Intensified Soil Moisture Extremes Decrease Soil Organic Carbon Decomposition: A Mechanistic Modeling Analysis

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Key Points:

- We conducted a mechanistic modeling analysis to study the response of SOC decomposition to intensified moisture extremes
- Active microbial biomass C and the corresponding turnover rates of SOC pools were more sensitive to extreme soil drying than soil wetting
- SOC decomposition decreased under intensified moisture extremes

Abstract

Earth system models have predicted that there will be more frequent and severe precipitation and drought events in terrestrial ecosystems. Microbially-mediated decomposition of soil organic carbon (SOC) tends to increase as soils wet and decrease as soils dry. However, the long-term SOC change under intensified moisture extremes remains poorly known as it depends on the frequency and intensity of soil drying and wetting. In this study, we explored long-term SOC dynamics under scenarios of alternating drying-wetting cycles using the Microbial-ENzyme Decomposition (MEND) model, a mechanistic microbial model. The model was parameterized with 11 years of observations from a temperate deciduous broadleaf forest site, showing satisfactory model performance in both model calibration ($R^2 = 0.67$) and validation ($R^2 = 0.69$) against heterotrophic respiration. We then used the model to simulate the long-term SOC dynamics under five scenarios of alternating drying-wetting cycles with different frequencies and severities over a period of 100 years. Results showed that the changes in active microbial biomass C and the corresponding turnover rates of SOC pools were more sensitive to soil drying than soil wetting. As a result, the cumulative soil C emission from microbial respiration decreased by 433.7 g C m^{-2} after the 100-year simulation in the highest frequency and intensity moisture scenario, but was not significantly affected by the lowest frequency and intensity scenario. This study emphasizes the nonlinear response of SOC decomposition to soil moisture changes, which causes decreased decomposition by microbes under drying that is not compensated by increased decomposition under wetting conditions.

Plain Language Summary

Soils store a large amount of carbon and thus play a critical role in regulating global carbon cycling and climate change. Soil organic carbon (SOC) decomposition is dependent upon microbes which are sensitive to moisture change. In this study, we explore microbially-mediated SOC decomposition in response to intensified dry and wet conditions using a mechanistic model. The model is calibrated at a temperate forest and used to predict future scenarios. Results suggest that SOC decomposition responds nonlinearly to moisture changes, showing a greater sensitivity to drying than wetting. The long-term CO_2 emissions from SOC decomposition decrease under scenarios with intensified moisture extremes.

1 Introduction

It is predicted that terrestrial ecosystems will experience intensified precipitation under global climate change (*IPCC*, 2013). Global climate models project more frequent extreme precipitation events and increased trends of dryness in many terrestrial ecosystems in the 21st century (*Field et al.*, 2012). Changes to soil moisture have the potential to significantly impact global carbon (C) cycling by altering the extent of soil organic C (SOC) decomposition during both extreme wet and extreme dry conditions (*Field et al.*, 2012).

The decomposition of SOC is dependent on microbial communities and their extracellular enzymes, both of which are sensitive to soil moisture changes. First, soil water availability directly impacts the activity and diffusion rate of extracellular enzymes, which in turn influences the accessibility of SOC substrates and the efficiency of decomposition (*Orchard and Cook*, 1983; *Criquet*, 2002; *Baldrian et al.*, 2010). Second, microorganisms may enter a state of relatively low metabolic activity or dormancy under unfavourable conditions, such as drought

(*Lennon and Jones*, 2011; *Stolpovsky et al.*, 2011). Microbial dormancy is usually reversible and dormant microbes may resuscitate to active states when environmental conditions improve (*Lennon and Jones*, 2011; *Stolpovsky et al.*, 2011; *Wang et al.*, 2015). Third, the lack of oxygen may limit aerobic decomposition of SOC during extremely wet conditions (*Linn and Doran*, 1984; *Franzluebbers*, 1999; *Sierra et al.*, 2017).

Generally, SOC decomposition peaks at an intermediate moisture level and decreases under both extremely dry or wet conditions (*Linn and Doran*, 1984; *Franzluebbers*, 1999; *Monard et al.*, 2012; *Sierra et al.*, 2017). As soil moisture is more often below the optimal levels, many studies have shown that the SOC decomposition rate is decreased under drought and increases with wetting (*Borken and Matzner*, 2009; *Shi et al.*, 2014; *German and Allison*, 2015; *Miao et al.*, 2017). However under intensified extreme moisture scenarios, soils may experience extremes in terms of both dryness and wetness. The long-term soil C emissions from SOC decomposition will be largely influenced by the relative impacts of soil drying versus wetting dynamics. Field manipulative experiments have shown inconsistent sensitivities of soil C fluxes to water reduction and water addition, depending on ecosystem types, treatment magnitudes, and experimental designs (*Harper et al.*, 2005; *Thomey et al.*, 2011; *Vargas et al.*, 2012; *Unger and Jongen*, 2015; *Zhou et al.*, 2016; *Luo et al.*, 2017; *Miao et al.*, 2017; *Zhang et al.*, 2019). These experiments usually do not mimic alternating drying and wetting cycles over time, or span only a few growing seasons. Thus, new studies are needed to understand how SOC decomposition and soil CO_2 emissions change under intensified soil moisture extremes.

