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Changing precipitation effect on forest soil carbon dynamics is driven by different attributes between dry and wet areas

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ABSTRACT

Changes in precipitation patterns have the potential to significantly affect the global carbon (C) cycle by altering soil organic carbon (SOC) dynamics. Comparing the patterns and drivers of soil C responses to precipitation changes in wet and dry forests can improve our understanding of soil carbon-water coupling. In this study, we conducted a *meta*-analysis to assess the effects of precipitation changes on soil dissolved organic carbon (DOC), microbial biomass carbon (MBC), SOC concentrations, and carbon dioxide (CO_2) flux across a broad range of forest sites in dry and wet regions. The results showed that both the soil DOC and MBC concentrations decreased significantly (by averages of 7.8 and 7.9%, respectively) at the wet sites, but increased (by 1.2 and 10.2%, respectively) at the dry sites under increased precipitation conditions. The soil MBC concentrations decreased by 17.5% at the wet sites but by 4.1% at the dry sites under reduced precipitation conditions. The soil CO_2 flux decreased by 18.9% and 14.3% at the wet and dry sites, respectively, under reduced precipitation. The responses of the soil MBC concentrations were influenced by precipitation intensity, whereas soil DOC and SOC concentration, and CO_2 flux were regulated by the soil texture and climate. Clearly, soil MBC was more sensitive to increased precipitation at the dry sites than at the wet sites. Under reduced precipitation, changes in soil MBC concentration and CO_2 flux were stronger at the wet sites than at the dry sites. To enhance forecasting of soil C cycles and functional alterations in a changing climate, the differing response mechanisms in dry and wet areas should be considered using process-based climate models.

1. Introduction

Climate warming has the potential to intensify hydrological processes over land, leading to altered global precipitation patterns that result in the increased frequency and intensity of heavy precipitation and drought events (IPCC, 2021). In the coming decades, wet and dry regions are expected to become wetter and drier (WWDD), respectively, as the hydrological cycle intensifies under climate warming (Kumar et al., 2015). This unbalanced change in soil moisture could have considerable effects on the soil carbon (C) cycles in forest ecosystems (Vicca et al., 2014; Green et al., 2019; Dong et al., 2021). Given the uncertainty of forest soil organic carbon (SOC) storage influenced by microscale soil factors (clay, bulk density) in different climatic zones (wet and dry regions) (Ni et al., 2022), it is crucial to clarify the mechanisms and drivers of soil C-related cycling under changing precipitation conditions. This information will help to improve the precision of the global C budget in climate change projections.

Previous studies have shown that the effect of changing precipitation on SOC dynamics can be explained by physical and physiological mechanisms (Vicca et al., 2014; Liang et al., 2021). For example, more dissolved organic carbon (DOC) is released from aggregates into soil solutions under increased precipitation scenarios (Moyano et al., 2013), resulting in the increased use of accessible substrates by rapidly stimulating microbial activity and increasing CO_2 emissions (Wu et al., 2011; Wang et al., 2021). Since oxygen is scarce when soil pores are filled with water, aerobic organisms may become less active in extremely moist environments (Robinson et al., 2019; Sánchez-García et al.; 2020 Liang et al., 2021). In contrast, decreased precipitation induces the disconnection between water and substrates in soil pores; thus, the microorganisms enter a relatively low metabolic activity or dormant state to

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buffer the water stress and attain osmotic equilibrium (Manzoni and Katul, 2014). In addition, drought conditions may improve physical protection of SOC by facilitating aggregate formation and stabilizing SOC (Zhang et al., 2019), and may cause a reduction in microbial carbon use efficiency (Tiemann and Billings, 2011). As a result, manipulation and *meta*-analysis studies have shown that the SOC decomposition rate decreases during droughts and increases after short-term wetting (German & Allison, 2015; Deng et al., 2021; Liang et al., 2021).

