forest, alpine, tundra, desert, wetland, and agricultural land (Table S3, Fig. S4).

There was some evidence for publication bias according to the funnel plots and Egger's regression for the studies exploring soil moisture under increased precipitation (Fig. S5a, Table S4), R_a under decreased precipitation (Fig. S6e, Table S4), and soil moisture under prolonged drought (Fig. S7a, Table S4). However, augmenting the data using the trim and fill method did not change the direction and the significance of these results (Table S4). In terms of the potential methodological moderators of the soil respiration studies, the time of year in which the manipulations occurred had a significant impact on the response of R_s under increased precipitation but not under decreased precipitation (Table S5). We could also not detect any significant differences among approaches to measuring R_s (Table S5). However, the R_s partitioning methods had significant
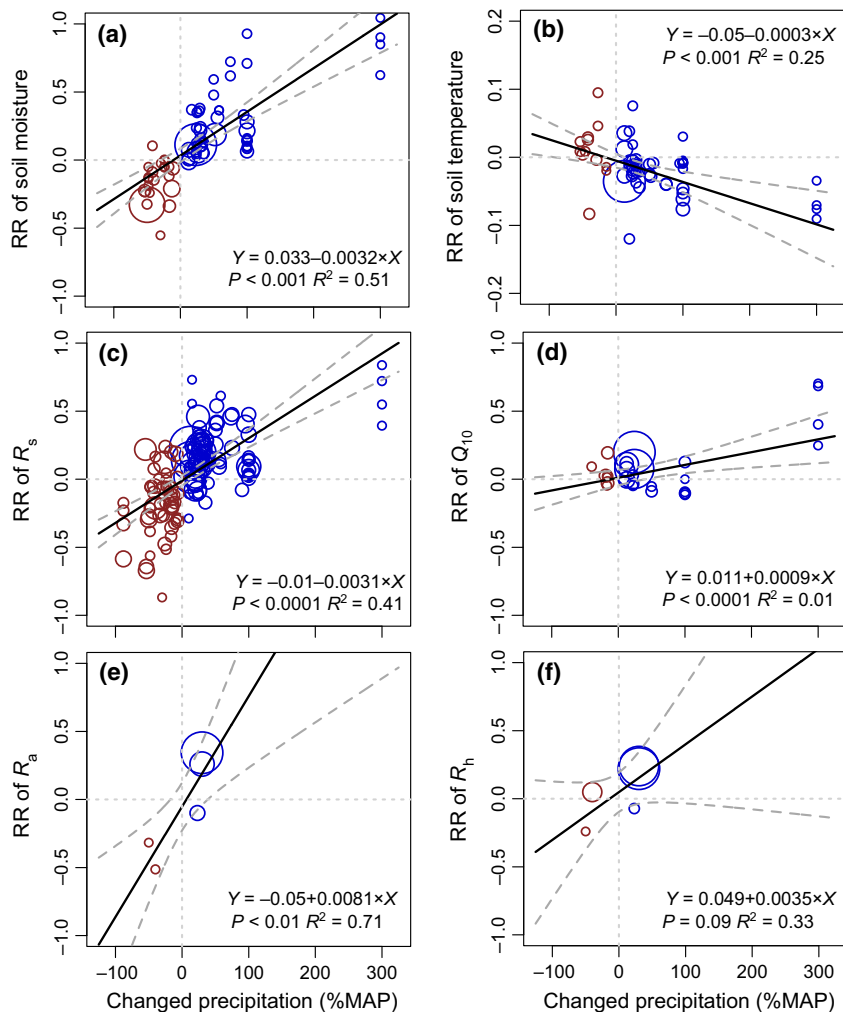
Fig. 1 Bubble plots of the meta-regression results between the responses of soil moisture (a), soil temperature (b), soil respiration (c), apparent temperature sensitivity (Q_{10}, d), autotrophic respiration (R_a, e), and heterotrophic respiration (R_h, f) to different manipulation levels under different precipitation treatments. Blue bubbles indicate increased precipitation treatments, red bubbles indicate decreased precipitation treatments, and the size of the bubble is the relative weight of the effect size (response ratio, RR) in the random-effects meta-regression. Larger bubbles indicate study outcomes that contributed a greater overall weight in meta-regressions.

impacts on the responses of R_a and R_h under increased precipitation. Further, the RRs derived from the trenching method were significantly lower than that from the clipping method for R_a and R_h (Table S5). However, our assessments of publication bias and potential methodological moderators have limited power because of the small number of studies available for each group.

