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Drought-Induced Soil Carbon Dynamics in Subtropical Forests: Emergent Divergence from Model Structures

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ABSTRACT

Accurately quantifying drought impacts on terrestrial carbon cycling is essential for advancing predictions of climate-carbon feedbacks. However, current biogeochemical models exhibit limited capability in simulating drought-induced transformations of soil organic carbon (SOC), particularly regarding microbial processes. Here, we conducted a systematic comparative evaluation of three prevailing SOC modeling structures, including conventional three-pool partitioning scheme (SM1), mineral and particulate-associated carbon partitioning scheme (SM2) and Michaelis-Menten regulated carbon-stabilization scheme (SM3), to elucidate their capacity in simulating soil carbon dynamics under decadal drought scenarios in a subtropical forest. We found divergent effects of drought in soil C input (SM1, 66%; SM2, 10%; SM3, -4%) and mean residence time (MRT; SM1, -31%; SM2, -14%; SM3, 65%), which lead to the predicted SOC substantial accumulation for both SM1 and SM3 (+39.5% and +56.9%, respectively) and moderate depletion (-6.1%) for SM2. The different C input directly affect the passive SOC (SM1) and mineral-associated organic carbon (SM2 and SM3). In comparison, the drought effects on passive SOC (SM1), microbe biomass (SM2) and MAOC (SM2 and SM3), lead to notable spread in MRT. These findings highlight critical model structural dependencies in simulating drought-affected soil carbon dynamics and emphasize the necessity for models to integrate microbial-physicochemical interactions for improved climate-carbon coupling projections.

Keywords: soil carbon stock, extreme drought, microbial enzyme activity, model comparison, data assimilation, traceability analysis.

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1 Introduction

Terrestrial ecosystems are facing increasing frequent stress from extreme drought which fundamentally alters plant-microbe-mineral interactions, serving as a key driver of carbon sequestration patterns (IPCC, 2013; Han et al., 2022; Choat et al., 2018; Hao et al., 2015). Initial drought exposure typically enhances soil organic carbon (SOC) stability via physicochemical protection mechanisms, such as reduced microbial decomposition from moisture limitation (Schimel, 2018), increased organo-mineral association due to soil contraction (Blankinship et al., 2016), and disrupted enzyme diffusion (Wu et al., 2025). However, plant-derived carbon inputs decline through productivity suppression which drives by hydraulic failure (Choat et al., 2018) and carbon allocation shifts away from roots (Yin et al., 2021a). Prolonged drought (e.g., >2 years) induces microbial adaptation strategies which may accelerate SOC loss (Barnard et al., 2013; Schimel et al., 2018). The shift toward filamentous fungi dominance enhances oxidative enzyme production, while necromass accumulation primes destabilization of mineral-associated carbon (Liang et al., 2020; Wang et al., 2024). However, predicting how terrestrial carbon storage responds to drought over decadal timescales remains a challenge, requiring the integration of long-term manipulative experiments with models capable of capturing drought-induced changes in plant-microbe-mineral interactions.

In most terrestrial ecosystem models, SOC is typically represented as discrete compartments defined by their turnover times (Krinner et al., 2005; Lawrence et al., 2019). Early modeling approaches, such as the single-pool model proposed by Jenny et

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al. (1941), treated SOC as a homogeneous system. Subsequent refinements led to the development of multi-pool frameworks. For example, Campbell et al. (1978) categorized SOC into labile and stable organic matter. The TECO model further advanced this by partitioning SOC into three pools (fast, slow, and passive SOM) with different turnover rates (Xu et al., 2006; Du et al., 2017; Wan et al., 2025). Later developments incorporated greater complexity, such as separating recalcitrant fractions and accounting for physically protected organic matter, which decomposes more slowly than unprotected forms (Paul et al., 1978; Willard et al., 2024). Despite these advancements, SOC pools remain conceptual constructs simulated via first-order kinetics. Importantly, the carbon content of individual pools cannot be empirically measured, model calibration relies solely on total SOC (Guo et al., 2022).