Despite this general understanding from a physiological perspective, whether the effects of changing precipitation regimes on the soil C cycle vary between wet and dry areas, and to what extent, remain unclear. For example, soil water potential changes asymmetrically, i.e., drought only induces slight changes in wet soils, but dramatic variations in dry soils (Sánchez-García et al., 2020; Patel et al., 2021; Ni et al., 2022). The adaptation or tolerance of soil microorganisms in dry regions to water stress causes regional heterogeneities to be more uncertain (Zeglin et al., 2013; Manzoni et al., 2014; Xu et al., 2020). While the hydrologic connectivity in wet soil is even less affected by changes in precipitation, microorganisms in wet regions are sensitive to changes in the bioavailable C pools, which in turn influence respiration and C loss from the soil. More importantly, soil physical structures (e.g., soil texture, pore distribution, and aggregate level) control the soil infiltration rate, substrate diffusion, and osmotic stress (van Groenigen et al., 2011; Zhou et al., 2018; Zhang et al., 2019). This implies that highly spatially heterogeneous soil DOC may not respond to changes in precipitation along the simple linear trend that is typically assumed in such case. Moreover, fine-textured soil tends to reduce infiltration and limit the displacement of soil pore CO_2. CO_2 pulse from such soil after wetting are lower than that those of coarse-textured soil (Strudley et al., 2008; Sánchez-García et al., 2020). Therefore, the feedback of soil C dynamics to changing precipitation regimes depends on the interactions among multiple environmental attributes, including the soil hydraulic functions and microbial activity. Although recent studies have focused on determining the non-linear response of SOC to environmental changes (Robinson et al., 2019; Wang et al., 2021), SOC storage is the result of long-term climatic processes. Great uncertainty remains regarding assessments of the responses of key soil C processes (i.e., DOC, microbial biomass carbon (MBC), CO_2, and SOC) to changing precipitation over a broad range of climates and soil textures in wet and dry regions, which limit the accuracy of global predictions under changing climatic conditions.

We conducted a *meta*-analysis to evaluate the effects of precipitation changes on the soil water, DOC, MBC, and SOC concentrations as well as the CO_2 flux in forest soils, induced by precipitation manipulation, water addition or reduction, and rewetting. Here, we hypothesized that (1) soil DOC and MBC concentrations decrease at wet sites and increase at dry sites under increased precipitation conditions, and (2) reductions in the MBC concentration and CO_2 flux are more pronounced at wet sites than at dry sites under decreased precipitation conditions.

2. Materials and methods

2.1. Data collection

We used a *meta*-analysis to assess the effects of precipitation changes on key soil C cycle processes in forest ecosystems. We searched for peer-reviewed journal articles before December 2021 using the Web of Science and China National Knowledge Infrastructure by using the following keywords: (altered/decreased/increased/reduction) AND [(precipitation/rainfall/snowfall) OR (moisture control/wetting/irrigation)] AND (dissolved organic carbon OR microbial biomass carbon OR soil respiration OR CO_2 flux OR CO_2 emission OR soil organic carbon). Each article included in the dataset met the following criteria:

1) We used the Standardized Precipitation-Evapotranspiration Index (SPEI) (Beguería et al., 2014) to determine whether the conditions were wet (SPEI > 0) or dry (SPEI < 0) at each site. The Global SPEI database offers long-term and robust information about drought conditions at a global scale, with 0.5 degree spatial and monthly temporal resolutions. We retrieved the SPEI (timescale: 48 months) from the Global SPEI Database (https://spei.csic.es/database.html) for each site, from which we calculated the annual SPEI for the sampling year.
2) Precipitation manipulation experiments were conducted in forest ecosystems, that included different forest types, such as primary forest, plantations, and shrubland. The data were collected empirically from field experiments or observational studies. Data that were modeled or estimated were not included.
3) Given that changes in precipitation duration and intensity may have very different effects than changes in the total amount of precipitation on soil microbial activity in forest soil (Ni et al., 2022), we examined the effect of treatment duration in this *meta*-analysis. Data collected under different precipitation manipulation intensities were considered to be independent and were included in the dataset.
4) Control and treatment plots were studied under the same ambient natural conditions, ensuring that only one independent variable (precipitation manipulation). The initial environmental, soil, and plant conditions (including climate, soil type, and species composition of the control plots) were the same as those in the precipitation manipulation plots.
5) Soil CO_2 fluxes were estimated based on soil respiration. Therefore, only total soil respiration data were included in the dataset, while microbial (heterotrophic) and root (autotrophic) respiration were excluded.
6) Ancillary site information, including the latitude, longitude, mean annual temperature (MAT), and precipitation (MAP), was also compiled. The MAT and MAP were directly retrieved directly from the original studies or from other studies in which experiments were conducted at the same site.
7) Edaphic factors, including soil texture (clay, silt, or sand), pH, and N concentration, were included if the values were reported in the corresponding articles. Missing soil clay contents, bulk density, and pH data were obtained using SoilGrids250m 2.0 (Hengl et al., 2017) according to the coordinates provided in the articles.

Data were extracted from the selected articles using the GetData software (version 2.22), including the soil moisture, DOC, MBC, CO_2 flux, and SOC. A total of 547 observations were compiled from 80 articles. Among the observations, 287, 153, 328, 153, and 122 paired observations were obtained for soil moisture, DOC, MBC, CO_2, and SOC, respectively (Fig. 1).

