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REGULAR ARTICLE

Intensified rainfall in the wet season alters the microbial contribution to soil carbon storage

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Abstract

Aims Precipitation patterns in the tropics of southern China are predicted to change with an increase of the rainfall in the wet season (WW) and a delay of the wet season into autumn (DW). To explore how soil C cycles respond to a changing precipitation pattern, we established a precipitation manipulation experiment through water exclusion or addition.

Methods We assessed soil physicochemical properties, microbial communities, glomalin-related soil protein (GRSP), and microbial residual carbon (MRC) to indicate whether there are differences in soil C cycling after altered precipitation patterns.

Results Changes in precipitation patterns did not affect soil properties at 0-10 cm soil depth. However, the WW treatment significantly increased microbial biomass (by 52%) at 10-20 cm soil depth owing to its long-term promotion. At the same time, the increment of microorganisms significantly decreased the contribution of fungal MRC to SOC (by 32%), and there was an increasing trend in bacterial MRC and SOC.

Conclusions Over a long time, the facilitation of microbes and the alteration of microbial contribution to SOC by intensified precipitation in the wet season will enhance the carbon sequestration capacity of tropical forest soils, which is of great importance in mitigating global warming.

Keywords Precipitation patterns · Tropical coastal forests · Microbial communities · Microbial residual carbon · Soil organic carbon

Abbreviations

AMF	Arbuscular mycorrhizal fungi
ANOVA	One-way analysis of variance
BP	Brey phosphorous
CT	Control
DW	The delayed wet season treatment
F/B	The ratio of fungi to bacteria
GalN	Galactosamine
GluN	Glucosamine
GRSP	Glomalin-related soil protein

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MRC	Microbial residual carbon
MurN	Muramic acid
NH_4^+-N	Soil ammonium
NO_3^--N	Soil nitrate
PLFAs	Phospholipid fatty acids
PLS-PM	Partial least squares path modeling
SOC	Soil organic carbon
WW	The wetter wet season treatment

Introduction

Tropical forests play a critical role in global carbon (C) cycling, as they store a quarter of global terrestrial carbon in biomass and soil (Guo and Gifford 2002; Jobbágy and Jackson 2000). Containing twice the amount of C as vegetation does, the soil is a structurally and functionally complex system, which is controlled by multiple variables such as vegetation, texture, moisture, temperature, and microbial community composition (Lal 2004; Srivastava et al. 2016; Tharammal et al. 2019). Under changing precipitation patterns (amount, timing, and intensity), soil microbial activities may be influenced (positive or negative) (Ren et al. 2017), thus altering litter decomposition, SOC mineralization, and other biogeochemical processes (Alvarez-Clare and Mack 2011; Schlesinger et al. 2016; Smith et al. 2015). However, how microbial activities and metabolisms respond to changing precipitation patterns in tropical forests raises many concerns, as they closely relate to global warming via changing soil C cycling (Barnard et al. 2015; Bouskill et al. 2013; Ma et al. 2017; Yang et al. 2021; Yu et al. 2019; Zhao et al. 2018).

Soil microorganisms play important roles in regulating soil nutrient availabilities and biogeochemical cycles, which are considered a fundamental part of terrestrial ecosystems (Banning et al. 2011; Harris 2009). In addition, they are involved in several aspects of C cycling, *e.g.*, arbuscular mycorrhizal fungi (AMF)-mediated C input (Treseder and Allen 2000; Wilson et al. 2009), and the formation of microbial residual C (Khan et al. 2016; Ma et al. 2017). Changes in precipitation patterns may influence the composition and structure of soil microbial communities, and therefore change the volume and components of SOC pools (Ma et al. 2017; Malik et al. 2016).

AMF is one of the most predominant soil microbial communities and able to establish symbiotic associations, namely, arbuscular mycorrhizas (AMs), with up to 80% of terrestrial plants (Keymer and Gutjahr 2018). Glomalin-related soil protein (GRSP), the production of AMF, is a kind of extracellular polymeric substance produced by the hyphae and spores. It accounts for 4-5% of soil C (Lovelock et al. 2004; Rillig et al. 2001) and can be preserved for a long time due to its low water solubility and resistance to degradation (Staddon et al. 2003; Treseder and Allen 2000). Microbial residual carbon (MRC) accounts for 25-40% of SOC and is mainly derived from microbial metabolites and residues (Ding et al. 2013; Khan et al. 2016). In contrast to soil microbial biomass carbon (MBC) and phospholipid fatty acids (PLFA) that degraded rapidly after cell death, MRC is more stable, and makes a greater and more stable contribution to SOC (Dong et al. 2015; Zelles 1999). To date, many studies of MRC have focused on manipulated nutrient addition experiments (Engelking et al. 2007; Fan et al. 2020; Griepentrog et al. 2014; Ma et al. 2017; Yuan et al. 2021). However, few studies have addressed the effects of changes in precipitation patterns on microbial activities and MRC in tropical forests (Nielsen and Ball 2015; Wu et al. 2011).

Affected by the tropical monsoon climate, tropical forests in southern China have distinctly dry and wet seasons, where the wet season is generally from April to September and the dry season is from October to March of each year. According to long-term monitoring and model predictions, precipitation patterns in southern China are changing (*e.g.*, increased precipitation during the wet season, and a delayed wet season: a prolonged wet season into relatively dry season; Fang et al., 2004; Barros et al. 2014; Luo et al. 2008). Precipitation patterns strongly affect soil moisture. In a seasonal tropical forest, even when annual total precipitation is constant, seasonal changes in precipitation might lead to a dramatic upheaval in soil moisture (Schimel et al. 2007; Zhou et al. 2011). As a result, the soil moisture of tropical forests in southern China will be altered by changes in precipitation patterns, thus altering crucial soil processes through variation in soil microorganisms (Wang et al. 2020; Wu et al. 2011). It has been proved that soil microorganisms are sensitive to environmental change, such as soil moisture, and growing season irrigation

have a positive effect on bacterial and fungal richness (Nielsen and Ball 2015).