Theoretical advancements in soil organic matter formation and decomposition improve the representation of SOC in land-surface and terrestrial ecosystem models (Doelsch et al., 2020; Si et al., 2023; Cotrufo et al., 2022; Sokol et al.,2019). Measured SOC fractions, such as particulate organic carbon (POC), mineral-associated organic carbon (MAOC) and dissolved organic carbon (DOC), have been proposed to link conceptual SOC pools (Lee et al., 2020). POC is typically considered as fragments of plant residues with a particle size > 53 μm, and it is more susceptible to external environment changes (Cotrufo et al., 2019; Benbi et al., 2014; Lugato et al., 2022). MAOC generally consists of microbial and plant-derived organo-mineral complexes rich in nutrients, typically < 53 μm, while also being associated with minerals and embedded in soil aggregates (Si et al., 2023; Hansen et al., 2024; Villarino et al., 2021).

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Some studies have revealed that models constrained by measurable SOC pools can provide more accurate estimation of model parameters thereby more accurate projections of SOC dynamics (Guo et al., 2022; Tao et al., 2024; Abramoff et al., 2022). Dissolved organic carbon (DOC), derived from living roots or transformed from recalcitrant macromolecular organic matter, is approximately 2 to 3 times more efficient than litter in forming soil organic matter (Sokol et al., 2019; Cotrufo et al., 2013). Moreover, the adsorption and desorption processes of DOC represent a key link in SOC decomposition (Camino-Serrano et al., 2018; Wu et al., 2014). Consequently, incorporating DOC and its interaction with SOC into models represents a crucial advance.

Soil organic matter decomposition is a stepwise process in which microbes secrete extracellular enzymes to catalyze the substrate, converting soil organic matter into assimilable subunits (Caldwell et al., 2005; Ma et al., 2024; Szejgis et al., 2024). Extensive manipulative experiments reveal that short-term drought limits microbial activities and substrate decomposition rates by inducing osmotic stress and constraining substrate diffusion (Honeker et al., 2024; Citerne et al., 2021). In contrast, long-term drought alters microbial community structure and carbon utilization patterns (Hueso et al., 2012; Preece et al., 2019; Wang et al., 2024). As catalysts of decomposition, microbial enzyme activities are impacted by drought (Sardans et al., 2010; Stursová et al., 2012; Wu et al., 2025). For example, drought significantly reduces the activities of β-glucosidase, acid phosphatase and polyphenol oxidase, although certain oxidases remain unaffected by soil moisture (Su et al., 2020a; Allison et al., 2023; Ficken et al.,

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2019). In recent years, microbial models, which focus on the process of microbial decomposition, have become increasingly incorporated in process-based ecological models (Moorhead et al., 2006; Lawrence et al., 2009; Allison et al., 2010; Huang et al., 2018). However, most microbial models focus only on simulating carbon dynamics under warming and nitrogen deposition scenarios (Luo et al., 2020; Knorr et al., 2005; Eastman et al., 2024), while studies investigating drought effects on SOC dynamics and microbial decomposition remain scarce. Consequently, incorporating microbial enzymes to terrestrial ecosystem model are necessary to elucidate microbial regulation of soil carbon responses to drought.

In this study, we evaluate three SOC modeling schemes with increasing complexity, including conventional three-pool partitioning scheme [SM1], mineral and particulate-associated carbon partitioning scheme [SM2] and Michaelis-Menten regulated carbon-stabilization scheme [SM3]. Using observational data from long-term drought experiments, we assess their validity and predictive performance. Our study addresses two key questions: (1) how does decadal drought affect SOC storage in subtropical forests? (2) do different model structures yield consistent drought impacts on SOC projections?

2 Materials and methods

2.1 Site description and data source

The Zhejiang Tiantong Forest Ecosystem National Field Scientific Observation and Research Station (28°48′N, 121°47′E, 163 m a.s.l) is located in Ningbo, Zhejiang

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Province. The site has a typical mid-subtropical monsoon climate with relatively distinct seasons. Summers are generally mild and rainy, while winters are dry with little precipitation. The annual average temperature in the study area is approximately 16.2 ℃. The annual average precipitation and evaporation are 1384 mm and 1320 mm, respectively, and the relative air humidity can reach 85%. The predominant soil type in the site is red-yellow soil and soil parent materials are mainly weathered products of some granite and sedimentary rocks. The soil texture consists of sand (6.8%), silt (55.5%), and clay (37.7%), with a pH ranging from about 4.4 to 5.1 (Gao et al., 2014). The vegetation type in the study area is typical subtropical evergreen broad-leaved forest, with secondary forests being the main vegetation type. The forest stocking density is approximately 3400 trees·hm^{-2}. The drought experiment was established in July 2013, which is composed of three experimental plots with similar terrain, vegetation type and stand condition (Su et al., 2020b).