2.2. Data analysis

The individual response ratio (*lnR*) was calculated to quantify the effects of increased/decreased precipitation on soil moisture, DOC, MBC, and SOC concentrations, as well as on the CO_2 flux, following the methods of Ni et al. (2022). The mean values (Xt for treatment and Xc for control), standard deviations (St for treatment and Sc for control), and sample sizes (nt for treatment and nc for control) for both the treatment and control plots were used to calculate their response ratios (*lnR*; Eq. (1)), variances (v; Eq. (2)), and weighting factors (w; Eq. (3)). The frequencies of the individual response ratios of altered precipitation on the DOC, MBC, and SOC concentrations and the CO_2 flux were assumed to follow normal distributions and fit Gaussian functions (all $P < 0.001$; Supplemental Figure S1).

$$lnR = ln(X_t/X_c) \tag{1}$$

$$v = S_t^2/n_tX_t^2 + S_c^2/n_cX_c^2 \tag{2}$$

$$w = 1/v \tag{3}$$

We ran a multivariate *meta*-analytic model (Konstantopoulos, 2011;

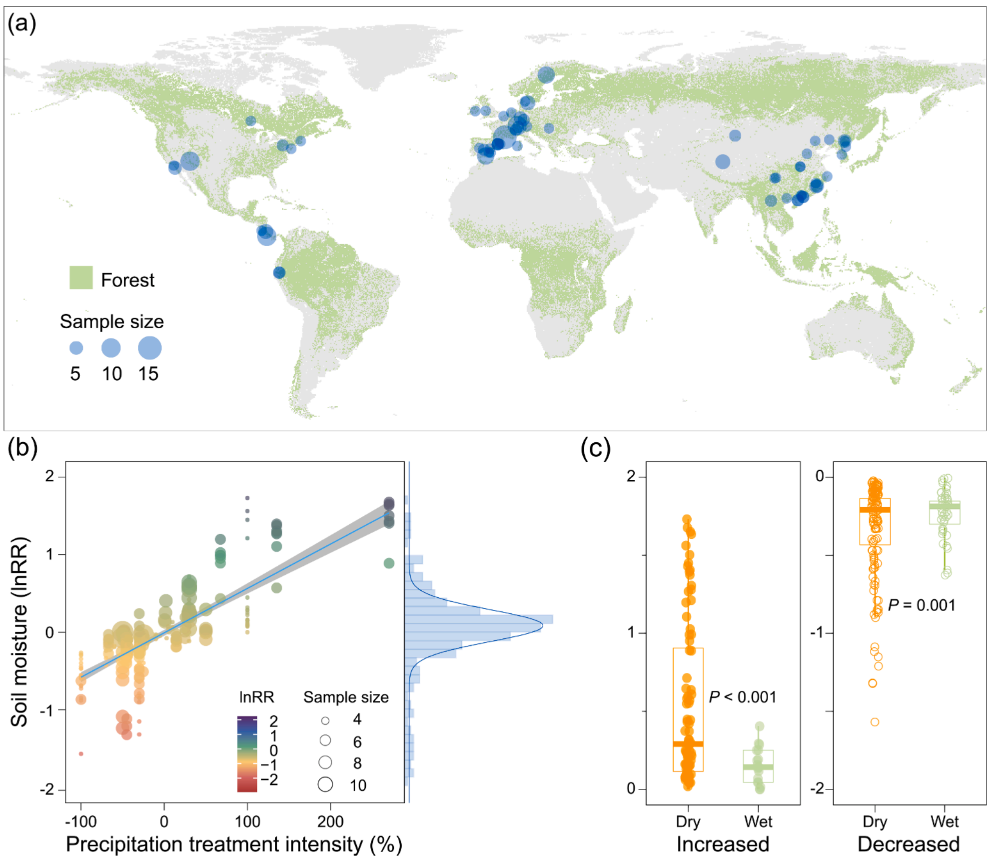

Fig. 1. (a) Global distribution of the study sites included in the *meta*-analysis; (b, c) Response of soil moisture to precipitation manipulation.