Soil microorganisms have different resource preferences and life history strategies under environmental stresses. Therefore, microbial taxa might diversely respond to changing precipitation patterns (Ren et al. 2017). Increased precipitation in the wet season can stimulate microbial activities by alleviating water stress and increasing the diffusion of substrates to microbes (Hartmann et al. 2017), while microbial activities also decline due to a lack of oxygen and nutrient leaching in humid ecosystems (Weil and Brady 2017). Intensified precipitation in the wet season increased the phyla Gemmatimonadetes and Basidiomycota but decreased Ascomycota, indicating that different soil microorganisms respond differently to intensified precipitation (Zhao et al. 2018). As for the delayed wet season, the microbial community composition and function generally are enhanced because of the alleviation of water limitation in the dry season (Landesman and Dighton 2010; Schimel et al. 2007). For instance, water addition in autumn increased bacterial and fungal abundance, leading to elevations in microorganisms and enzyme activities and thus faster soil C cycles (Gong et al. 2021; Huang et al. 2018).

In this study, we established a precipitation manipulation experiment through water exclusion or addition to simulate the projected delayed wet season (DW) and wetter wet season (WW) in a tropical forest, aiming to better understand how microbial activities and associated C cycles respond to changes in precipitation patterns. We hypothesized that (a) both DW and WW treatments promoted microorganisms, while the WW and DW treatments more strongly alleviated the water stress of microorganisms in the dry season; (b) the enhancement of microbial activities accelerated the accumulation of GRSP and MRC, which are two vital sources of stable SOC, and thus the quantity of SOC increased.

Materials and Methods

Sample collection

Our study was conducted at the Xiaoliang Research Station of Tropical Coastal Ecosystems, Chinese Academy of Sciences (21°27′N; 110°54′E), Guangdong province, China (Fig. 1a). The climate of the region is a tropical monsoon climate with a noticeable variation of the wet (April–September) and dry season (November–March), where the mean annual temperature and precipitation are 23°C and 1400–1700 mm, respectively. The field manipulation experiment was conducted in 2012, which was established in a

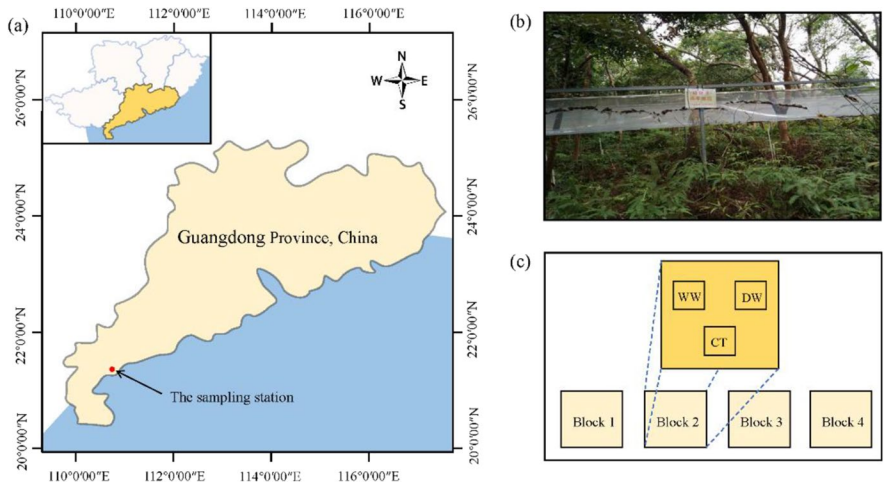

Fig. 1 (a) The sampling site (indicated by the red point), Xiaoliang Research Station for Tropical Costal Ecosystem, Chinese Academy of Sciences was located in Xiaoliang Town, Dianbai District, Maoming City (110°54′18″E, 21°27′49″N). (b) Precipitation manipulation plots in a seasonally dry tropical forest in southern China. (c) The experiment design of seasonal precipitation changes, where each plot was 12 m × 12 m and at least 3 m away from each other

secondary tropical forest using a completely randomized block design. Within four replicate blocks, delayed wet season (DW: reducing two months throughfall during the early wet season and then adding the same amount of reduced water after the wet season), wetter wet season (WW: adding 30% annual precipitation water during mid-wet season additionally), and control (without changes in precipitation patterns) were randomly assigned to three 12 m × 12 m plots (Fig. 1b, c). A detailed description of these treatments can be found in Yu et al. (2019). There was a gap of at least 2 m between plots, and they were separated by a PVC board to avoid interference caused by the treatments. In August 2020, we randomly took three soil cores at 0 to 10 cm and 10 to 20 cm depth in each plot and homogenized cores from the same plot into one soil sample, resulting in 24 soil samples. The soils were sieved through 2 mm mesh to remove stones and roots and stored at -20°C before use (Yu et al. 2020).

Soil physicochemical characteristics

Soil moisture was assessed by oven-drying 10 g fresh soil samples at 105°C for 24 h in a cylindrical stainless-steel container of known weight (Chen et al. 2017). Soil pH was determined in a 1:2.5 soil: water slurry using a glass pH electrode (METTLER TOLEDO, FiveGO^{TM}, Zurich, Switzerland). The determination of SOC was based on the $K_2Cr_2O_7$ titration method (Lu 1999). Soil NH_4^+-N and NO_3^--N were extracted by 2 *M* KCl (Page et al. 1982), Bray P was extracted by the Bray 1 method (0.03 *M* NH_4F and 0.025 *M* HCl; Bray and Kurtz 1945). The above-mentioned soil NH_4^+-N, NO_3^--N, and BP were analyzed by automated discrete analyzers (SKALAR BluVison^{TM}, Breda, the Netherlands).