As an alternative to field experiments, process-based modeling can be used to gain insights into SOC decomposition (*Jenkinson et al.*, 1987; *Parton et al.*, 1988; *Kätterer et al.*, 1998; *Rey and Jarvis*, 2006; *Liang et al.*, 2015; *Luo et al.*, 2016). Conventionally, SOC

decomposition is simulated in such models using first-order decay equations with empirical parameters that are adjusted by environmental modifiers. More recent studies suggested that such conventional models have difficulty representing nonlinear responses of SOC dynamics to environmental changes (*Allison et al.*, 2010; *Abramoff et al.*, 2018; *Liang et al.*, 2018a). To represent nonlinear SOC processes, different strategies have been reported, such as using flexible parameters (*Xu et al.*, 2006; *Luo et al.*, 2016; *Liang et al.*, 2018b), adding nonlinear processes based on the first-order decay model (*Guenet et al.*, 2016; *Liang et al.*, 2018a), and explicitly including microbial pools and processes (*Allison et al.*, 2010; *German et al.*, 2012; *Wang et al.*, 2013; *Wieder et al.*, 2013). Among those strategies, explicitly including microbial biomass C (MBC) and enzyme pools may more mechanistically simulate the role of microbial organisms and extracellular enzymes in SOC decomposition and have recently been applied to study SOC dynamics in response to climatic and environmental changes (*Li et al.*, 2014; *Hararuk et al.*, 2015; *Wang et al.*, 2015; *Wieder et al.*, 2015; *Georgiou et al.*, 2017; *Wang et al.*, 2019).

In this study we explored long-term SOC dynamics under intensified moisture extremes using a microbial-explicit (i.e., Microbial-ENzyme Decomposition, MEND) model that was parameterized with 11 years of measurements from a temperate deciduous forest. The model explicitly represents microbial dormancy, resuscitation, different types of SOC-degrading enzymes, and how they vary in response to soil moisture potential. A combination of two levels of frequency and severity of soil moisture, as well as a control with normal interannual variability, were used to simulate scenarios of alternating drying and wetting cycles over 100 years. The study was conducted to answer the following questions: (i) How do microbial processes respond to intensified moisture extremes with different frequency and severity? and (ii) How does long-term SOC decomposition change with intensified moisture extremes?

2 Materials and Methods

2.1 Data collection

Data used in this study were collected at the Missouri Ozark AmeriFlux (MOFLUX) forest site (latitude 38º44'39"N, longitude 92º12'W), which is located in the University of Missouri's Baskett Wildlife Research and Education (*Gu et al.*, 2016). It is a temperate, upland oak-hickory (*Quercus*-*Carya*) forest, with monthly mean temperature of −1.3 °C in January and 25.2 °C in July and mean annual precipitation of 1083 mm, ranging from 563 mm to 1351 mm. Dominant soils belong to soil orders Alfisols (Weller silt loam) and Mollisols (Clinkenbeard very flaggy clay loam) (*Young et al.*, 2001).

Soil respiration, along with soil temperature and soil moisture, have been measured *in situ* since 2005. Soil temperature was measured using a soil temperature profile sensor (model STP01, HukseefluxUSA, Inc., Center Moriches, NY) at five depths down to 0.5 m, and volumetric soil water content (SWC) was measured using water content reflectometers (model CS616, Campbell Scientific Inc., Logan UT). Measurements at 0.2 m were used for modeling analyses. The soil respiration measurements were conducted using a custom built automated eight-chamber system of the *Edwards and Riggs* (2003) design from 2005 to 2013 (*Gu et al.*, 2008). The system was replaced with an automated sixteen-chamber respiration system (LI-8100, Li-Cor Inc., Lincoln, Nebraska) in 2014. The two systems operated side-by-side for a period to ensure comparable responses before discontinuing measurements with the original system (Paul Hanson, Oak Ridge National Laboratory, personal communication). Respiration measurements from multiple chambers were aggregated to a single time series at hourly

149 resolution for the purposes of this research. Microbial respiration was calculated based on the
150 ratio of heterotrophic respiration to total soil respiration in the calibrated Energy Exascale Earth
151 System Model (E3SM) Land Model (ELM) at the same site which was validated by a trenching
152 experiment (*Liang et al.*, 2019). The ratio varies between 0.5 and 0.9, with lower ratio during the
153 growing season and higher ratio in the non-growing season.

154 Aboveground litter production was measured along five transects radiating from the base
155 of an eddy covariance tower adjacent to the soil respiration chambers. Each transect had five
156 plots except for one with four due to the presence of a pond at the terminus. In each plot, two
157 collectors (i.e., storage tubs, 68 L, 0.225 m^2 surface area) were deployed randomly. Litter was
158 collected weekly to bi-weekly during leaf-off, and at approximately monthly intervals during the
159 remaining seasons, oven-dried at 60 ºC until constant weight is achieved.