Cooper et al., 2019) with random effects using the "*metafor*" package to estimate the overall weighted effects (*lnRR*) of precipitation on the soil C pools. The responses of the variables to precipitation manipulation were considered significant if the 95 % bootstrap *CI* did not overlap zero. For ease of interpretation, *lnRR* and the corresponding 95 % *CIs* were back transformed to percentage changes (Eq. (4)):

$$\text{Percent change}\,(\%) = \left(e^{lnEE} - 1\right) \times 100\% \qquad (4)$$

2.3. Statistical analysis

To evaluate the relative importance of treatment intensity, duration, climatic conditions, and soil clay content affecting *lnR*, we adopted mixed-effects *meta*-regression model selections using the "*glmulti*" package (Calcagno and de Mazancourt, 2010) in R (version 4.2.1) (R Core Team, 2020), which is based on the maximum likelihood estimation. The importance of each factor was computed as the sum of the Akaike weights for the models in which it was included, with a cutoff of 0.8 to differentiate essential from non-essential factors following the cutoffs used in previous studies (Yue et al., 2021). To assess the effects of treatment intensity, soil clay content, SPEI, and MAT on *lnR*, we performed mixed-effects *meta*-regression models (Berkey et al., 1995) using the "*rma.mv*" function in R, with the response ratio as a response variable and treatment intensity, soil clay content, SPEI, or MAT as a random effect. These analysis was carried out using R with the "*metafor*" package (version 3.4.0) (Viechtbauer, 2010).

2.4. Publication bias

To address potential publication bias that can arise when studies published and included in the database were not a random subset of the total number of studies performed, we used Egger's regression test along with a funnel plot (Egger et al., 1997) and trim-and-fill test (Duval and Tweedie, 2000). Both Egger's regression and the trim-and-fill tests were applied using the *meta*-analytic residuals, which consisted of sampling errors and the effect-size-level effects equivalent to normal residuals (Nakagawa and Poulin, 2012). The R_0 estimator was used and implemented with the "*trimfill*" function of the "*metafor*" package to perform the trim-and-fill tests (Viechtbauer, 2010). Egger's regression test on the metanalytic residuals of the soil DOC under decreased precipitation showed potential funnel asymmetry ($P = 0.001$; Supplemental Table S1), however, the trim-and-fill test suggested no evidence for publication bias (Supplemental Figure S2). From these combined results, it is likely that publication bias in the data used in this study was very limited, and the studies included in the database were a representative sample of the available studies.

3. Results

Both the DOC and MBC concentrations decreased significantly (by averages of 7.8 and 7.9 %, respectively; all $P < 0.05$) at the wet sites, but increased (by 1.2 and 10.2 %, respectively) at the dry sites under increased precipitation (Fig. 2a). Soil DOC concentrations increased slightly at both wet and dry sites (by averages of 4.8 % and 8.2 %, respectively; all $P > 0.05$) under decreased precipitation (Fig. 2b). Soil MBC concentrations decreased by 17.5 % at the wet sites ($P < 0.05$) under reduced precipitation but only decreased by 4.1 % ($P > 0.05$) at the dry sites (Fig. 2b). SOC concentrations did not change significantly, except for an 8.5 % increase ($P < 0.05$) at wet sites under increased precipitation (Fig. 2). The soil CO_2 flux decreased by 18.9 % at the wet site and by 14.3 % at the dry sites (all $P < 0.05$) under reduced precipitation (Fig. 2b).

At the wet sites, soil clay content was the most important driver of precipitation effects on soil DOC concentrations and CO_2 flux, while the