Glomalin-related soil protein extraction and quantification

To analyze GRSP, we extracted 1.0 g air-dried milled samples with sodium citrate by an improved procedure (Rillig et al. 2003; Zhang et al. 2020). Briefly, easily extracted GRSP (EE-GRSP) and total extracted GRSP (T-GRSP) were extracted by 8 ml sodium citrate (20 *mM*, pH = 7.0 for EE-GRSP; 50 *mM*, pH=8.0 for T-GRSP) at 121°C for 30 min (EE-GRSP) or 60 min (T-GRSP). The T-GRSP was extracted three times until the solution was straw-colored. The supernatant was centrifuged and analyzed by a spectrophotometer (Multiskan^{TM} FC, ThermoFisher, Waltham, MA, USA) using bovine serum albumin as the standard.

Soil microbial community composition

Soil microbial community composition was characterized by the phospholipid fatty acid (PLFA) methods. Briefly, 8 g of freeze-dried soil samples were extracted in chloroform–methanol–phosphate buffer (1:2:0.8 v/v/v), and the extracted lipids were fractionated into neutral lipids, glycolipids, and polar lipids on a 0.5 g silica gel solid-phase extraction column by successive elution with chloroform, acetone, and methanol (Schimel et al. 2007; Veum et al. 2019). The methanol fraction (containing phospholipids) was subjected to mild alkaline methanolysis to transform the fatty acids into free methyl esters and analyzed on a gas chromatograph (GC7890, Agilent, CA, California, USA). The ratio of fungi to bacteria (F/B) was calculated to represent changes in community structure. The total PLFAs biomass of the soil microbial community was calculated as the sum of the groups, while the abundance of each group was calculated by classifications of PLFAs. Detailed assignments of signature PLFAs into functional groups are presented in Table S1 (Bardgett et al. 1996; Bossio et al. 2006; Cusack et al. 2011; Frostegård and Bååth 1996).

Soil amino sugars and microbial residual carbon

To calculate MRC and its contribution to the SOC pool, we extracted and transformed soil amino sugars. Aliquots of 0.5 g of air-dried soil were hydrolyzed with 10 ml 6 *M* HCl at 105°C for 6 hours. After hydrolysis, samples were uniformly mixed and cooled to room temperature, and then filtered. An aliquot of 0.5 ml of filtrate was evaporated to dryness by nitrogen gas at 40-45°C to remove HCl. The dried residues were dissolved in 0.5 ml of deionized water, dried by nitrogen gas again, and redissolved in 2 ml of deionized water and stored at −20°C before analysis (Mou et al. 2020; Zhang and Amelung 1996). The four amino sugars (GluN, MurN, GalN, and ManN) were pre-column derivatized with orthophthaldialdehyde. The concentrations of four amino sugar were determined using a high-performance

liquid chromatograph (Dionex Ultimate 3000, Thermo Fisher Scientific, Waltham, MA, USA) equipped with an octadecylsilylated silica gel column (Acclaim120 C18; 150 mm, 4.6 mm, 3 μm; Thermo Fisher Scientific, Waltham, MA, USA). The individual amino sugars (GluN, GalN, and MurN) were identified and quantified according to the chromatograms of standard solutions containing mixed amino sugars. The concentrations of individual and total amino sugars were expressed as μg g^{-1} dry soil. The formula for identifying the fungal residue carbon amino sugars was:

$$\mathrm{F-GluN}\left(\mu g\ g^{-1}\right) = \mathrm{total\ GluN}\left(\mu g\ g^{-1}\right) - 2 \times \mathrm{MurN}\left(\mu g\ g^{-1}\right) \times (179.2/251.2),$$

where F-GluN was fungal-derived GluN. Since GluN was present in both fungal and bacterial cell walls, F-GluN was calculated by subtracting bacterial-derived GluN from total GluN, assuming that MurN and GluN occurred at a 1 to 2 molar ratio in bacterial cell walls. 179.2 and 251.2 were the molecular weights of GluN and MurN, respectively (Engelking et al. 2007; Shao et al. 2017).

Therefore, MRC was calculated as:

$$\text{Fungal MRC}\left(\mu g\ g^{-1}\right) = \mathrm{F-GluN} \times 9,$$

$$\text{Bacterial MRC}\left(\mu g\ g^{-1}\right) = \mathrm{MurN} \times 45,$$

where 9 and 45 were conversion factors (Appuhn and Joergensen 2006). The relative contribution of the residual carbon to the soil carbon pool was viewed by analyzing the fungal or bacterial MRC compared to SOC.

Data analysis

Before statistical analysis, the data were subject to the Shapiro–Wilk test for normality and the Levene test for homogeneity of variance. When data were not normally distributed, they were logarithmically transformed. Then we used two-way ANOVAs to evaluate the changes of precipitation patterns, soil depths and their interaction on soil physicochemical characteristics, GRSP, microbial community composition and MRC by the "rstatix" package (Kassambara 2021) in R software (R Core Team, R 4.0.3 2020). Where the effects were significant, post hoc tests (LSD) were conducted to assess the differences among treatments and depths at $P < 0.05$. The general linear model analysis was also used to examine the relationships between GRSP, MRC and SOC. Partial least squares path modeling (PLS-PM) was applied to further identify the possible pathways by which measured variables mediated the response of microbial community, GRSP, MRC and their contribution to effects of precipitation changes, using the "plspm" package (Sanchez et al. 2015). Five blocks of reflective indicators were defined as "Soil properties", "Microbial communities", "Glomalin-related soil protein", "Microbial residual carbon", "SOC". The goodness-of-fit index was met to ensure the model was valid (the goodness of fit > 0.7).

Results

Overview of measured indicators

Overall, the interactions between treatment and depth were not significant, indicating that there was no combined effect of treatment and depth on these variables (Table S2; $P>0.05$). However, the differences between the variables at different soil depths were almost all significant (only moisture, pH and F/B were exceptions), which showed obvious differences between 0-10 cm and 10-20 cm soil depths. Treatment had significant impacts on soil moisture, Bray P, microbial communities (including bacteria, fungi, Gram-positive and actinomycetes) and bacterial MRC ($P<0.05$), while there were no significant effects on GRSP and fungal MRC.