Responses of soil moisture and soil temperature

The RR of soil moisture were positively correlated with the precipitation manipulation levels (Fig. 1a). When the treatment levels were normalized to 28% of the MAP and averaged across biomes, increased precipitation levels significantly increased the soil moisture by 17% and decreased precipitation levels reduced the soil moisture by −14% (Table 1). The effect sizes for the prolonged drought treatments were not normalized by the precipitation amount because prolonged drought did not alter the precipitation amount. Across all of the ecosystems, prolonged drought decreased the soil moisture by an average of −12% (Table 2). There was also significant heterogeneity in responses to increased and decreased precipitation in soil moisture across biomes. Deserts showed the most pronounced increase in soil moisture under the normalized increased precipitation, whereas tropical and subtropical forests showed the greatest reductions under the normalized decreased precipitation (Table 1).

Table 1 Pooled normalized effect sizes (%) and 95% confidence intervals (CIs) of the soil moisture, soil temperature, and soil respiration caused precipitation manipulation among different precipitation levels and across biomes

Biomes	Manipulation level Mean ± SE (%MAP)	Soil moisture Effect size (%)	95% CI (%)	Soil temperature Effect size (%)	95% CI (%)	Soil respiration Effect size (%)	95% CI (%)
Increased precipitation							
Total mean	51 ± 6 (100)	**17 (49)**	**12, 22**	**−1.3 (47)**	**−2.4, −0.1**	**16 (85)**	**12, 20**
Trop. forest	69 ± 11 (11)	**21 (9)**	**11, 32**	−0.2 (6)	−4.5, 4.3	**11 (11)**	**3, 21**
Trop. Savanna	219 ± 51 (6)	18 (6)	−7, 50	−0.6 (4)	−13, 13.5	11 (6)	−14, 43
Temp. forest	63 ± 9 (10)	9 (3)	−4, 24	−1.5 (3)	−5.9, 3.2	5 (6)	−6, 16
Temp. grassland	29 ± 4 (30)	**9 (18)**	**3, 15**	−1.4 (13)	−3.5, 0.8	**17 (30)**	**11, 24**
Mediterranean	26 ± 3 (20)	–	–	−1 (9)	−3.6, 1.7	**8 (14)**	**0.3, 16**
Desert	46 ± 6 (18)	**29 (12)**	**20, 39**	−1.6 (12)	−3.7, 0.6	**28 (16)**	**20, 37**
		Q_B = 15.4, df = 5, P = 0.009		Q_B = 0.39, df = 6; P = 0.996		**Q_B = 18.7, df = 6; P = 0.009**	
Decreased precipitation							
Total mean	30 ± 2 (71)	**−14 (23)**	**−20, −7**	1.0 (12)	−1.3, 3.3	**−17 (50)**	**−24, −10**
Trop. forest	33 ± 5 (10)	**−31 (5)**	**−39, −21**	0.4 (5)	−5.3, 7.0	**−18 (10)**	**−32, −1**
Temp. forest	18 ± 3 (5)	–	–	−3.3 (2)	−20.2, 17.1	−24 (5)	−42, 0
Temp. shrubland	15 ± 2 (14)	–	–	–	–	−19 (7)	−38, 7
Temp. grassland	41 ± 5 (24)	−8 (14)	−15, 1	1.9 (4)	−4.2, 8.3	**−15 (21)**	**−26, −3**
Mediterranean	26 ± 4 (15)	−7 (2)	−25, 15	1.4 (6)	−3.2, 6.3	−14 (7)	−30, 8
Alpine	54 ± 0 (2)	−11 (2)	−26, 8	0.8 (2)	−5.5, 7.6	−25 (2)	−50, 12
		Q_B = 23.4, df = 4, P < 0.001		Q_B = 0.35, df = 5; P = 0.987		Q_B = 0.89, df = 6; P = 0.978	

Positive values indicate a percentage increase relative to the ambient precipitation condition, and negative values indicate a percentage decrease. The bold numbers indicate that 95% CIs do not overlap with zero. The number of effect sizes from each biome is shown in parentheses. Bolded Q_B values indicate a significant between-group heterogeneity. df indicates degrees of freedom; Trop. indicates tropical and subtropical; Temp. indicates temperate; and Agri. indicates agricultural; MAP, mean annual precipitation.