160 Soil water potential (Ψ_s), which was calculated from observed SWC and soil water
161 retention curves that were developed for the site, was used to determine the effect of water stress
162 on SOC decomposition. To derive the soil water retention curves, soil samples were collected
163 from the area of the flux tower base. Samples were evaluated periodically for soil water potential
164 using a dewpoint potentiometer (Decagon Devices, Model WP4C) and a pressure plate as they
165 dried over time. Then, the soil water retention curve was derived by fitting the van Genuchten
166 model (*van Genuchten*, 1980) which is shown in Fig. S1a.

167

168 **2.2 Model description and calibration**

169 The MEND model simulates hourly microbially-mediated SOC decomposition (*Wang et*
170 *al.*, 2015; *Wang et al.*, 2019). It is driven by C inputs from roots and aboveground litter, soil

171 temperature, moisture, and pH. It was assumed that the annual soil carbon input to the top layers
172 were similar from aboveground and belowground litter. Therefore, the measured aboveground
173 litter-C was doubled as the soil carbon input. The fractions of C input to POC1, POC2 and DOC
174 were 0.15, 0.53 and 0.32, respectively. The MEND model explicitly includes microbial and
175 enzymatic physiology to control SOC decomposition (Fig. S2) (*Wang et al.*, 2014; *Wang et al.*,
176 2015; *Wang et al.*, 2019), which has been proven effective to simulate microbially-mediated
177 SOC dynamics in various ecosystems (*Li et al.*, 2019; *Wang et al.*, 2019). It includes an active
178 and a dormant microbial pool to model microbial dormancy and resuscitation depending on the
179 abiotic environment. In MEND, the active and dormant microbial pools are dynamic depending
180 on the substrate availability, soil temperature and moisture, with the modifiers of microbial
181 dormancy (i.e., from active to dormant state, f_{A2D}) and resuscitation (i.e., from dormant to active
182 state, f_{D2A}) expressed as:

183 $$f_{A2D} = \left(1 - \frac{DOC}{K_D + DOC}\right) \times \exp\left(-\frac{E_a}{R}\left[\frac{1}{T} - \frac{1}{T_{ref}}\right]\right) \times \frac{(-\Psi_s)^{\omega}}{(-\Psi_s)^{\omega} + (-\Psi_{A2D})^{\omega}} \quad (1)$$

184 $$f_{D2A} = \frac{DOC}{K_D + DOC} \times \exp\left(-\frac{E_a}{R}\left[\frac{1}{T} - \frac{1}{T_{ref}}\right]\right) \times \frac{(-\Psi_{D2A})^{\omega}}{(-\Psi_s)^{\omega} + (-\Psi_{D2A})^{\omega}} \quad (2)$$

185 where DOC is the pool size of dissolved organic C, K_D is the half-saturation constant for
186 microbial uptake of DOC, E_a is the energy of activation (kJ mol^{-1}), R is the gas constant (8.314 J
187 mol^{-1} K^{-1}), T (K) is the soil temperature, T_{ref} (K) is the reference soil temperature, Ψ_s is soil
188 water potential (MPa), Ψ_{A2D} and Ψ_{D2A} are soil water potential thresholds for microbial
189 dormancy and resuscitation, and ω is to determine the steepness of the curve (*Manzoni et al.*,
190 2014; *Wang et al.*, 2020). Figure S3 showes the rates of microbial dormancy and resuscitation
191 changing with soil moisture.

192 The active microbial pool produces different functional enzymes to target corresponding
193 substrates, including two particulate organic C (POC) pools and one mineral-associated organic
194 C (MOC) pool. Enzyme-decomposed POCs enter the MOC and the dissolved organic C (DOC)
195 pools. Decomposed MOC also become DOC, which is then available to be taken up by the active
196 microbes. The decomposition fluxes (F_x) of POCs and MOC were calculated using the
197 Michaelis-Menten equation,

198 $$F_x = \frac{[V_x \times f(T) \times f(\Psi_s)] \times E_x \times P_x}{K_x \times f(T) + P_x} \qquad (3)$$

199 where *x* denotes POC1, POC2 or MOC, V_x and K_x are the maximum specific decay rate and half-
200 saturation constant for the targeting pool (P_x), and E_x is the corresponding enzyme concentration,
201 $f(T)$ and $f(\Psi_s)$ are temperature and soil water potential modifiers, respectively. The $f(T)$
202 relationship is represented by the Arrhenius equation

203 $$f(T) = \exp\left(-\frac{E_a}{R}\left[\frac{1}{T} - \frac{1}{T_{ref}}\right]\right) \qquad (4)$$

204 where E_a is the energy of activation (kJ mol^{-1}), R is the gas constant (8.314 J mol^{-1} K^{-1}), T (K) is
205 the soil temperature and T_{ref} (K) is the reference soil temperature.