Soil physicochemical properties

Soil physicochemical properties did not vary drastically among different precipitation conditions (Table 1). Intensified precipitation in the wet season increased soil moisture at 10-20 cm depth (increased by 15%; $P<0.05$), while there was no significant difference at 0-10 cm depth, which might result from rapid surface evapotranspiration. SOC also showed an increasing tendency between DW and WW at 10-20 cm depth ($P<0.05$), indicating the accumulation of

Table 1 Soil physiochemical characteristics at 0-10 cm and 10-20 cm depth under changing precipitation patterns, where DW was delayed wet season treatment, WW was wetter wet season treatment, and CT was control. SOC was soil organic carbon, NH_4^+-N was ammonium-N, NO_3^--N was nitrate-N, and BP was Bray P; values were means ±SE; n = 4, different superscript letters within a row indicated significant differences among treatments at $P < 0.05$ (after correction for multiple comparisons)

Soil physiochemical properties	Topsoil (0~10 cm)			Subsoil (10~20 cm)		
	CT	DW	WW	CT	DW	WW
pH	4.25±0.19	4.51±0.35	4.22±0.18	4.44±0.09	4.53±0.24	4.34±0.07
Moisture (%)	20.08±1.59	20.15±2.73	22.15±1.57	18.25±1.52^{b}	19.78±0.85^{ab}	20.88±0.46^{a}
SOC (g kg^{-1})	22.49±4.11	28.80±3.36	24.41±6.94	9.04±1.40^{ab}	8.62±1.85^{b}	12.03±2.49^{a}
NO_3^--N (mg kg^{-1})	0.60±0.19	0.54±0.10	0.71±0.09	0.20±0.03	0.21±0.09	0.23±0.07
NH_4^+-N (mg kg^{-1})	0.69±0.54	1.03±0.68	0.91±0.27	0.38±0.27	0.35±0.19	0.45±0.16
BP (mg kg^{-1})	0.10±0.02^{ab}	0.08±0.02^{b}	0.12±0.01^{a}	0.04±0.01	0.04±0.01	0.05±0.01

SOC in the WW treatment. Therefore, intensified precipitation in the wet season increased soil moisture at 10-20 cm depth, while other soil physicochemical properties were affected to a limited extent by changed precipitation patterns.

Glomalin-related soil protein

Both T-GRSP and EE-GRSP were significantly differed between 0-10 cm and 10-20 cm sampling depth, especially in the DW and WW treatments (Fig. 2a, b; $P<0.05$). However, their contribution to SOC (both T-GRSP/SOC and EE-GRSP/SOC) was fairly constant in the DW or WW treatments (Fig. 2c, d; $P>0.05$). Neither DW nor WW treatment significantly influenced them at 0-10 cm or 10-20 cm depth, indicating that GRSPs and their contribution to SOC were relatively constant under changing precipitation patterns.

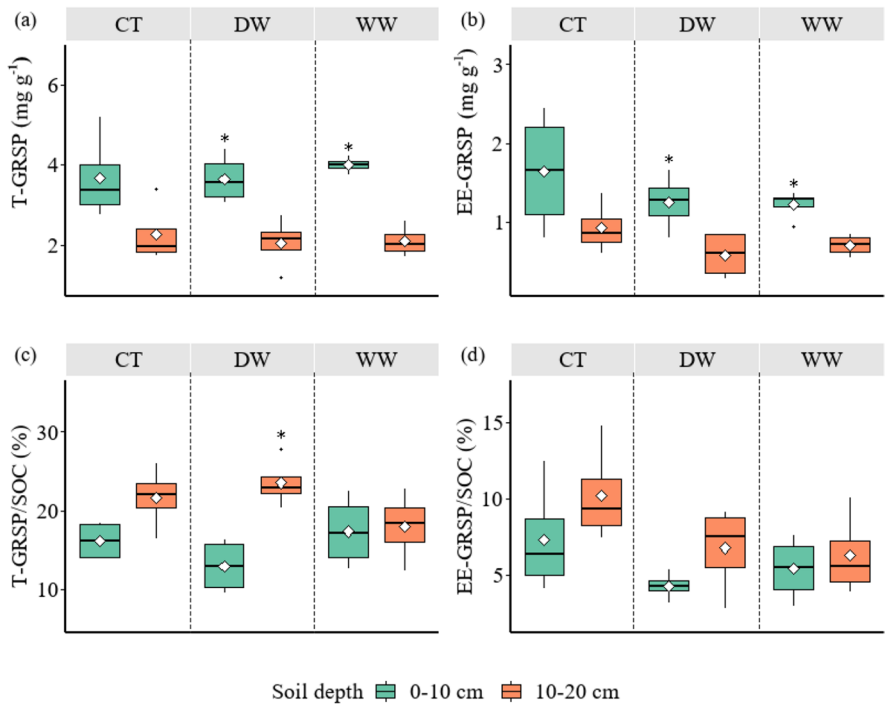

Fig. 2 Total, easily-extractable glomalin-related soil protein (T/EE-GRSP) and their contribution to SOC (T-GRSP/SOC and EE-GRSP/SOC) were assessed in (a) (b) (c) (d), where DW was delayed wet season treatment, WW was wetter wet season treatment, and CT was control. The asterisks indicated significant differences between soil depths and different lowercase letters indicated significant differences among precipitation conditions at $P < 0.05$ (after correction for multiple comparisons)

Soil microbial community

For PLFAs, the WW treatment significantly increased microbial biomass at 10-20 cm depth including bacterial abundance, fungal abundance and Gram-positive bacterial (G +) abundance, respectively (Fig. 3a, b, c; $P<0.05$), while the abundance of Gram-negative bacteria (G-), actinobacteria and AMF were relatively stable (Fig. 3d, e, f; $P>0.05$). As far as the total PLFA biomass was concerned, the WW treatment significantly increased the microbial biomass by 52% compared with the control at 10-20 cm depth (Fig. 3h; $P<0.05$), showing the effect of WW treatment on favoring soil microbes. The increasing results of microbial biomass were consistent with changes in soil moisture, indicating that intensified precipitation in the wet season strengthened the microbial activity. However, the WW treatment did not change microbial biomass at 0-10 cm depth (Fig. 3a, b, c, d, e, f; $P>0.05$).