The RRs of soil temperature were negatively correlated with the precipitation manipulation level (Fig. 1b). When the treatment levels were normalized to 28% of the MAP, increased precipitation levels decreased the soil temperature by an average of 1.3%, whereas the decreased precipitation levels did not affect the soil temperature (Table 1). The responses of temperature were not different among the biomes (Table 1).

Responses of soil respiration

The RRs of R_s were positively correlated with the precipitation manipulation level (Fig. 1c). When the precipitation treatments were normalized to 28% of the MAP, the increased precipitation levels increased R_s by an average of 16% and the decreased precipitation levels reduced R_s by an average of −17% (Table 1). For the individual biomes, the normalized increased precipitation levels stimulated R_s with amounts ranging from 8% to 28% (Table 1). The normalized decreased precipitation treatment reduced the R_s values by −14% to −25% for the studied biomes, although

the reduction was only significant for tropical forests and temperate grasslands (Table 1). Prolonged drought decreased the R_s values by an average of −6% (Table 2). For the individual biome types, the effect of prolonged drought was only significant in temperate grasslands (−10%).

The response of R_s was positively correlated with the RRs of soil moisture (Fig. 2a), and negatively correlated with the RRs of soil temperature (Fig. 2b). When the soil moisture was controlled using a partial regression, the negative correlation between the responses of R_s and soil temperature was no longer significant (Fig. S9a).

To compare whether the responses of R_s in planted forests differed from natural forests, we further parsed forest studies among these two groups. For the normalized increased and decreased precipitation treatments, the responses of R_s in the planted and natural forests were not significantly different (Table S6).

The interaction between precipitation changes and the other manipulation factors, including elevated CO_2, elevated temperature, additional N, and additional litter, was also assessed. Overall, the RRs of R_s under the

Table 2 Pooled effect sizes (%) and 95% CIs of the soil moisture and soil respiration caused by prolonged drought across biomes

Biomes	Soil moisture		Soil respiration	
	Effect size (%)	95% CI (%)	Effect size (%)	95% CI (%)
Total mean	**−12 (8)**	**−17, −6**	**−6 (14)**	**−11, −1**
Temp. grassland	**−13 (7)**	**−18, −7**	**−10 (7)**	**−15, −4**
Agri. land	–	–	−2 (5)	−9, 6
	–		$Q_B = 9.72$, df = 2; $P = 0.021$	

Positive values indicate a percentage increase relative to the ambient precipitation condition, and negative values indicate a percentage decrease. The bold numbers indicate that 95% CIs do not overlap with zero. The number of effect sizes from each biome is shown in parentheses. Bolded Q_B value indicates a significant between-group heterogeneity. df indicates degrees of freedom; Temp. indicates temperate; and Agri. indicates agricultural.

combined treatments did not significantly differ from those under the single-factor treatments except for the increased precipitation plus litter addition treatment.

The RRs of R_s under the increased precipitation plus litter addition treatment were significantly greater than that under the increased precipitation only or litter addition only treatment (Fig. S8).

Responses of Q_{10}, R_a, and R_h

The RRs of Q_{10} were positively correlated with the precipitation manipulation level (Fig. 1d). After the treatment levels were normalized to 28% of the MAP, the increased precipitation levels increased the Q_{10} by 6% (Table 3). The normalized decreased precipitation and prolonged drought treatments did not significantly impact the Q_{10} value (Table 3). When categorized according to the biomes, the normalized increased precipitation treatment increased the Q_{10} value for temperate grasslands (17%) and deserts (17%), whereas the normalized decreased precipitation and prolonged drought treatments had no effect on the Q_{10} value for the individual biomes (Table 3).