The forcing datasets used in this study span from 2014 to 2022, including photosynthetically active radiation (PAR), leaf area index (LAI), air temperature (Ta), relative humidity of air (RH), soil temperature (Ts) and moisture content of soil (SWC). These data were mainly measured by the station meteorological observation device. The above-ground biomass data of plants were mainly estimated by allometric growth equation. The C content of litter was determined by potassium dichromate oxidation method. Soil total organic carbon and its physical and chemical properties were measured by elemental analyzer. Microbial biomass carbon was determined by chloroform fumigation. DOC was determined by hot water extraction and element

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analyzer (Zhou et al., 2013). Soil enzyme activities were determined by microplate enzyme assay (Saiya-Cork et al., 2002; Su et al., 2020b) and was expressed by substrate conversion per gram of dry soil per hour. The soil respiration rate was measured using the *LI-COR 8100 portable system* (LI-COR. Inc., Lincoln, NE, USA) between 9 a.m. and 1 p.m. on 1 - 2 sunny days per month, and accumulated the data on daily scale.

2.2 Model description

All three soil models are coupled to a common vegetation submodule, which requires identical environmental drivers and provides the same input data (Fig. 1). In SM1, soil organic carbon is divided into three pools, including (1) a microbial pool with fast turnover; (2) a slow (chemically protected) pool, and (3) a passive (physically protected) pool (Xu et al., 2006; Du et al., 2015). In SM2, SOM is divided into four pools (Si et al., 2023), including (1) a dissolved organic carbon pool (DOC), which is converted from organic matter with high molecular weight and difficult to decompose. Microbes can utilize DOC and release CO_2 (Allison et al., 2010; Lawrence et al., 2009); (2) a microbial pool; (3) a particulate organic carbon pool (POC), and (4) a mineral-associated organic carbon (MAOC). SM3 is an extension of SM2 that incorporates three enzyme components (β-1, 4-glucosidase (BG), polyphenol oxidase (PPO), and cellobiohydrolase (CBH)), which directly catalyze the decomposition of POC and MAOC. Given that enzymes have a low carbon content and their inclusion a pool could lead to model overparameterization, we therefore assign them a catalysis role instead of considering them as carbon pools. In these three model schemes, SM1 and SM2 implicitly represent microbial activities, where the decomposition of SOM governed by

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linear, first- order dynamics. Soil C turnover times are defined by biome and pool-specific decay constants, which are modified by environmental scalars such as soil temperature and soil moisture availability (Du et al., 2017; Du et al., 2025). In contrast, the SM3 adopted reverse Michaelis- Menten kinetics to explicitly represent the catalytic progress of microbial extracellular enzymes. The turnovers of DOC, POC and MAOC are depended on the size of both the donor (substrate) and the receiver (microbial biomass) pools. SM1 was expressed by the following equations:

$$\frac{dC_M}{dt} = I + C_S c_7 a_{67} + C_P c_8 a_{68} - C_M c_6 \quad (1)$$

$$\frac{dC_S}{dt} = I + C_M c_6 a_{76} - C_S c_7 \quad (2)$$

$$\frac{dC_P}{dt} = C_M c6 a_{86} + C_S c_7 a_{87} - C_P c_8 \quad (3)$$

Where C_M, C_S, C_P represent the C content of microbe, slow SOM and passive SOM. I represents the C input from litters, c_6, c_7, c_8 represent the exit rate of C from microbes, slow SOM and passive SOM, and a_{67}, a_{68}, a_{76}, a_{78} represent the allocation of slow SOM to microbes, passive SOM to microbes, microbes to slow SOM and passive SOM to slow SOM, respectively.