Soil microbial residual carbon

MRC was obtained after a conversion of soil amino sugars. In terms of the quantity of total MRC and fungal MRC, there were significant differences between 0-10 cm and 10-20 cm sampling depths in the DW and WW treatments (Fig. 4a, e; $P<0.05$). Bacterial MRC in the WW treatment was significantly higher than DW treatment at 10-20 cm depth (Fig. 4c;

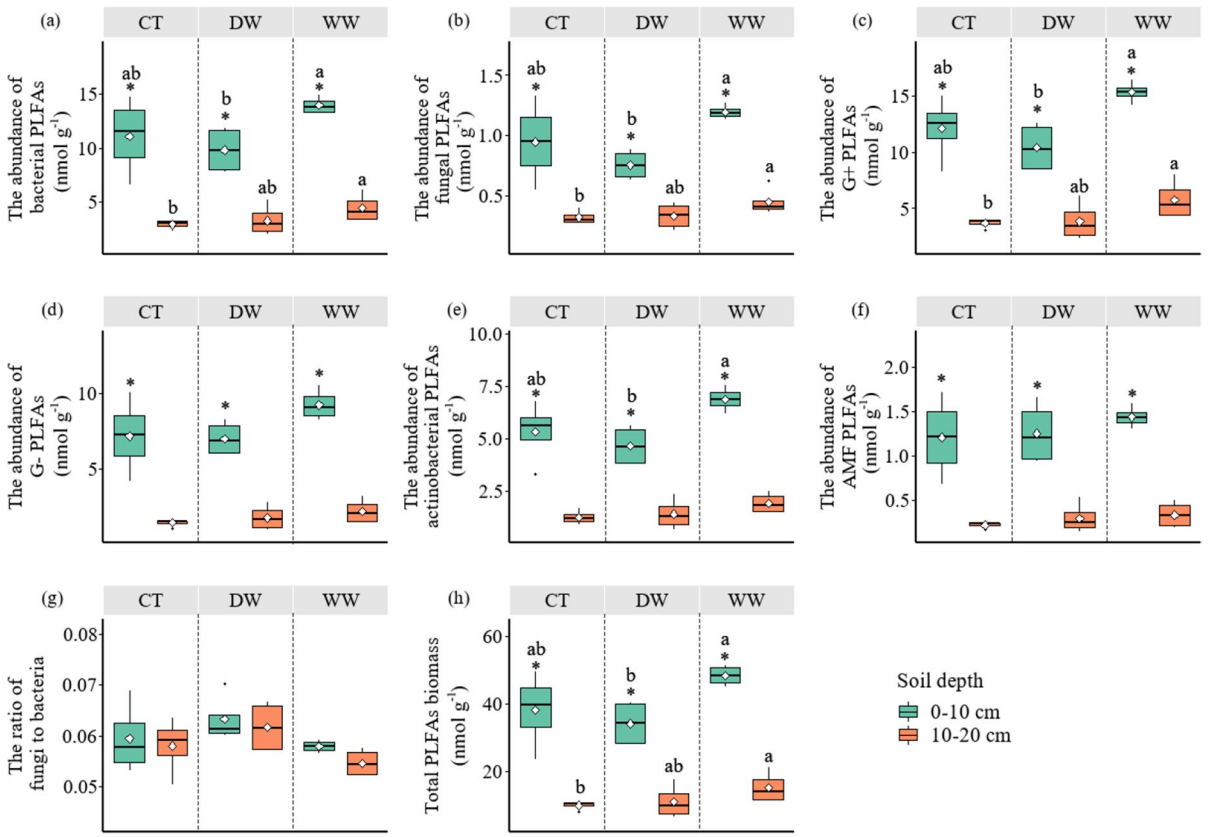

Fig. 3 Phospholipid fatty acid (PLFAs) biomarkers represented microbial community composition in soil, showing the abundances of (a) bacterial PLFAs, (b) fungal PLFAs, (c) Gram-positive (G+) bacterial PLFAs, (d) Gram-negative (G-) bacterial PLFAs, (e) actinomycete PLFAs, (f) arbuscular mycorrhizal fungal (AMF) PLFAs, (g) the ratio of fungi to bacteria (F/B ratio), and (h) total PLFAs biomass, where DW was delayed wet season treatment, WW was wetter wet season treatment, and CT was control. The asterisks indicated significant differences between soil depths and different lowercase letters indicated significant differences among precipitation conditions at $P < 0.05$ (after correction for multiple comparisons)