206 Different moisture functions were used to modify the decomposition according to
207 oxidative versus hydrolytic enzymes (Fig. S3b). The oxidative enzyme modifier, $f_o(\Psi_s)$ has an
208 optimal moisture range (*Wang et al.*, 2020) and was expressed as:

209 $$f_o(\Psi_s) = \begin{cases} 0.0 & , \quad \Psi_s \leq -10^{2.5} \\ 0.625 - 0.25 \times log_{10}(-\Psi_s) & , \quad -10^{2.5} < \Psi_s \leq -10^{-1.5} \\ 1.0 & , \quad 10^{-1.5} < \Psi_s \leq -10^{-2.5} \\ \dfrac{(2.5 + 0.4 \times log_{10}(-\Psi_s))}{1.5} & , \quad -10^{-2.5} < \Psi_s \leq -10^{-4.0} \\ 0.6 & , \quad \Psi_s > -10^{-4.0} \end{cases} \qquad (5)$$

The hydrolytic enzyme modifier $f_h(\Psi_s)$, was expressed following (*Manzoni et al.*, 2012),

$$f_h(\Psi_s) = \begin{cases} 0.0 & , \quad \Psi_s \le \Psi_{min} \\ 1.0 - \left(\dfrac{ln(\Psi_s/\Psi_{FC})}{ln(\Psi_{min}/\Psi_{FC})} \right)^b & , \Psi_{min} < \Psi_s \le \Psi_{FC} \\ 1.0 & , \quad \Psi_s > \Psi_{FC} \end{cases} \qquad (6)$$

where Ψ_{FC} $(= -0.033\ MPa)$ is the soil water potential at field capacity, Ψ_{min} is the microbial stress soil water potential threshold, and *b* determines the curve shape (*Manzoni et al.*, 2012). Further details of the MEND model can be found in *Wang et al.* (2015).

The model was calibrated with data from 2005 through 2012 and validated with data from 2013 through 2015. Selected parameters based on their sensitivities were estimated by applying the Shuffled Complex Evolution algorithm, a stochastic optimization method that is capable of obtaining global optimal model parameters (*Duan et al.*, 1992; *Wang et al.*, 2015). During the calibration, the objective function is calculated as $(1 - R^2)$, where R^2 is the coefficient of determination between the simulated and calculated heterotrophic respiration fluxes. As the calibration algorithm runs, the objective function is minimized to optimize the model performance. The remaining parameters were adjusted based on values from previous modeling and synthesis studies (*Manzoni et al.*, 2012; *Wang et al.*, 2013; *Wang et al.*, 2015).

2.3 Scenario analyses

The mean annual precipitation ranges from 563 mm to 1351 mm, indicating significant inter-annual variation in soil moisture. In this study we focus on inter-annual moisture extremes. We developed five scenarios extending over a simulation period of 100 years (Fig. 1). Within each of the scenarios, the frequency of extreme drought and wetting, as well as the magnitude

(i.e., severity) of moisture increase in wet years and decrease in dry years were set to keep the long-term mean soil moisture content over the 100 years unchanged. The five scenarios were:

1. Control: hourly abiotic environment and C input with seasonal and interannual variations in 2005-2015 were repeated until the end of simulation (100 years) (Fig. 1a);
2. Low frequency and low severity (LF+LS): based on Scenario (1), SWC reduced by 5% (v/v) in 10 random years and increased by 5% (v/v) in 10 random years (Fig. 1b);
3. Low frequency and high severity (LF+HS): based on Scenario (1), SWC reduced by 10% (v/v) in 10 random years and increased by 10% (v/v) in 10 random years (Fig. 1c);
4. High frequency and low severity (HF+LS): based on Scenario (1), SWC reduced by 5% (v/v) in 20 random years and increased by 5% (v/v) in 20 random years (Fig. 1d);
5. High frequency and high severity (HF+HS): based on Scenario (1), SWC reduced by 10% (v/v) in 20 random years and increased by 10% (v/v) in 20 random years (Fig. 1e).

In the last four scenarios, extreme events were randomly distributed within 25-year time periods, with 10% of total extreme events allocated to years 1-25, 20% to years 26-50, 30% to years 51-75, and 40% to years 76-100 (Fig. 1). In this study, two terms, “control” and “normal”, were used. To clarify, the term “control” was used to represent Scenario 1. The term “normal” was used to represent simulation years from any of the scenarios that lacked moisture increases or decreases. The maximum volumetric SWC was always less than 70%, so the prescribed moisture treatments never fully saturated the soils.

252 With the changed SWC, soil water potential at each simulating time step was calculated
253 based on the calibrated van Genuchten model (Fig. S1a). The magnitude of soil water potential
254 change resulting from the prescribed SWC changes was dependent on the baseline SWC and the
255 moisture change at each time step. The magnitude of soil water potential change decreased with
256 the increase in baseline SWC. With the same baseline SWC, reduced SWC generally resulted in
257 greater soil water potential change than increased SWC. For example, soil water potential at 20%
258 of SWC was -0.96 MPa, which changed to -4.99 MPa when SWC reduced to 15% and changed
259 to -0.33 MPa when SWC increased to 25%. Soil water potential at 40% of SWC was -0.04 MPa,
260 which changed to -0.08 MPa when SWC reduced to 35% and changed to -0.02 MPa when SWC
261 increased to 45%. Annual values of soil water potential over the 100-year simulation in all the
262 five scenarios were shown in Fig. S1b.