The soil C pools of SM2 were expressed as follows:

$$\frac{dC_{DOC}}{dt} = I + C_{POC} c_7 a_{67} + C_{MAOC} c_9 a_{69} - C_{DOC} c_6 \quad (4)$$

$$\frac{dC_{POC}}{dt} = I + C_M c_8 a_{78} - C_{POC} c_7 \quad (5)$$

$$\frac{dC_M}{dt} = C_{DOC} c_6 a_{86} - C_M c_8 \quad (6)$$

$$\frac{dC_{MAOC}}{dt} = C_{POC} c_7 a_{97} + C_M c_8 a_{98} - C_{MAOC} c_9 \quad (7)$$

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Where C_{DOC}, C_{POC}, C_{MAOC} represent the C content of DOC, POC, MAOC. Parameters c_6, c_7, c_8, c_9 denote the exit rate of DOC, POC, microbes and MAOC, and a_{67}, a_{69}, a_{78}, a_{86}, a_{97}, a_{98} represent the allocation of POC to DOC, MAOC to DOC, microbes to POC, DOC to microbes, POC to MAOC and microbes to MAOC, respectively.

SM3 was expressed by the following equations:

$$\frac{dC_{DOC}}{dt} = I + a_{67}(V_{CBH.P} + V_{PPO.P} + V_{BG.P})C_{POC} + a_{69}(V_{CBH.M} + V_{PPO.M} + V_{BG.M})C_{MAOC} - \frac{V_{max.assim}C_M C_{DOC}}{KM_{assim} + C_{DOC}} \quad (8)$$

$$\frac{dC_{POC}}{dt} = I + C_M c_8 a_{78} - (V_{CBH.P} + V_{PPO.P} + V_{BG.P})C_{POC} \quad (9)$$

$$\frac{dC_M}{dt} = C_{DOC} c_6 a_{86} - C_M c_8 \quad (10)$$

$$\frac{dC_{MAOC}}{dt} = a_{97}(V_{CBH.P} + V_{PPO.P} + V_{BG.P})C_{POC} + a_{98}c_8 C_M - (V_{CBH.M} + V_{PPO.M} + V_{BG.M})C_{MAOC} \quad (11)$$

Where $V_{max.assim}$ and KM_{assim} denote microbe maximum assimilation rate and half-saturation for assimilation. $V_{CBH.P}$, $V_{PPO.P}$, $V_{BG.P}$ represent catalytic rate of CBH, PPO, BG to POC. $V_{CBH.M}$, $V_{PPO.M}$, $V_{BG.M}$ represent catalytic rate of CBH, PPO, BG to MAOC.

$$V_{enzy.P} = \frac{V_{max.enzy} f_{enzy} C_M}{KM_{enzy} + C_{POC}} \quad (12)$$

$$V_{enzy.M} = \frac{V_{max.enzy} f_{enzy} C_M}{KM_{enzy} + C_{MAOC}} \quad (13)$$

Where $V_{max.enzy}$ represent the maximum reaction rate. KM_{enzy} represent half-saturation for reaction, f_{enzy} represent the C ratio of CBH, PPO, BG to microbes, respectively. The enzyme activities were calculated as following:

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$$V_{enzy} = \frac{V_{max.enzy} f_{enzy} C_M C_{sub}}{KM_{enzy} + C_{sub}} \quad (14)$$

Where C_{sub} denotes the C content of the enzyme-catalyzed substrate contained within a soil block with an area of 1 m^2 and a depth of 10 cm, and it maintains a consistent ratio of enzyme to substrate as required for experimental measurements.

We estimated model parameters using the Markov Chain Monte Carlo (MCMC) and evaluated changes in the simulated ecosystem C storage capacity using a traceability analysis framework (Supplement). The effect of drought on C storage is calculated as follows:

$$Drought\ Effect = \frac{(C_{drought} - C_{ctr})}{C_{ctr}} \times 100\% \quad (15)$$

Where $C_{drought}$ represents the C content of drought, C_{ctr} represents the C content of control condition.