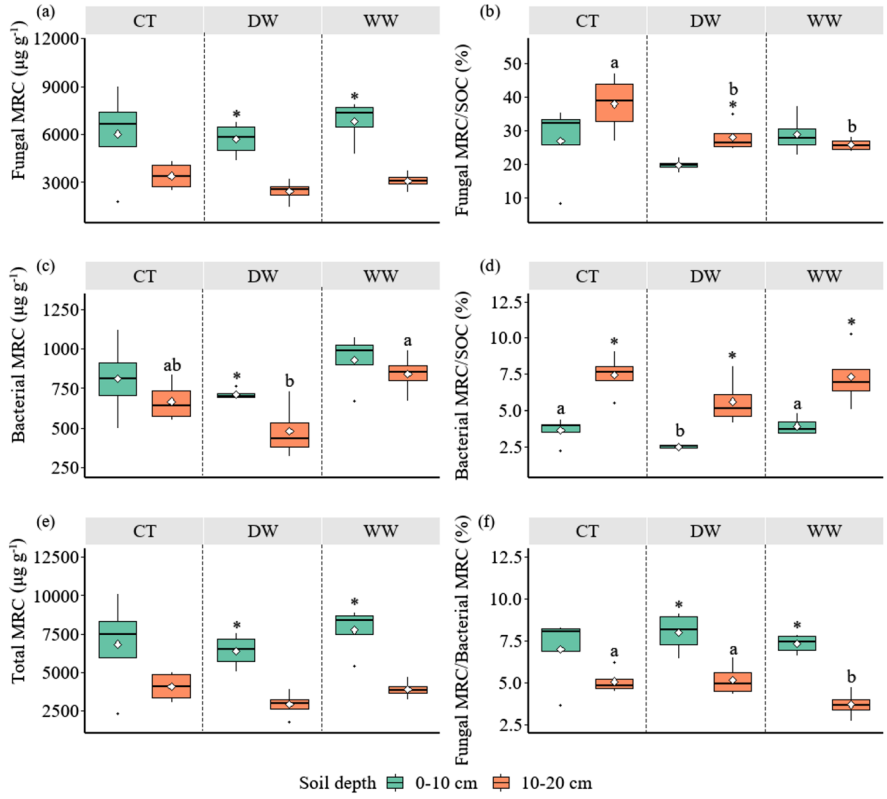

Fig. 4 Changes of precipitation on concentrations of microbial residual carbon (MRC: including fungal MRC, bacterial MRC, and total MRC), their contribution to soil organic carbon (SOC) accumulation, and the ratio of fungal MRC to bacterial MRC (fungal MRC/bacterial MRC), where DW was delayed wet season treatment, WW was wetter wet season treatment, and CT was control. The asterisks indicated significant differences between soil depths and different lowercase letters indicated significant differences among precipitation treatments (LSD test; $P < 0.05$)

$P<0.05$), manifesting the accumulation of bacterial MRC in the WW treatment, which also corresponded with the increase in SOC. However, WW treatment significantly decreased the contribution of fungal MRC to SOC (fungal MRC/SOC, by 32%) and the ratio of fungal MRC to bacterial MRC (fungal MRC/bacterial MRC, by 27%; Fig. 4b, f; $P<0.05$), indicating that fungal MRC contributed lower to SOC caused by intensified rainfall in the wet season.

PLS-PM and linear regression

PLS-PM was used to identify the pathways mediating the factors affecting SOC under changing precipitation patterns (Fig. 6). Soil properties altered SOC by changing the biomass and metabolism of microbial communities (GRSP: AMF-mediated C and MRC: microbial residual C), where there were strongly positive effects on all pathways that affected the SOC pool (The goodness of fit was 0.74). Thereby, the response of SOC to changes of the precipitation patterns were mainly mediated by the alteration of living microbial communities, and their metabolisms and residues.

From linear regression outcomes, all of BMRC, FMRC, TMRC, T-GRSP, and EE-GRSP showed a strongly positive relationship with SOC (Fig. 5a, b, c, d, e; $P<0.05$), indicating that both MRCs and GRSPs had profound effects on SOC accumulation. Simultaneously, the amount of GRSPs was relatively stable and the fungal MRC had a decreasing tendency in the WW treatment, thus the accumulation of SOC might be promoted by rising bacterial MRC.

Discussion

Soil microbial communities

Our results showed that at 10-20 cm soil depth, the WW treatment significantly increased microbial activity and biomass, while there were no remarkable differences between DW and CT. It was partly verified our hypothesis (a) that intensified precipitation in the wet season enhanced microbial biomass. Moreover, soil microbial biomass was strongly correlated with soil moisture (Fig. S1; $P<0.01$), indicating