The RRs of Q_{10} were positively correlated with RRs of soil moisture (Fig. 2c) and negatively correlated with the RRs of soil temperature (Fig. 2d); however, these correlations were not significant when the effects of soil moisture were controlled (Fig. S9b).
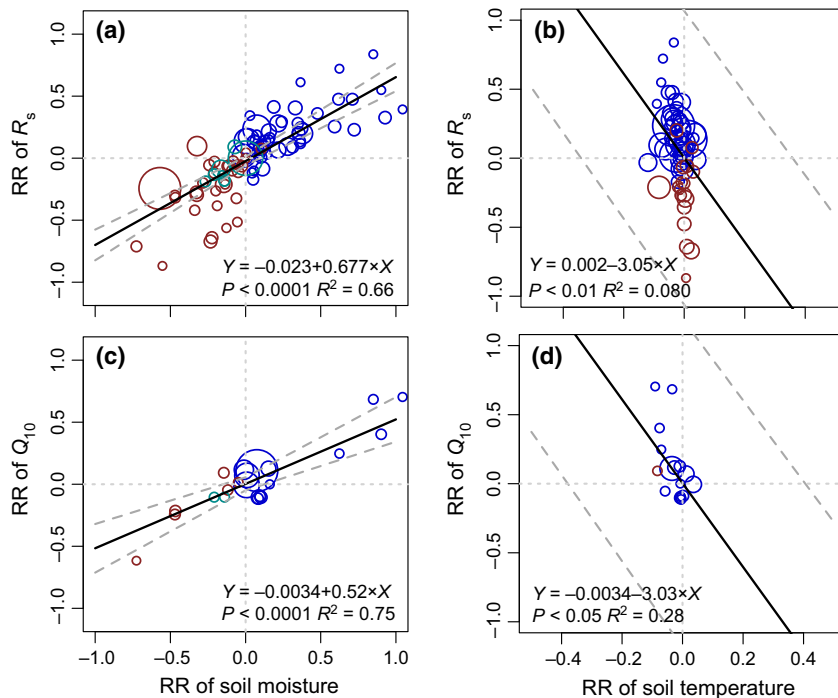

Fig. 2 Bubble plots of the meta-regressions on the effects of precipitation-induced changes in soil moisture and soil temperature on soil respiration (a, b) and Q_{10} (c, d). Blue bubbles indicate increased precipitation treatments, red bubbles indicate decreased precipitation treatments, green bubbles indicate prolonged drought treatments, and the size of the bubble is relative the weight of the effect size (response ratio, RR) in the random-effects meta-regression. Larger bubbles indicate study outcomes that contributed a greater overall weight in meta-regressions.

Table 3 Pooled normalized effect sizes (%) and 95% CIs of the apparent temperature sensitivity (Q_{10}) caused by increased precipitation and decreased precipitation, and non-normalized effect sizes and 95% CIs of the Q_{10} caused by prolonged drought period treatments

Biomes	Increased precipitation		Decreased precipitation		Prolonged drought	
	Effect size (%)	95% CI (%)	Effect size (%)	95% CI (%)	Effect size (%)	95% CI (%)
Total mean	**6 (21)**	**0.2, 12**	7 (7)	−5, 19	−11 (7)	−22, 2
Trop. forest	−1 (6)	−9, 8	–	–	–	–
Trop. Savanna	5 (4)	−19, 37	–	–	–	–
Temp. forest	−4 (2)	−17, 10	–	–	–	–
Temp. grassland	**17 (4)**	**8, 26**	−3 (2)	−27, 28	−10 (2)	−27, 12
Mediterranean	−18 (3)	−12, 9	9 (5)	−4, 23	–	–
Agri. Land	–	–	–	–	−12 (5)	−26, 5
Desert	**17 (2)**	**5, 31**	–	–	–	–
	$Q_B = 15.34$, df = 6, $P = 0.009$		$Q_B = 0.58$, df = 2, $P = 0.447$		$Q_B = 0.02$, df = 2, $P = 0.886$	

Positive values indicate a percentage increase relative to the ambient precipitation condition, and negative values indicate a percentage decrease. The bold numbers indicate that 95% CIs do not overlap with zero. The number of effect sizes from each biome is shown in parentheses. Bolded Q_B value indicates a significant between-group heterogeneity. df indicates degrees of freedom. Trop. indicates tropical and subtropical; Temp. indicates temperate; and Agri. indicates agricultural.

Table 4 Pooled normalized effect sizes (%) and 95% CIs of autotrophic (R_a) and heterotrophic (R_h) respiration caused by precipitation manipulation among different precipitation levels and across biomes

	Increased precipitation		Decreased precipitation	
	Effect size (%)	95% CI (%)	Effect size (%)	95% CI (%)
Autotrophic respiration (R_a)				
Total mean	16 (3)	−8, 47	−22 (2)	−42, 5
Heterotrophic respiration (R_h)				
Total mean	13 (3)	−5, 35	−4 (2)	−23, 19

Positive values indicate a percentage increase relative to the ambient precipitation condition, and negative values indicate a percentage decrease. The number of effect sizes from each biome is shown in parentheses.