3 Results

3.1 Model validation

In this study, we used the Markov Chain Monte Carlo (MCMC) algorithm to constrain model parameters (Figs. 2 and S3). All three schemes incorporate 8 vegetation-related parameters (Fig. S3). SM1 included 8 soil carbon-related parameters (Fig. 2), with 5 well-constrained under control conditions (c_7, a_{86}, a_{67}, a_{87}, a_{68}) and 5 under drought conditions (c_7, c_8, a_{76}, a_{86}, a_{68}). SM2 consisted 14 soil carbon-related parameters, with 7 well-constrained in the control scenario (c_9, c_{10}, a_{74}, a_{65}, a_{67}, a_{97}, a_{78}) and 9 in the drought scenario (c_9, c_{10}, a_{64}, a_{74}, a_{86}, a_{67}, a_{97}, a_{98}, a_{69}). SM3 had 11 well-constrained

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parameters under control conditions ($V_{max.assim}$, $V_{max.CBH}$, KM_{CBH}, f_{CBH}, f_{BG}, f_{PPO}, a_{64}, a_{74}, a_{75}, a_{97}, a_{78}) and 12 under drought conditions (c_6, $V_{max.assim}$, $V_{max.CBH}$, KM_{CBH}, KM_{BG}, $V_{max.PPO}$, KM_{PPO}, f_{BG}, f_{PPO}, a_{65}, a_{86}, a_{97}) in all 22 soil carbon-related parameters.

All three schemes calibrated by observations from the drought experimental which had overall good agreement (Figs. S1 and S2). The simulation of vegetation C (leaf, fine root, wood) and soil respiration exhibited high accuracy. The simulated MBC by SM1 was inferior to those simulated by SM2 and SM3, suggesting that incorporating measurable C pools can improve the accuracy of MBC simulation. By comparing the accuracy of POC and MAOC, we found that SM3 generally outperformed SM2, indicating that the incorporation of enzyme activities can enhance the simulation of the SOC fractions, particularly with respect to MAOC.

3.2 Carbon simulation and prediction by three model schemes

Carbon storage from 2023 to 2100 was predicted using three different model schemes. All models consistently indicated an increasing trend in vegetation C (VegC) and a decreasing trend in soil organic carbon under both control and drought conditions (Figs. 3 and S4). Specifically, under control conditions, SM1 simulated growth rates of 260% for VegC, -56.9% for SOC and 188% for total organic carbon (TOC). Under drought conditions, the corresponding rates were 223%, -50.4% and 159%. SM2 projected growth rates of 263% for VegC, -60.8% for SOC and 179% for TOC under control conditions, and 217%, -55% and 151% under drought. For SM3, the simulated growth rates were 230% for VegC, -88% for SOC and 146% for TOC in the control scenario, while under drought the values were 169%, -55% and 106%, respectively.

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3.3 Drought effects on carbon storage

All three modeling schemes consistently indicated that drought reduced C content in MBC (SM1, -36.9%; SM2, -56.9%; SM3, -27.3%), VegC (SM1, -16.8%; SM2, -19.9%; SM3, -25.4%) and TOC (SM1, -15%; SM2, -19.4%; SM3, -24.4%). However, the simulated responses of SOC to drought varied among the schemes (Fig. 4). SM1 predicted an increase in SOC under drought conditions (+39.5%) compared to the control, driving by increases in both the slow (+13%) and passive (+57%) C pools. Similarly, SM3 projected a rise in SOC (+56.9%), accompanied by increases in POC (+82.3%), MAOC (+88.1%), and DOC (+6.7%). In contrast, SM2 simulated a decrease in SOC (-6.1%), with reductions in DOC (-35.3%) and MAOC (-3.7%), through POC increased (+43.4%).

By comparing the proportion of drought effects on each soil C pool simulated by each scheme, it is apparent that different modeling schemes exhibit distinct sensitivities to drought across specific carbon pools (Fig. 4). Specifically, SM2 demonstrated greater sensitivity to drought effects on microbial biomass (-54%) and DOC (-84%) compared to SM3 (-18% and +16%, respectively). Conversely, SM3 showed higher sensitivity to drought-induced changes on POC (+82%) and MAOC (+74%) relative to SM2 (-26% and +18%, respectively).