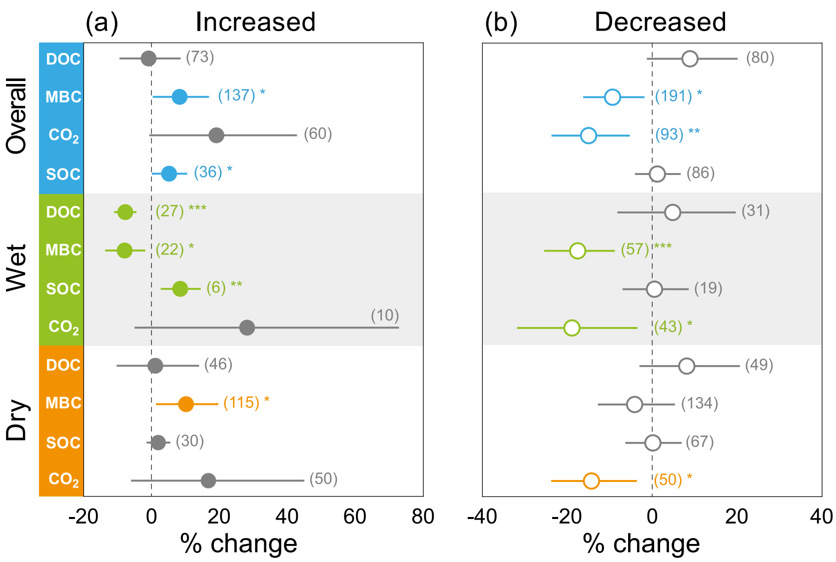

Fig. 2. Changes in dissolved organic carbon (DOC), microbial biomass carbon (MBC), and soil organic carbon (SOC) concentrations and CO_2 efflux under precipitation manipulation. Points represent the percent changes and 95% confidence intervals (*CIs*). Solid and hollow circles indicate increased and decreased precipitation, respectively. Blue represents the overall results, orange represents the dry sites, and green represents the wet sites. Colored symbols depict significant effects; grey indicates a non-significant statistical result. The sample sizes of each group are provided on the left. The response of the variable to altered precipitation was considered to be significant if the 95% bootstrap *CI* did not overlap with zero.

treatment intensity was the key driver of soil MBC and SOC concentrations (Fig. 3a-d). In addition, we found consistent positive (all $P < 0.05$) linear relationships between soil clay content, treatment intensity and the response ratio (Fig. 4a, b, and d).

At the dry sites, the response of the DOC concentration was best predicted by MAT, MAP, and the treatment intensity (Fig. 3e). The response of the MBC concentration was mediated by the treatment intensity, soil clay content, MAP, and treatment duration (Fig. 3f), and was positively related to the treatment intensity ($P < 0.001$, Fig. 4f). The response of the SOC concentration was mediated by the SPEI and MAP (Fig. 4g) and was positively related to the SPEI (Fig. 4g). The treatment intensity was the most important driver of the soil CO_2 flux response (Fig. 3h), and had a positive effect on the *lnRR* of the soil CO_2 flux ($P < 0.001$, Fig. 4h).

4. Discussion

Changes in precipitation are a major imprint of climate change and affect soil C cycling by changing environmental conditions, including the water potential, oxygen diffusion, and dissolved substrates (Berdugo et al., 2020; Ni et al., 2022). Based on this review, soil DOC and MBC concentrations decreased significantly at the wet sites but increased at the dry sites under increased precipitation. Reduced precipitation lowered the soil MBC concentration and CO_2 flux, which was more obvious in wet regions than in dry regions. The global analysis performed here demonstrates that the responses of the soil C pools and flux to precipitation changes varied depending on the climate (dry vs wet regions), which was mainly due to differences in the experimental intensity, soil texture, and soil moisture conditions.