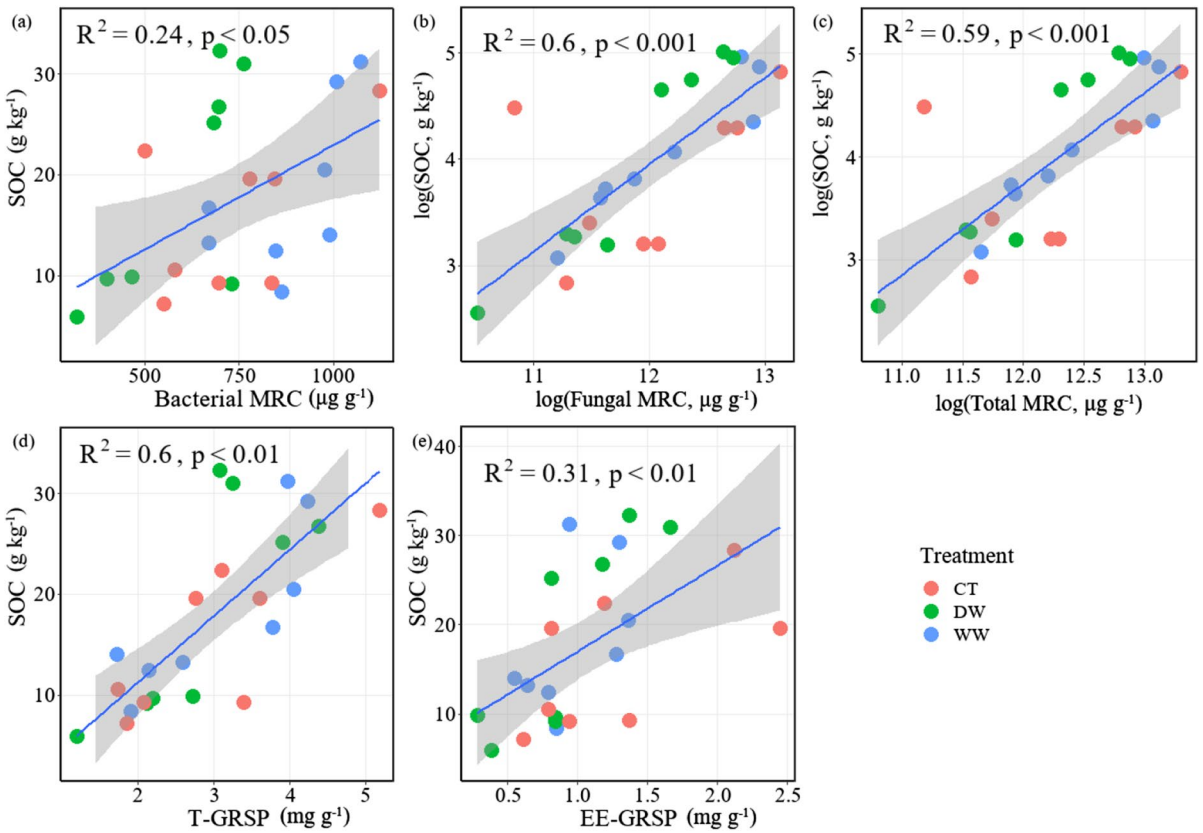

Fig. 5 Relationships of soil organic carbon (SOC) content with (a) bacterial microbial residual carbon (BMRC), (b) fungal microbial residual carbon (FMRC), (c) total microbial residual carbon (TMRC), (d) total glomalin-related soil protein (T-GRSP), (e) easily-extractable glomalin-related soil protein (EE-GRSP). When data were not normally distributed, they were logarithmically transformed. The determination coefficients (R^2) and *P*-values were generated from linear regression ($P < 0.05$). DW was delayed wet season treatment, WW was wetter wet season treatment, and CT was control

that the facilitation of microorganisms in the WW treatment at 10-20 cm soil depth was driven by soil moisture.

The variation of microbial communities in the DW treatment was inconsistent with our hypothesis, and also contrasted with a previous study conducted in the same plot three years ago (Yu 2019). Our early results showed that DW treatment significantly enhanced microbial activity and changed the microbial community structure owing to a prolonged life cycle of soil microorganisms, while WW treatment did not (Yu 2019). The DW treatment extended the wet season to autumn which alleviated the water stress in autumn and prolonged the life cycle of microorganisms; and microbial activities rapidly increased (Gong et al. 2021). However, microorganisms were adapted to environment with adequate moisture (Hartmann et al. 2017), so the promotion of water availability gradually decreased, and the microbial activities tended to decline over time. The WW treatment promoted microbes but not as strongly as DW, as there was no water stress in the wet season (Bossio et al. 2006; Tan et al. 2021). This might explain our results, where microorganisms were rapidly boosted in the short term by the DW treatment, but the facilitation gradually became steady in the long run, resulting in no changes. However, the WW treatment showed a slow long-term promotion of microbes which caused a significant increment in microorganisms after accumulating for several years. On longer time scales, the WW treatment might still have a stimulating effect on microbial communities which would further strengthen microbial activities, leading to a greater

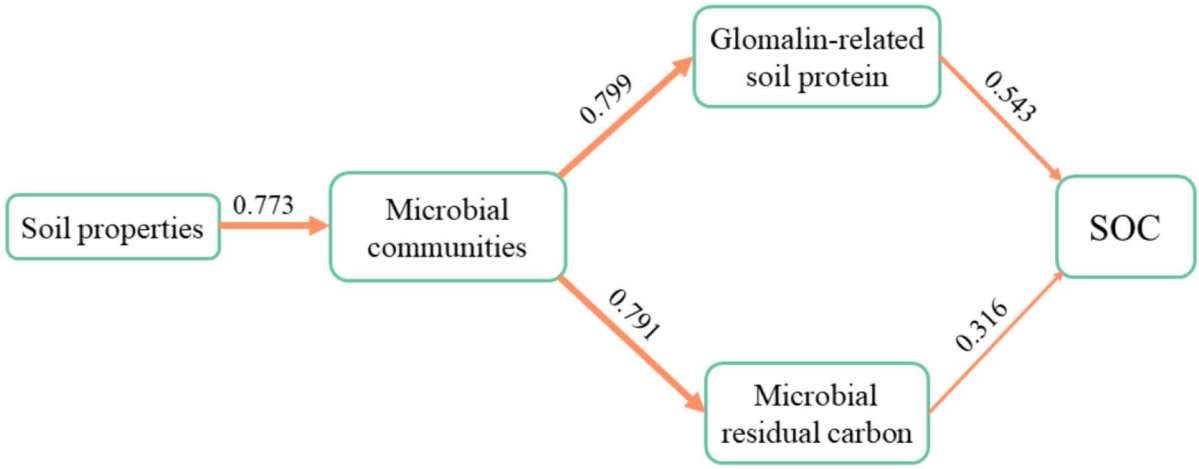

Fig. 6 Factors in manipulating soil organic carbon (SOC) under the background of changes in precipitation patterns (The goodness of fit of the model is 0.74). Five blocks of reflective indicators were indicated: "Soil properties" was considered as a combination of soil moisture, pH, ammonium-N, nitrate-N and Bray P; "Microbial communities" was indicated by latent variables of fungal PLFAs and bacterial PLFAs; "Glomalin-related soil protein" was the integration of easily-extracted glomalin-related soil protein (EE-GRSP) and difficultly extracted glomalin-related soil protein (DE-GRSP); "Microbial residual carbon" was indicated by the MRC of fungi and bacteria, respectively. Orange lines showed positive paths and the width of lines indicated the effect size

transformation of related biogeochemistry cycles in the future.

GRSP and MRC

The GRSP contents were unchanged under changes in precipitation patterns at both 0-10 cm and 10-20 cm soil depths, and the abundance of AMF community was also stable. The closely associated relationship between GRSP and AMF community was demonstrated by the outcome of linear regression that existed a strong positive correlation (Fig. S2; $P<0.001$). Generally, soil AMF community responded more strongly to changes in nutrient availability than in soil moisture (Sheldrake et al. 2018). Therefore, our finding that neither AMF community nor GRSP contents were altered in the DW or WW treatment further demonstrated that AMF community and related productive contents were less sensitive to changing precipitation patterns.