263 Soil C processes in the latter four moisture simulation scenarios were compared with that
264 in the control, i.e., x = (treatment – control)/control×100%. Within each scenario, results were
265 summarized in three groups depending on soil moisture change (i.e., normal, increased moisture,
266 and decreased moisture) to derive the overall microbial responses to moisture changes. The
267 change in each group was tested using the *t*-test with the null hypothesis that the change
268 comparing with the control was not significantly different from zero. The magnitude of change
269 ($|x|$) between the years of reduced and increased soil moisture was tested using the *t*-test with the
270 null hypothesis of insignificant difference. The statistical analyses were conducted at $P < 0.05$
271 for significance and at $P < 0.1$ for marginal significance.

272

3 Results

3.1 Model calibration and validation

The MEND model parameters were either predetermined based on previous studies (*Manzoni et al.*, 2012; *Wang et al.*, 2013; *Wang et al.*, 2015) or calibrated against observations (Table 1). Values of the calibrated parameters were determined using calculated heterotrophic respiration data from 2005 to 2012, showing a R^2 value of 0.67 (Fig. 2). The calibrated MEND model was then validated using data from 2013 to 2015. Once calibrated, the model adequately simulated both seasonal and inter-annual variability of SOC decomposition during the validation period, with $R^2 = 0.69$ (Fig. 2). The simulated SOC under the control scenario was at equilibrium with seasonal and inter-annual variations (Fig. S4).

3.2 Responses of SOC decomposition to intensified moisture extremes

Figure 3 shows the percent change in active microbial biomass C (MBA) as a result of changes in frequency and severity of soil moisture with respect to the control scenario (Fig. 1). With the intensified soil moisture extremes, MBA was reduced during drier periods (for LF+HS, HF+LS and HF+HS, $P < 0.05$; and for LF+LS, $P < 0.1$) (Fig. 3). During wetter periods, MBA increased (for LF+LS, $P < 0.05$; and for LF+HS, $P < 0.1$), but did not change for the more frequent extreme event (i.e., HF+LS and HF+HS) scenarios (Fig. 3). The magnitude of MBA change was significantly higher during dry periods than wet periods in all scenarios except LF+LS (Table 2, Fig. 3). The response of total enzyme concentrations to soil moisture extremes was similar to that of MBA (Table 2, Fig. S5).

294 Generally, DOC appeared to be reduced in dry periods and increased in wet periods, but
295 the differences were insignificant across the pairs of drying and wetting in LF+LS, LF+HS and
296 HF+LS (Table 2, Fig. 4). Only in the HF+HS scenario, the magnitude of change during the dry
297 periods was significantly smaller than that of the wet periods ($P < 0.01$; Table 2, Fig. 4d).

298 Turnover rates of C pools, which were computed from the Michaelis-Menten kinetics,
299 were equivalent to the first-order decomposition rate. The turnover rate of DOC did not change
300 during wet periods, whereas that of POCs and MOC increased except POC1 (POC degraded by
301 oxidative enzymes) in the HF+HS scenario (Fig. 5). The turnover rates of DOC, POCs and MOC
302 were significantly decreased during dry periods in all four scenarios. In low-frequency scenarios
303 (i.e., LF+LS and LF+HS), the magnitude of moisture-induced turnover changes between dry and
304 wet periods was similar for all the four C pools except POC1 in LF+HS, which was marginally
305 higher in drying than wetting periods (Table 2, Fig. 5a, b). However, the directions were
306 different; i.e., turnover rates increased under wet conditions and decreased under dry conditions.
307 In high-frequency scenarios (i.e., HF+LS and HF+HS), the magnitude of moisture-induced
308 turnover changes was generally higher in dry compared to wet periods (Table 2, Fig. 5c, d).

309 The responses of microbial C processes to intensified moisture extremes resulted in
310 changes in CO_2 emissions that depended on event frequency and severity (Fig. 6). In the LF+LS
311 scenario, the cumulative CO_2 emission was barely changed, showing a slight increase of 9.9 g C
312 m^{-2} in comparison to the control after the 100-year simulation. However, the cumulative CO_2
313 emission decreased by 54.7 g C m^{-2}, 101.4 g C m^{-2}, and 433.7 g C m^{-2} in the LF+HS, HF+LS,
314 and HF+HS scenarios, respectively.

315

4 Discussion

The influence of soil water change on heterotrophic respiration is dependent on different mechanisms, such as substrate accessibility, oxygen diffusion and microbial stress (*Yan et al.*, 2018; *Ghezzehei et al.*, 2019). These factors collectively shape the response of microbial respiration to soil water changes. In the MEND model, the microbial stress was mainly simulated by the microbial dormancy and resuscitation, which were modified by environmental factors including substrate availability, soil temperature and moisture. The substrate availability is controlled by enzyme-catalyzed decomposition influenced by soil pH, temperature and moisture. Under saturated conditions, the oxygen limitation to microbial respiration is represented by the declined oxidative decomposition (Fig. S3b).