3.4 Traceability analysis of drought effects

The traceability analysis revealed that both SM1 and SM3 simulated higher SOC under drought condition (SM1, 2.5 kg C m^{-2}; SM3, 1.2 kg C m^{-2}) compared to the control (SM1, 2.1 kg C m^{-2}; SM3, 0.8 kg C m^{-2}) at the end of forecast period (Fig. 5). In contrast,

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SM2 simulated lower SOC under drought (2.3 kg C m^{-2}) compared to the control (2.5 kg C m^{-2}). The increase of SOC in SM1 during drought was driven by higher soil carbon input (drought, 1.0 kg C m^{-2} $year^{-1}$; control, 0.6 kg C m^{-2} $year^{-1}$) (Figs. 5 and 6), while in SM3, it resulted from an extended soil carbon residence time (drought, 4.3 years; control, 2.6 years). However, SM2 simulated a reduction in soil carbon residence time under drought, leading to decreased SOC.

We further analyzed the C residence times of individual pools simulated by the three modeling schemes under both control and drought conditions (Fig. 6). In SM1, drought increased the C residence time of passive SOM which resulted from the allocation proportions from slow SOM to passive SOM and from passive SOM to microbes were elevated. For SM2, drought reduced the C residence time of microbes and increased that of MAOC. The allocation proportions from POC to DOC and from DOC to microbes were enhanced, while the allocation from MAOC to DOC declined. In SM3, drought resulted in a longer C residence time for MAOC. The allocation proportions from DOC to microbes, from MAOC to DOC, and from microbes to MAOC all increased, while the allocation from microbes to POC decreased.

4 Discussion

4.1 Response of ecosystem carbon dynamics to long-term drought

In this study, all three modeling schemes consistently indicate that drought leads to decrease in vegetable carbon (VegC), microbes carbon (Microbe C) and total organic carbon (TOC), while particulate organic carbon (POC) increases under drought

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conditions (Figs. 3, 4 and S4). These findings are consistent with multiple fields manipulated experiments (Zhou et al., 2020; Pennisi., 2022; Schwalm et al., 2017). During drought, plants undergo physiologically adjustments and shifts in community structure in accordance with species-specific water use strategies to prevent excessive water loss (Rowland et al., 2023). These responses in turn affect C uptake via photosynthesis and C release via respiration at the ecosystem level, potentially decoupling these two processes (Meir et al., 2008).

Drought consistently reduced microbial biomass carbon (MBC) across all three models, and sensitivity analysis indicated this reduction was primarily driven by increased microbial decay rates (Figs. 2 and S5). With prolonged drought duration, microbial C content exhibited a pattern of initial decline followed by a gradual recovery (Fig. 3a). Drought-induced water stress directly impairs microorganisms, leading to decreased metabolic activity (Quiroga et al., 2024). However, microorganisms can adapt to drought through physiological changes, community turnover, and evolutionary mechanisms (Martiny et al., 2015; Allison., 2023). At the community scale, drought-sensitive microbes may be replaced by more resilient taxa that immigrate into the area (Allison et al., 2008; Ricks & Yannarell., 2023). Several studies have showed that fungi exhibit greater drought adaptability compared to bacteria (Preece et al., 2019; Bastida et al., 2018; de Vries et al., 2018). Gram-positive bacteria are also better adapted to low-moisture soils compared to Gram-negative bacteria, due to their thicker and harder cell walls, which render them less affected by drought (Castro et al., 2010; Uhlírová et al., 2005). Through in situ manipulation experiments, Bu et al (2018) and Su et al (2020b)

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have observed shifts in microbial community structure under drought condition, which may explain the gradual increase in microbial biomass under prolonged drought conditions. Besides, given that microbes directly consume DOC, the incorporation of measured DOC pools in SM2 and SM3 enhances the model's ability to simulate microbial sensitivity to drought.

Simulation results from all three modeling schemes consistently showed that drought initially decreased soil respiration, followed by a subsequently recovery (Fig. 3a). This trend mirrors variations in microbial carbon content, indicating that drought regulates soil respiration primarily through its control of microbial biomass (Zhao et al., 2025; Ficken & Warren., 2019). Sensitive analysis further revealed a strong positive correlation between the C content of POC and the allocation proportion of litters to POC (Figs. 2 and S5). These results imply that drought enhance both the carbon content in litter and its transfer to POC, resulting in an overall increase in POC. Furthermore, since POC are directly influenced by enzymatic catalysis, SM3's heightened sensitivity to drought effects on these pools underscores the model's effectiveness in capturing enzyme-mediated processes under drought conditions.