The RRs of R_a and R_h showed a positive linear correlation with the precipitation manipulation level (Fig. 1e, f). When the precipitation treatment level was normalized to 28% of the MAP, significant responses were not observed for R_a and R_h. However, the few available studies limited the statistical power of these analyses (Table 4).

Response of soil moisture, R_s, and Q_{10} along climate gradients

Under the normalized increased precipitation treatments, the responses of soil moisture, R_s, and Q_{10} decreased as the aridity indices increased (Fig. 3a, c, e).

Under the normalized decreased precipitation treatments, the responses of soil moisture were negatively correlated with the aridity indices, whereas the responses of R_s and Q_{10} did not present significant trends (Fig. 3b, d, f); however, the sample sizes for these analyses were too limited to offer a robust analysis for the response of Q_{10}.

We further binned the study sites in 20 arid index intervals and compared the responses of soil moisture, R_s, and Q_{10} under the normalized precipitation treatments for each climate zone. The asymmetrical response to the wet and dry climate treatments was only significant for soil moisture in two climate zones. Soil moisture was more sensitive to the increased precipitation treatments in areas with aridity indices ranging from 40 to 60 and more sensitive to the decreased precipitation treatments in areas with indices ranging from 60 to 80 (Fig. 4a). However, these results must be interpreted carefully because of the small sample size and the lack of wet experiments in arid areas and drought experiments in humid areas.

Discussion

Global patterns of soil respiration

Our meta-analysis found that increased precipitation stimulated R_s, although the stimulation rates decreased with increases in climate humidity, as indicated by the negative correlation between normalized RR of R_s and aridity index (Fig. 2c). Our results also found that increases in Q_{10} induced by increased precipitation also decreased with aridity (Fig. 3c). Overall, these findings
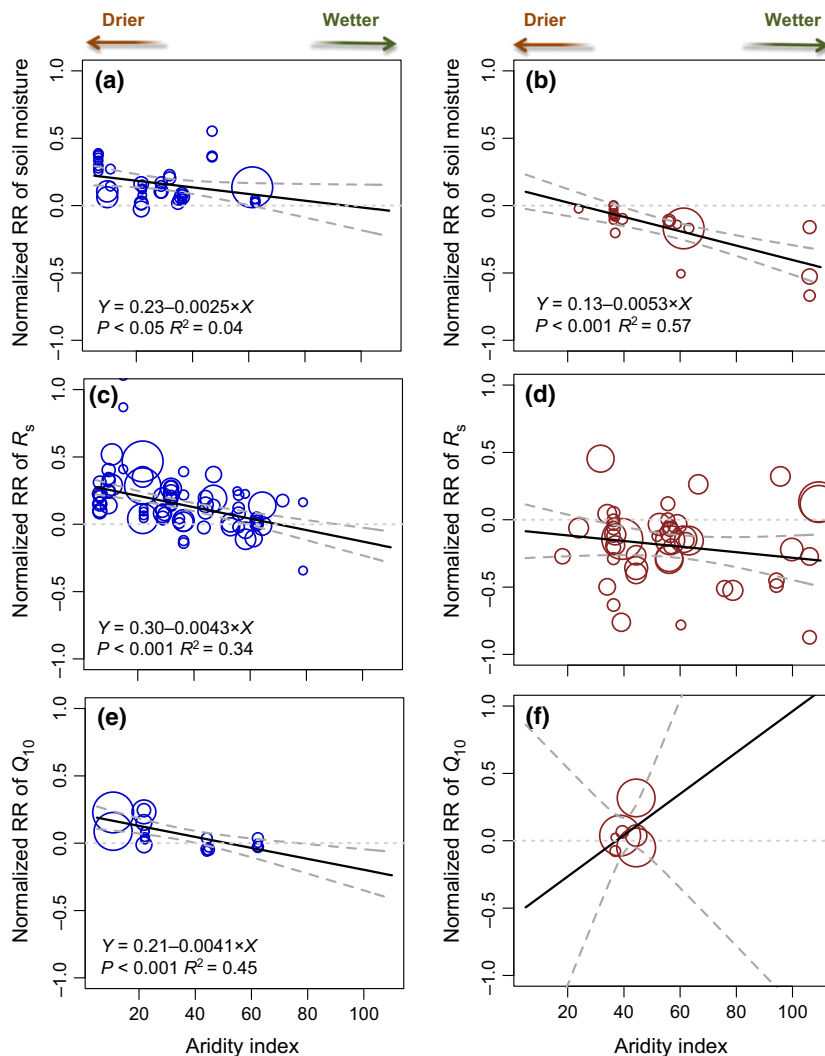
Fig. 3 Bubble plots of the meta-regression results between the aridity index and the normalized response ratios (RRs) of soil moisture (a, b), soil respiration (c, d) and Q_{10} (e, f) under the increased and decreased precipitation treatments. High aridity index means a humid climate while a low aridity index means an arid climate. Blue bubbles indicate increased precipitation treatments, red bubbles indicate decreased precipitation treatments, and the size of the bubble is relative the weight of the effect size (RR) in the random-effects meta-regression. Larger bubbles indicate study outcomes that contributed a greater overall weight in the analyses.