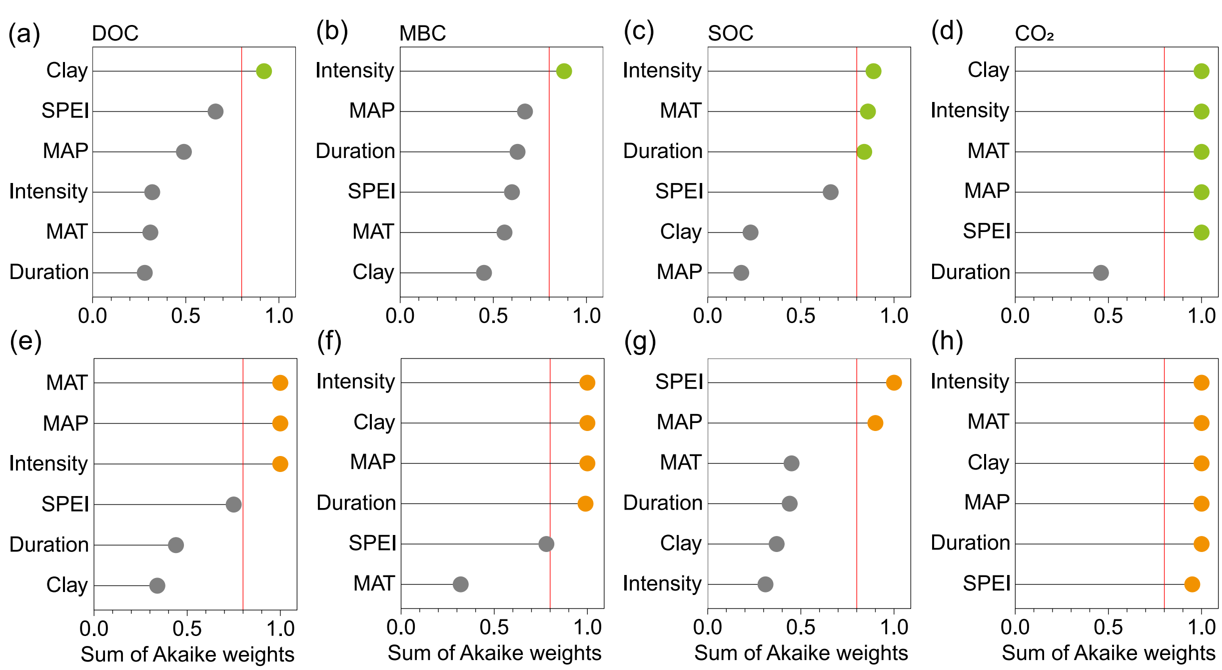

Fig. 3. Key predictors explaining changes in the soil carbon turnover processes. Green represents wet areas (a-d), and orange represents dry sites (e-h). Factor importance was estimated from the sum of the Akaike weights, based on model selection analysis using corrected Akaike's information criteria. The cut-off (red vertical line) was set as 0.8 to differentiate between the essential and non-essential factors. MAT: mean annual temperature, MAP: mean annual precipitation, SPEI: standardized precipitation-evapotranspiration index, Intensity: manipulation intensity, Duration: manipulation duration, Clay: clay content.

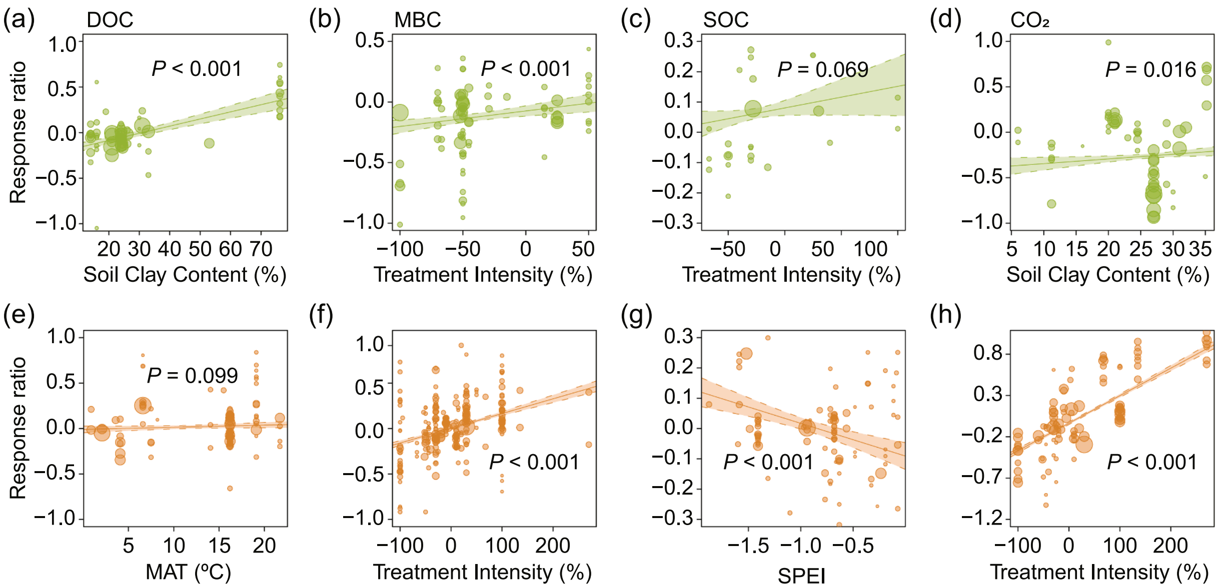

Fig. 4. Relationships between predictors and individual response ratios using pairwise data. Green represents wet areas (a-d) and orange represents dry sites (e-h). Linear fitted lines and 95% confidence intervals are shown. The size of each point was proportional to the weight that the study received in the analysis (larger points indicate studies that received more weight). MAT: mean annual temperature, SPEI: standardized precipitation evapotranspiration index.

4.1. Precipitation effects on soil carbon cycle at wet forests

Supporting our first hypothesis, soil DOC and MBC decreased at the wet sites under increased precipitation, but soil MBC increased at the dry sites. Surprisingly, we also found that soil DOC at the wet sites decreased when precipitation increased (Fig. 2a). Potential mechanisms explaining this result may be that increased leaching after precipitation pulses, which cause soil DOC loss (Sánchez-García et al., 2020). This result was further supported by decreased soil MBC at the wet sites under elevated precipitation (Fig. 2a), indicating that microbial utilization does not decrease the soil DOC. Microbial activity is also limited by oxygen when the soil pores reach a saturation state (Moyano et al., 2013). The filling of soil pores with water would partly explain the increased soil CO_2 flux at the wet sites (Fig. 2a). In contrast, soil DOC would accumulate slightly without leaching from the soil under less precipitation conditions (Brangarí et al., 2020; Deng et al., 2021). At an optimal level, microorganisms use the substrate in solution to conduct enzyme–catalyzed decomposition to achieve reproductive activities (Moyano et al., 2013; Deng et al., 2021). Under reduced precipitation, microbial activity and C absorption would be low (Manzoni et al., 2016), and most of the C would be utilized to synthesize osmotic control products, such as osmolyte C, which is released near cells and has a poor usage efficiency for growth