The accumulation of MRC depends on the balance between production and degradation of microbial products (Joergensen 2018; Six et al. 2006). When microbial biomass and activity increase, their reproduction and metabolism speed up, while the decomposition rates of SOC also accelerate (Griepentrog et al. 2014; Vitousek et al. 2010). When the rate of residual production exceeds the decomposition, MRC begins to accumulate (Wang et al. 2021). Unlike the soil surface where SOC mainly comes from inputs from plants, MRC is primarily a stable fraction of SOC at 10-20 cm soil depth; the change in MRC was less at 0-10 cm but SOC was more susceptible to MRC at 10-20 cm depth (Brockett et al. 2012; Coleman et al. 2018; Landesman and Dighton 2010). Therefore, there was no notable difference in MRC at 0-10 cm depth in our experiment.

The WW treatment significantly increased the amount of bacterial MRC at 10-20 cm soil depth compared with the DW treatment, while the fungal MRC had a downward trend. This may be because the bacterial community is less stable than the fungal community, the bacterial community being more sensitive to environmental factors such as soil moisture and nutrient availability (de Vries et al. 2018). The stronger promotion on the bacterial community by increased soil moisture, would enhance their metabolism and growth, leading to more living bacterial biomass and also more residual products (Bardgett and Caruso 2020; Koyama et al. 2018).

However, intensified rainfall in the wet season did not change the total MRC, which did not support

our hypothesis (b). This may be due to the fact that microbial necromass did not react to environmental changes as quickly as living microorganisms, because it requires a longer time accumulation of residual formation. The strong linear relationship between living microorganisms and dead residual carbon, as well as the asynchronous change between them, can partly explain the lag of MRC accumulation in time series (Fig. S3 & S4).

Dynamics of SOC

As the two main sources of steady SOC, both GRSP and MRC play crucial roles in SOC accumulation (Angst et al. 2021). The AMF-mediated C that is present in T-GRSP is considered highly recalcitrant, lasting for a minimum of 12–22 years, while EE-GRSP is considered the newly-produced or nearly-decomposed fraction that plays an active role in the development of soil structure (Rillig 2004; Wright and Upadhyaya 1996; Wu et al. 2014a). GRSP not only directly promotes SOC accumulation, because it is hard to degrade (Zhang et al. 2017), but also forms a recalcitrant structure of soil aggregates to conserve steady SOC (Dai et al. 2015; Wu et al. 2014b). In summary, GRSP is crucial to the accumulation and turnover of SOC in soils. In our study, the quantity of GRSPs (both T-GRSP and EE-GRSP) was relatively stable owing to the insensitivity of the AMF community which meant that the AMF community and AMF-mediated C did not alter the SOC pool under changing precipitation patterns.

MRC provides meaningful insights into the sequestration of SOC in microbial residues and shifts in soil organic matter (SOM) turnover (Amelung et al. 2008; Joergensen et al. 2010; Zhang and Amelung 1996). According to a global-scale meta-analysis, microbial necromass plays an essential role in SOC accumulation in major global ecosystems, comprising cropland, grassland, and forest ecosystems which further emphasizes the importance of MRC in SOC circulation (Wang et al. 2021). As some studies reported a dominance of bacterial instead of fungal necromass in steady SOC, these results indicate that the bacterial biomass near reactive mineral surfaces and the factors influencing microbial biomass might be important variables that determine the quantity of microbial residues stabilized in SOC (Gillespie et al. 2014; Zhang et al. 1999). In our study, we found that MRC, as the main source of SOC at 10-20 cm soil depth, showed different trends in the context of changing precipitation patterns; fungal MRC had a decreasing trend, while bacterial MRC showed an increasing trend. This partly confirmed our hypothesis. The increasing trend was significant between the DW and WW treatment, consistent with the alteration of SOC, revealing the critical contribution of bacterial MRC to the SOC pool.

Moreover, the upward trend of bacterial MRC and SOC and the downward trend of fungal MRC in this study further indicated that the WW treatment significantly decreased fungal MRC/SOC and fungal MRC/bacterial MRC. It was because the absolute values of these indicators were not significantly affected by the WW treatment, but their ratio showed a distinct difference, which confirmed that they changed in an opposite way. The alteration of bacterial MRC was synchronous with that of SOC, and there was a strong positive correlation between them, which suggested that the accumulation of SOC was primarily driven by bacterial MRC. Although the accumulation of SOC at 10-20 cm depth was not significant compared with the CT in our study, it might ultimately increase the accumulation of bacterial MRC under long-term promotion of microorganisms by more intensified wet season precipitation in the future, which would strengthen the C sequestration capacity of tropical forest soils. Therefore, it is a meaningful finding that more concentrated precipitation in the wet season has a positive effect on the accumulation of SOC through the increase of bacterial MRC, especially under more frequent extreme precipitation and drought events in the future.

Conclusion

In summary, the DW and WW treatment did not change the soil properties and microbial community at 0-10 cm soil depth. In contrast, at 10-20 cm soil depth, the soil microbial community and the contribution of residues to SOC were altered. We also found that the relative contribution of fungal MRC to SOC decreased, while the contribution of bacterial MRC to SOC increased, indicating that SOC was driven by bacterial MRC. Combined with previous research, we surmised that a delayed wet season promoted microorganisms significantly in the

short term and tended to stabilize over a long time, whereas a wetter wet season caused insignificant differences in microorganisms in the short term but the cumulative effect of long-term promotion eventually produced an increment prominently. Therefore, the findings that intensified precipitation in the wet season facilitates the growth of microbial biomass after a long-term promotion, and accelerates the accumulation of SOC arising from the elevation of bacterial MRC, may have a far-reaching impact on global climate change.

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Author contributions Faming Wang designed the experiment. Jinge Zhou, Jingfan Zhang, Yingwen Li, and Yongxing Li performed the experiments. Jinge Zhou analyzed the data. Jinge Zhou, Hans Lambers and Faming Wang wrote this manuscript. All co-authors revised the manuscript.

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Data Availability The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

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