suggest that the sensitivity of R_s to increases in precipitation can be greater in arid areas relative to humid areas.

Several studies have found that the carbon cycle in arid and semi-arid areas is more sensitive to increases in precipitation. The degree of increased productivity and NEE was greater in wet years relative to the degree of decreased productivity in drought years (Knapp & Smith, 2001; Flanagan *et al.*, 2002), which is consistent with the results presented here. Similarly, a recent global study demonstrated that the greatest increase in the NEE caused by increased precipitation occurred in semi-arid areas of the southern Hemisphere (Poulter *et al.*, 2014). These findings suggest that in those arid and semi-arid

regions where are expected to receive more precipitation, carbon turnover could be greatly accelerated, and this acceleration may be greater with continued climate warming because the Q_{10} values were also increased under increased precipitation.

How drought affects terrestrial carbon cycling has received great attention because of the increasing frequency of extreme climate conditions (Knapp *et al.*, 2015). Our meta-analysis suggests that under the normalized decreased precipitation treatments, the reduction in soil moisture was greater in the more humid areas. Although significant trends were not detected between the normalized reduction of R_s and the aridity index, the pooled RR_{norm} of R_s tended to be higher in the more humid areas (Fig. 4b).
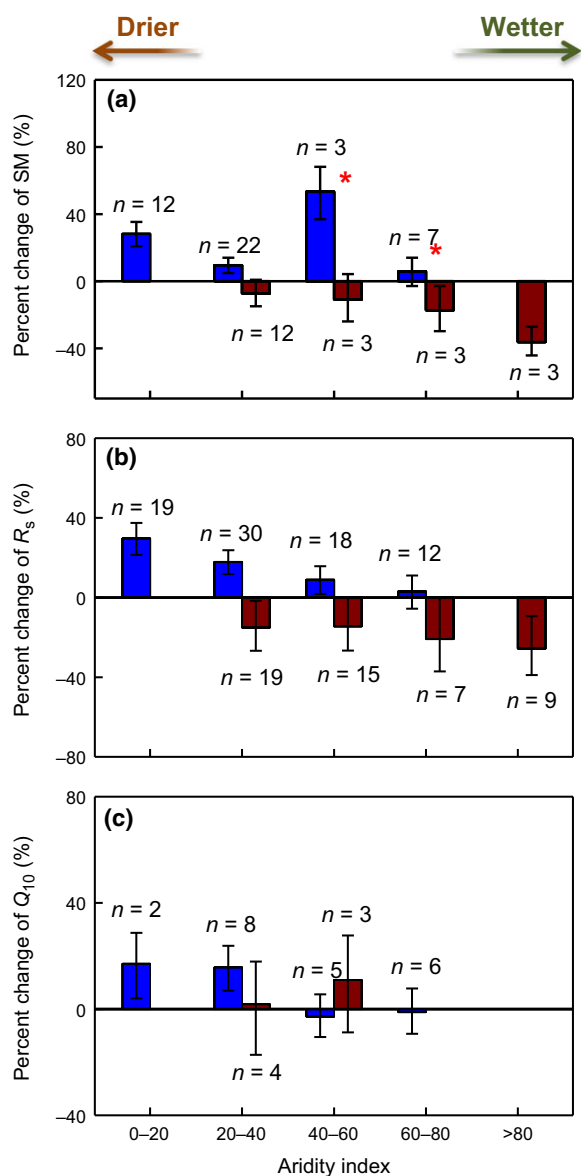
Fig. 4 Pooled effect sizes (%) of the normalized soil moisture (SM, a), soil respiration (R_s, b) and Q_{10} (c) for different aridity indexes binned to 20 intervals. Blue bars show increased precipitation treatments and red bars show decreased precipitation treatments. Results are based on a random-effects meta-analysis.