After calibration, the MEND model was validated with multi-year measurements, showing similar R^2 values (Fig. 2). The MEND model also simulated the inter-annual variability, including an extremely dry year (2012). Synthetic analyses show that drought generally reduces SOC decomposition rates, but its effect on MBC varies from negative to neutral and to positive (*Zhou et al.*, 2016; *Homyak et al.*, 2017). One vital reason for the inconsistent responses of SOC decomposition rate and MBC is that total MBC consists of both active microbial biomass C (i.e., MBA) and dormant MBC (MBD). Dormant microbes utilize limited substrates to maintain basic functions and the decomposition of SOC is determined by the pool size of MBA and related enzyme production (*Lennon and Jones*, 2011; *Stolpovsky et al.*, 2011; *Wang et al.*, 2015). In this study, total MBC was not changed by drought under the LF+LS, LF+HS and HF+LS scenarios, and was increased by the HF+HS drought (Fig. S6), indicating that microbial dormancy could maintain the total biomass. Our results are within the observed range by synthetic analyses, which show that the effect of drought on total microbial biomass could vary from negative to

neutral and to positive (*Zhou et al.*, 2016; *Homyak et al.*, 2017). Meanwhile, the ratio of active to total microbial biomass carbon (MBA/MBC ratio) was reduced by drought (Fig. S7). Therefore, the depressed CO_2 emission was primarily because of the change in active, instead of total, microbial biomass. The incorporation of microbial dormancy and resuscitation make the model more precisely responsive to changes in soil moisture (Wang *et al*., 2019), as found in this study.

The relative magnitude of microbial and enzymatic responses to extreme wet and dry conditions influenced the overall C budget. In this study, MBA decreased in drying periods in all the scenarios (Fig. 3). In contrast, MBA increased during the wetting periods in the low-frequency scenarios but did not change in the high-frequency scenarios (Fig. 3). The magnitude of the change in MBA induced by the extreme drought was higher than that imposed by extreme wetting. This is likely because the soil water potential does not change symmetrically with changes in SWC, i.e., the decrease in soil water potential during dry conditions is steeper than the increase during wet conditions (*van Genuchten*, 1980; *Tuller and Or*, 2004; *Seki*, 2007) (Fig. S1). Thus, the water limitation is more severe under extreme drying conditions, whereas the alleviation of water limitation under wetting conditions is relatively mild. In addition, extreme wet conditions can restrain oxidative microbial activity, instead of stimulating it, prohibiting the microbial water use efficiency (*Linn and Doran*, 1984; *Franzluebbers*, 1999; *Sierra et al.*, 2017).

Additionally, extracellular enzymatic processes represent critical microbial feedbacks to SOC decomposition, directly regulating the turnover of SOC pools through the activities of oxidative and hydrolytic enzymes. Low soil water potential can affect the activity of both oxidative and hydrolytic enzymes by limiting substrate accessibility and physiology (*Orchard and Cook*, 1983; *Criquet*, 2002; *Baldrian et al.*, 2010). Consequently, under dry conditions, enzymatic decomposition will become limiting, which more strongly affects hydrolytic versus

oxidative enzyme activity (Fig. S3b). These constraints are reflected by stronger decreases in enzyme concentrations under dry conditions (Fig. S5). In addition, POC1/POC2 ratio was generally decreased under drought and increased under wetter conditions (Fig. S8). This was because hydrolytic decomposition (the decomposition of POC2) was more sensitive to moisture change than oxidative decomposition (the decomposition of POC1), which was represented by a steeper soil water function for the POC2 decomposition below the optimal point (Fig. S3b). Thus, the magnitude of decrease in POC2 decomposition tended to be larger than that in POC1 decomposition, leading to a greater proportion of undecomposed POC2 remaining in the soil. As a result, the POC1/POC2 ratio was reduced under drought, and increased under wetter conditions. Oxygen limitation under extreme wet conditions also restrains the activity of oxidative enzymes (*Linn and Doran*, 1984; *Franzluebbers*, 1999; *Sierra et al.*, 2017) (Fig. S3b). The hydrolytic enzymes regulating decomposition, in contrast, are not limited by oxygen availability, meaning that enzyme activity stays at a relatively high level under wet conditions (*Manzoni et al.*, 2012; *Wang et al.*, 2015; Fig. S2). This explains the decreasing enzyme concentrations with increased moisture in the HF + HS scenarios, although the differences compared to normal conditions were not significant (Fig. S5). Additional feedbacks may occur because enzyme production is related to MBA. Under dry conditions, lower MBA produces fewer enzymes. As a result of these combined effects, the decrease in SOC turnover rates under drying periods was more evident than the increase under wetting periods (Fig. 5), leading to decreased long-term CO_2 emissions when soil experiences both extremely dry and wet conditions, particularly under high frequency (Fig. 6). The asymmetric response of soil microbial activity has a similar pattern with plants in response to extreme moisture conditions. For example, long-term observational and modeling studies show strong decreases in plant growth

with extreme dryness, which cannot be offset by growth increases during wet periods, resulting in long-term declines of plant growth, C assimilation, and net biome productivity (*Dannenberg et al.*, 2019; *Green et al.*, 2019; *Xu et al.*, 2019). These results, along with our findings in this study, imply that both plants and microbes respond to moisture extremes asymmetrically due to strong moisture stress induced by dry extremes, but relatively moderate relief of water stress during wet periods (*van Genuchten*, 1980; *Tuller and Or*, 2004; *Seki*, 2007).