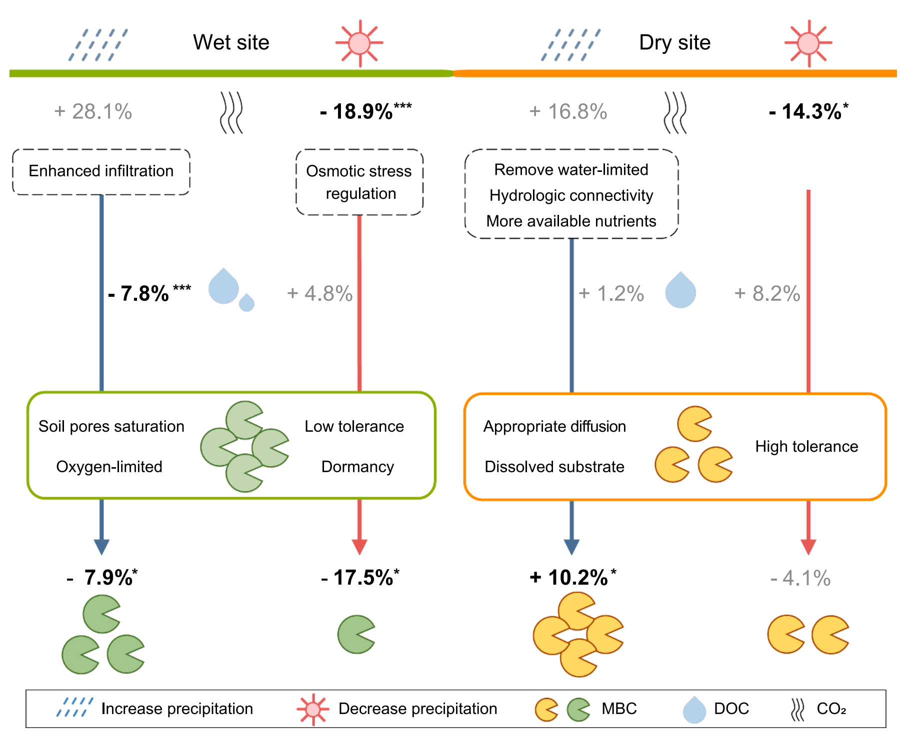

Fig. 5. Schematic diagram of the response of soil organic carbon to precipitation changes in forest soil in dry and wet regions. DOC: dissolved organic carbon, MBC: microbial biomass carbon. Asterisks denote significant differences (95 % bootstrap *CI* does not overlap with zero). * $P < 0.05$, *** $P < 0.001$.

(Wood et al., 2001; Schimel, 2018). Generally, microbes at wet sites face less osmotic stress (Fig. 5), suggesting that more resources and energy are available for microbial growth (Brangarí et al., 2020).

However, we observed that microbial biomass declined significantly under decreased precipitation (Fig. 2b), probably because microbes invest more resources in regulating osmotic stress when facing a rapid reduction in water potential entering a dormant state, or even death (Slessarev et al., 2020). Therefore, soil DOC concentrations increased slightly when the precipitation decreased (Fig. 2b), which might be due to lower soil DOC consumption by microorganisms or newly produced dissolved C in the soil solution due to microbial cell lysis (Patel et al., 2021). In addition, the CO_2 flux in wet forest soil exhibited a positive relationship with the precipitation treatment (Table S3), which can be explained by the dependence of microbial activity on the soil moisture level (Manzoni et al., 2012; Vicca et al., 2014). When the precipitation decreased, the capacity of the soil microorganisms to tolerate drought stress in humid locations was low; thus, the CO_2 produced by microbial activity reduced significantly (Fig. 2b).