Over the past 100 years, arid areas have presented greater relative increases (%) in annual precipitation in extremely wet years, and tropical humid areas have experienced more pronounced relative reductions (%) in annual precipitation during extremely dry years (Knapp *et al.*, 2015). Such precipitation regime shifts could amplify the annual fluctuation of global R_s fluxes because increased precipitation results in greater increases in R_s in more arid areas, whereas drought tends to induce greater reductions in R_s in more humid areas.

Factors driving the response of soil respiration

Our global synthesis indicates that precipitation manipulation experiments altered both soil moisture and temperature. Although the moisture and temperature of soil are known to play critical roles in determining the variability of R_s, our results indicated that responses of R_s and Q_{10} to precipitation changes were predominantly driven by changes in soil moisture. The RRs of soil moisture explained 66% and 75% of the variances for the RRs of R_s and Q_{10}, respectively. A partial regression further indicated that precipitation-induced changes in temperature had little impact on R_s and Q_{10} (Fig. S9). The lack of soil temperature impact on R_s may have been caused by the small changes in soil temperature, from −0.05 to −0.74 °C under the normalized increased precipitation treatments and 0.04–0.70 °C under the decreased precipitation treatments. These temperature ranges may be not sufficient to affect the activities of plants and decomposers. However, the result may also have been caused by the soil moisture effects dominating and overriding the soil temperature effects under the altered precipitation regimes, and such conditions have been observed in several field experiments (Liu *et al.*, 2009; Matias *et al.*, 2012; Suseela & Dukes, 2013).

The response of R_s to precipitation changes represents an integrated effect of two components, R_a and R_h. We found that the responses of R_a and R_h increased with increases in the precipitation manipulation levels (Fig. 1e, f). However, under precipitation levels normalized to 28% of the MAP, R_a and R_h did not show significant responses to precipitation changes. This lack of the response could have been caused by the limited number of studies reporting R_a and R_h values. If we applied unweighted regressions (i.e. a quantitative review approach instead of a meta-analysis) that include the outcomes of additional studies that did not report the variances required to calculate weights, then the normalized reduced precipitation treatments decreased R_h and the increased precipitation treatments stimulated R_h (Table S7). Compared with the R_h responses, the increased and decreased precipitation treatments did not induce changes in R_a (Table S7). Although these unweighted regressions have a limited in power to generalize, they indicate potential differences between the R_a and R_h responses. However, because of the limited number of studies partitioning R_a and R_h and the potential bias caused by partitioning methods (Table S5), whether these two components show different responses to precipitation remains inconclusive. Clearly, additional long-term experiments are required to better understand how changes in precipitation affect the dynamics of R_h and R_a.

Moving beyond the precipitation amount

The frequency and magnitude of climate extremes are expected to increase as temperatures continue to increase (IPCC, 2014). In addition to changes in the size of events, increases in precipitation extremes are also characterized by certain changes, including the number of precipitation events and the intervals between events (Knapp *et al.*, 2015).

Our meta-analysis suggests that the prolonged drought experiments in which the precipitation intervals were increased, but the quantity of precipitation remained unchanged, significantly reduced the R_s value by an average of 7% (Table 1). In temperate grasslands, the decrease in R_s under prolonged drought (−10%, −15% to −4%) was similar to the results of the normalized drought treatment (−15%, −26% to −3%). The reduction of R_s under prolonged drought could be caused by the length of increasing drought stress, which reduces plant primary productivity and the amount of C allocated to respiration (Harper *et al.*, 2005). However, prolonged drought also reduces the frequency of drying/rewetting cycles in soils. Rewetting dry soil could result in CO_2 pulses by degassing the CO_2 that accumulated in the soil during the dry period (Maranon-Jimenez *et al.*, 2011), this can stimulate microbial activity via increases in the labile C supply and accelerating soil aggregate turnover (Birch, 1964; Huxman *et al.*, 2004; Unger *et al.*, 2010). Prolonged drought can decrease the frequency of drying/rewetting cycles, which may reduce C losses via respiration. Studies with higher measurement frequencies will be needed to elucidate these issues given they can capture soil CO_2 efflux pulses after episodic rain events.