Soil water potential controls the aqueous movement as well as enzymatic production and activity (*Moyano et al.*, 2012; *Ghezzehei et al.*, 2019). However, it is relatively difficult to directly measure soil water potential *in situ*. The calculation of soil water potential largely relies on the soil water retention curve which describes the relationship between soil water contents and potentials (*van Genuchten*, 1980; *Tuller and Or*, 2004; *Seki*, 2007). Therefore, an appropriate soil water retention curve is critical to simulate the moisture effects on microbial respiration. Under dry conditions, e.g., the permanent wilting point with a soil metric water potential of -1.5 MPa, soil water is not available to many plants (*Briggs and Shantz*, 1912). The soil water potential of -1.5 MPa is usually the low limit of a typical soil water retention curve. However, the water stress threshold for soil microbial organisms could be as low as -14 MPa (*Manzoni et al.*, 2012). Therefore, a typical soil water retention curve may not be adequate for microbial respiration. In this study, we merged measurements from the WP4C and pressure plate methods in order to derive a more appropriate soil water retention curve, though the relatively large variance of our measurements from the WP4C may bring uncertainties to our analyses. Therefore, precise measurements and estimates of soil water retention curve, with a wide soil water potential range (e.g., below -1.5 MPa), may improve the simulations of microbial activity and SOC decomposition in response to soil water content changes.

5 Conclusions

In this study, we explored the impact of intensified soil moisture extremes on microbial processing of soil C and the consequent long-term CO_2 emissions. The sensitivities of MBA, extracellular enzyme activities, and corresponding turnover rates of SOC pools to soil drying and wetting were different, showing a greater magnitude of decrease by soil drying than increase by wetting. Thus, the intensified soil moisture extremes decreased long-term microbial CO_2 emission after the 100-year simulation. Our study suggests that intensified soil drying and wetting, even without changes in average soil moisture content, may still alter SOC dynamics and long-term CO_2 emissions from soil.

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626 **Table 1** Parameter values of the MEND model to represent soil organic carbon (SOC) dynamics at the MOFLUX site.

Parameter name	Description	Predetermined value	Priori range	Calibrated value	Unit
LF_0	Initial fraction of POC_1 in POC	-	(0.1, 1.0)	0.8	-
r_0	Initial active fraction of microbes	-	(0.01, 1.0)	0.7	-
V_{P1}	Max specific decay rate for POC_1	2.0	-	-	h^{-1}
V_{P2}	Max specific decay rate for POC_2	2.0	-	-	h^{-1}
V_M	Max specific decay rate for MOC	2.0	-	-	h^{-1}
K_{P1}	Half-saturation constant for POC_1	18.0	-	-	mg C cm^{-3} soil
K_{P2}	Half-saturation constant for POC_2	6.0	-	-	mg C cm^{-3} soil
K_M	Half-saturation constant for MOC	650.0	-	-	mg C cm^{-3} soil
Q_{max}	Max sorption capacity	3.6	-	-	mg C cm^{-3} soil
K_{ba}	Binding affinity	9.1	-	-	(mg C cm^{-3} soil)$^{-1}$
K_{des}	Desorption rate	4.0×10^{-3}	-	-	mg C cm^{-3} soil h^{-1}
r_E	Turnover rate of enzymes	-	(0.0001, 0.01)	3.1×10^{-3}	h^{-1}
p_{EP}	Enzyme production constant for POCs	-	(0.0001, 0.05)	3.5×10^{-2}	-
fp_{EM}	Ratio of enzyme production constant for MOC to p_{EM}	-	(0.5, 5.0)	3.50	-
f_D	Fraction of decomposed POC allocated to DOC	-	(0.05, 1.0)	1.9×10^{-1}	-
g_D	Fraction of dead microbes allocated to DOC	-	(0.01, 1.0)	0.1	-
V_g	Max specific growth rate	-	(0.001, 0.1)	9.6×10^{-3}	h^{-1}
α	Ratio of max specific maintenance rate (V_m) to ($V_m + V_g$)	-	(0.01, 0.5)	4.9×10^{-2}	-
K_D	Half-saturation constant for microbial uptake of DOC	-	(0.01, 0.5)	1.0×10^{-2}	mg C cm^{-3} soil
Y_g	True growth yield at reference temperature	-	(0.2, 0.6)	0.2	-
Y_{g_sl}	Temperature slope for Y_g	-	(0.001, 0.03)	2.5×10^{-2}	1/°C
γ	Constant of max microbial mortality	-	(0.1, 20)	0.1	-
β	Ratio of dormant maintenance rate to V_m	-	(0.0005, 0.05)	5.0×10^{-2}	-
WP_{A2D}	Ψ_s threshold for microbial dormancy	-	(0.2, 6)	4.4	-MPa
τ	Constant to calculate Ψ_s threshold for resuscitation	-	(0.1, 0.95)	0.4	-
w	Exponential in Ψ_s function for dormancy	4.0	(1, 6)	-	-

627 *MOC: mineral-associated organic C; POC_1: particulate organic C decomposed by oxidative enzymes (EP_1); POC_2: particulate*
628 *organic C decomposed by hydrolytic enzymes (EP_2); DOC: dissolved organic C; QOC: absorbed DOC by minerals; Ψ_s: soil water*
629 *potential.*
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633 **Table 2** *P* values of the *t*-test between the magnitude of change (i.e., |change|) by drying and
634 wetting in intensified moisture scenarios compared with the control scenario.