4.2. *Precipitation effects on soil carbon cycle at dry forests*

At dry sites with lower water contents, increasing precipitation promotes a rapid DOC release from soil organic matter due to enhanced infiltration (Zhang et al., 2019; Deng et al., 2021). Under water deficit conditions, infiltration allows the diffusion of dissolved materials retained in the water films around mineral particles (Homyak et al., 2018). However, the results obtained herein indicated that increased precipitation did not induce increases in soil DOC (Fig. 2a). It is possible that enhanced hydrologic connectivity improves microbial access to dissolved substrates (Liang et al., 2021), which concurrently increases the assimilation of newly "activated" C for microbial growth (Homyak et al., 2018; Patel et al., 2021). The opposing responses of soil DOC and MBC to increases precipitation between wet and dry regions highlight the regulatory role of the initial soil moisture conditions (Patel et al., 2021).

Under decreased precipitation, the response of soil CO_2 flux was significant, while those of soil DOC and MBC concentration were not significant (Fig. 2). The degree to which MBC concentrations were reduced in dry forest soil was weaker than in wet forest soil (Fig. 2b, Table S2). It is possible that microbes at the dry sites are more drought-tolerant than those at the wet sites (Fig. 5). Even so, reduced soil moisture may decrease the C use efficiency of soil microorganisms, thereby decreasing soil CO_2 flux significantly (Manzoni et al., 2012; Selsted et al., 2012). Differences in microbial C utilization strategies and water stress tolerance (Fig. 5) indirectly drive the responses of soil microbial biomass and metabolic activity to drought (Schimel, 2018). In addition, we did not observe notable changes in SOC for either increased or decreased precipitation at the dry sites (Fig. 2). Based on several process-based models and studies, it has been predicted that drought, which occurs under extremely low precipitation intensity and duration, would decrease the SOC concentration (Green et al., 2019; Liang et al., 2021). Most of the precipitation manipulations included in this review did not reach the threshold, and the results did not indicate that the soil DOC and SOC response were related to the treatment duration (Supplementary Fig. S3a, c). Instead, consistent with the idea that an extended drought or wet period may render the soil microbes inactive (Supplemental Fig. S3b) (Moyano et al., 2013; Ni et al., 2022).

4.3. *Soil texture and climate controls over the precipitation effects*

Soil water availability influences microbial metabolic activity and extracellular enzyme diffusion, which then influence the accessibility of SOC substrates and CO_2 emissions (Wu et al., 2011). The results clearly showed that increased precipitation had a negative effect on soil MBC concentrations, which suggests that soil moisture should be maintained at an intermediate level (Liang et al., 2021). Soil texture is another key factor, as the results indicated a positive relationship between the soil DOC response and soil clay contents at wet sites (Fig. 4a). It is possible that coarse-textured soils with lower clay content and bulk density hold less capillary water (Zhou et al., 2018) owing to their lower water retention ability and a smaller amount of substrate per unit mass of soil (Gómez-Guerrero and Doane, 2018). As discussed above, soil pore aeration is restricted when moisture conditions exceed suitable levels, which may account for the regulation of CO_2 emissions by soil clay content (Fig. 3d).

In dry regions, short-term changes in precipitation patterns may not alter the diffusion and production of dissolved substances, as determined by the physical structure or the climate, which could explain soil DOC response to precipitation changes mediated by MAT and MAP (Fig. 3e). Arid areas contain more coarse-textured soils and more limited water than wet areas (Liu et al., 2020). Therefore, microbial biomass C was controlled by moisture conditions and was positively correlated with the precipitation treatment intensity (Figs. 3 and 4). SPEI was an important regulator of the SOC response (Fig. 3g), suggesting that changes in SOC may require long-term and multi-factor changes in climatic patterns. The response of the soil CO_2 flux received a weighting over 0.8 for experimental treatment intensity, climate, and soil clay content at both the wet and dry sites (Fig. 3h), implying the presence of a more complex mechanism for CO_2 variations, as indicated by its large confidence interval (Fig. 2a).

5. Conclusions

In the context of changing precipitation regimes in different areas and given the high storage and sensitivity of forest soil C pools, understanding their coupling in different climatic conditions is critical for improving predictions of the soil C cycle. Our findings emphasize that the underlying physiological and physical mechanisms that derived soil DOC and microbial activity in response to changing precipitation are diametrically opposed in wet and dry regions. Moreover, the soil DOC, CO_2 flux, and SOC responses differed across climates due to initial moisture conditions and soil textures. Future studies should incorporate initial microscale conditions, including soil water retention capacity, pore connectivity, solute diffusivity, and the extent to which these attributes are influenced by precipitation, as they vary markedly under different climatic conditions and are closely related to soil moisture and texture.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.geoderma.2022.116279.

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