Our findings with prolonged drought experiments highlight the importance of considering the timing and frequency of precipitation events when studying the carbon cycle under changing precipitation regimes. Currently, precipitation manipulation experiments focus predominantly on changes in the precipitation amount, with only a few focusing on other precipitation regime attributes. For example, in our dataset of 220 study outcomes, 206 were from studies that manipulated the precipitation amount and only 14 explored prolonged drought conditions. This limited number of studies significantly restricts assessments of potentially distinctive ecosystem responses and hampers our ability to understand how diverse plant and microbe communities regulate response patterns.

For more realistic simulations of future precipitation regimes, the frequency, intensity, and seasonality of precipitation should be manipulated. Although such studies would require more complex experimental designs with greater replication, these experiments would provide the much needed insight required to predict drought effects under a warming climate (Knapp *et al.*, 2008; Beier *et al.*, 2012). These studies and a standardized protocol for devising comparable precipitation scenarios across regions would greatly advance the development of models and predictions of current and future global patterns.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. Boolean search terms used for identifying precipitation-manipulation experiments from Web of Science over the period 1994–2014 (Thomson Reuters).

Table S2. A list of the studies included in this soil respiration meta-analysis.

Table S3. Database structure and parameters. Values are the number of independent measurements, and values in parentheses are the number of measurements that reported standard error or standard deviation.

Table S4. Results of publication bias tests using Egger's regression and the comparison of adjusted effect sizes using the trim and fill method and no-adjusted effect sizes.

Table S5. The non-normalized response ratios (RR) of soil respiration (R_s) under different manipulation period, RR of R_s using different measurement methods, and RR of autotrophic respiration (R_a) and heterotrophic respiration (R_h) using different partitioning methods.

Table S6. The normalized response ratios (RR$_{norm}$) of soil respiration (R_s) of planted and natural forests under increased-precipitation and decreased-precipitation treatments.

Table S7. Pooled normalized effect sizes (%) and 95% CIs of autotrophic respiration (R_a) and heterotrophic respiration (R_h) to increased precipitation and decreased precipitation assessed by unweight meta-analysis.

Figure S1. Effects of experimental duration on soil respiration response of individual studies which precipitation manipulation (increased-precipitation, decreased-precipitation and prolonged-drought period) lasted for more than 2 years.

Figure S2. Effects of experimental duration on soil respiration response for all studies that included in our dataset.

Figure S3. Histograms for the frequency of precipitation manipulation levels for increased-precipitation treatments (a), decreased-precipitation treatments (b) and the absolute manipulation levels for increased- and decreased- precipitation treatments (c).

Figure S4. Global distribution of precipitation manipulation experiments included in this meta-analysis. Detailed information for each site, including authors, site name, latitude, longitude and other information are found in Table S2.

Figure S5. Funnel plots of soil moisture (a), soil temperature (b), soil respiration (c), temperature sensitivity (Q_{10}, d), autotrophic respiration (R_a, e) and heterotrophic respiration (R_h, f) under increased-precipitation treatment.

Figure S6. Funnel plots of soil moisture (a), soil temperature (b), soil respiration (c), temperature sensitivity (Q_{10}, d), autotrophic respiration (R_a, e) and heterotrophic respiration (R_h, f) under decreased-precipitation treatment.

Figure S7. Funnel plots of soil moisture (a), soil respiration (b), and temperature sensitivity (Q_{10}, c) under prolonged-drought period treatment.

Figure S8. The response ratios for experiments where altered precipitation and another environmental change factor, including increased CO$_2$, warming, N addition and litter addition, were tested simultaneously: overall response ratios for altered precipitation only, increased CO$_2$ only/warming only/N addition only or litter addition only, and the combined treatments.

Figure S9. Partial regression plots for response ratios of R_s (a) and response ratios of Q_{10} (b). Residuals of variables were calculated by controlling for response ratios of soil moisture. Blue and red circles represent increased- and decreased-precipitation treatments, respectively.