Scenario	MBA	EP	DOC	Turnover rates			
				DOC	POC_1	POC_2	MOC
LF+LS	0.942	0.823	0.247	0.626	0.709	0.918	0.834
LF+HS	0.048	0.051	0.222	0.101	0.083	0.272	0.405
HF+LS	0.072	0.055	0.670	0.024	0.009	0.025	0.070
HF+HS	< 0.001	< 0.001	0.001	< 0.001	< 0.001	< 0.001	< 0.001

635 *MBA: active microbial biomass C; DOC: dissolved organic C; EP: total enzyme concentration;*
636 *POC_1: particulate organic C decomposed by oxidative enzymes (EP_1); POC_2: particulate*
637 *organic C decomposed by hydrolytic enzymes (EP_2); MOC: mineral-associated organic C.*
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Figure legends

Figure 1. Scenarios of alternating drying and wetting cycles for the 100-year simulation used in this study. The number in each box is the year of simulation. Blue boxes represent normal levels of soil moisture, pink boxes represent -5% moisture, red boxes represent -10% moisture, light green boxes represent +5% moisture, green boxes represent +10% moisture. The five different simulations are: Control; LF+LS: low frequency (10 random years) and low severity (±5%); LF+HS: low frequency (10 random years) and high severity (±10%); HF+LS: high frequency (20 random years) and low severity (±5%); HF+LS: high frequency (20 random years) and high severity (±10%).

Figure 2. Observed (dots) and modeled (line) microbial respiration (R) at the MOFLUX site. Data from 2005 to 2012 (purple dots) and from 2013 to 2015 (red dots) were used to calibrate (black line) and validate (blue line) the model, respectively. The goodness of fit is shown as the coefficient of determination (R^2) in corresponding line colors.

Figure 3. Effect of intensified moisture extremes on active microbial biomass C (MBA) (Mean ± SE). LF+LS: low frequency (10 random years) and low severity (±5%); LF+HS: low frequency (10 random years) and high severity (±10%); HF+LS: high frequency (20 random years) and low severity (±5%); HF+LS: high frequency (20 random years) and high severity (±10%). In **a** and **b**, the number of replicates is 10, 10, and 80 for reduced, increased, and normal soil moisture, respectively. In **c** and **d**, the number of replicates is 20, 20, and 60 for reduced, increased, and normal soil moisture, respectively. Symbols above the error bars show the statistical difference of the bars from 0. #- $P < 0.10$; *- $P < 0.05$; **- $P < 0.01$; ***- $P < 0.001$.

663

664 **Figure 4. Effect of intensified moisture extremes on dissolved organic C (DOC)**
665 **concentration (Mean ± SE).** LF+LS: low frequency (10 random years) and low severity (±5%);
666 LF+HS: low frequency (10 random years) and high severity (±10%); HF+LS: high frequency (20
667 random years) and low severity (±5%); HF+LS: high frequency (20 random years) and high
668 severity (±10%). In **a** and **b**, the number of replicates is 10, 10 and 80 for reduced, increased and
669 normal soil moisture, respectively. In **c** and **d**, the number of replicates is 20, 20 and 60 for
670 reduced, increased and normal soil moisture, respectively. Symbols near the error bars show the
671 statistical difference of the bars from 0. #- $P < 0.10$; *- $P < 0.05$; **- $P < 0.01$; ***- $P < 0.001$.

672

673 **Figure 5. Effect of intensified moisture extremes on the turnover rates of soil C pools**
674 **(Mean ± SE).** LF+LS: low frequency (10 random years) and low severity (±5%); LF+HS: low
675 frequency (10 random years) and high severity (±10%); HF+LS: high frequency (20 random
676 years) and low severity (±5%); HF+LS: high frequency (20 random years) and high severity
677 (±10%). In **a** and **b**, the number of replicates is 10, 10 and 80 for reduced, increased and normal
678 soil moisture, respectively. In **c** and **d**, the number of replicates is 20, 20 and 60 for reduced,
679 increased and normal soil moisture, respectively. Symbols near the error bars show the statistical
680 difference of the bars from 0. #- $P < 0.10$; *- $P < 0.05$; **- $P < 0.01$; ***- $P < 0.001$.

681

682 **Figure 6. Ten-year running average of cumulative CO_2 emission in scenarios of alternating**
683 **drying and wetting cycles, normalized to the control scenario.**

684