4.2 Divergent simulations of drought effect on SOC among three modeling schemes

A key divergence among the three modeling schemes lies in their simulation of drought effects on SOC components, which is the key source of discrepancy in the projected carbon storage response (Figs. 4 and 6). SM1 divides SOC into three pools, including MBC, slow SOM, and passive SOM. However, since only total SOC data are available

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to constrain the model, the predictions of this scheme are highly sensitive to the quality and the duration of SOC observations (Fig. S5). Given the non-linear response of ecosystems to drought duration (Müller et al., 2022; Anderegg et al., 2020; Schwalm et al., 2017), models constrained by short-term observation data may introduce substantial deviation in long-term projections. In contrast, SM2 partitions the SOC into four observable carbon pools (i.e., Microbes, POC, MAOC and DOC), each independently constrained by corresponding measurements. The trajectory of SOC is thus jointly determined by these four fractions, leading to pronounced differences between the predictions of SM1 and SM2. Since both models use the same SOC data, this demonstrates the profound influence of carbon partitioning strategies on model predictions. Furthermore, drought causes the carbon input rates and carbon loss rates of individual carbon pools in SM2 deviate from the overall SOC change rate. These pool-specific discrepancies cause the SOC predictions to diverge increasingly over time between models with different structures.

Differences between SM2 and SM3 are mainly reflected in the dynamics of DOC and MAOC. SM2 employs first-order linear kinetics to describe the decomposition of DOC and MAOC, where the decomposition rate is proportional to their C content. In contrast, SM3 utilizes reverse Michaelis-Menten kinetics, indicates that the decomposition of SOC is not only dependent on C content but also on microbial C and enzyme activities (Chandel et al., 2023). Under drought condition, SM2 simulates a decrease in DOC, while SM3 predicts an increase (Fig. 4). Some studies report that drought can reduce DOC concentrations (Tiwari et al., 2022; Wu et al., 2023), whereas

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others suggest it may increase DOC due to the influence of factors such as air temperature, soil temperature, humidity, precipitation, pH, and sulfate concentrations (Evans et al., 2005; Sowerby et al., 2010). Sensitivity analysis reveals that DOC in SM2 is influenced mainly by the transfer ratio of POC to DOC and the transfer ratio of metabolic litter to DOC (Fig. S5). However, DOC dynamics are primarily controlled by the microbe maximum assimilation rate and half-saturation for assimilation in SM3, indicating that SM3 captures direct microbial regulation of DOC decomposition. Similarly, while SM2 simulates a slight decrease in MAOC under drought, SM3 predicts an increase (Fig. 4). This discrepancy stems the fact that SM3 explicitly incorporates the catalytic effects of three enzyme activities - BG, PPO and CBH – on MAOC decomposition. Drought reduces microbial enzyme activities (Figs. S1 and S2) (Bach et al., 2016; Waldrop et al., 2006), thereby weakening MAOC decomposition capacity and accumulating MAOC under drought condition. Moreover, the explicit inclusion of enzyme-mediated processes significantly improves the accuracy of POC and MAOC simulations, suggesting the importance of representing enzyme activities in SOC decomposition models.

Our study enhances the understanding how drought affects forest C dynamic across different model schemes. Nevertheless, we acknowledge that several uncertainties involved in our analysis. First, we only considered three enzymes that directly catalyze soil carbon decomposition, while other enzymes (e.g., Acid phosphatase, N-acetyl-glycosaminidase, Peroxidase) may also contribute indirectly to this process (Su et al., 2020b). Second, when calculating enzyme activities, we applied laboratory-derived

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proportional relationships between enzyme quantity and substrate quantity to field conditions, which assumes substrate availability far exceeds enzyme availability in field soils. Finally, laboratory enzyme activities measurements typically use specific substrates, whereas field soils contain multiple potential substrates that could be catalyzed, which introduces additional uncertainty in our simulations.

5 Conclusions

Accurately simulating the impacts of drought on soil carbon dynamics is of critical importance for terrestrial carbon sequestration. In this study, we integrated data assimilation and traceability analysis, devising three soil carbon decomposition schemes and exploring how different soil carbon decomposition models simulate soil carbon responses to drought. Our results revealed significant disparities in the drought effects on soil organic carbon as simulated by the three models, with these differences primarily driven by carbon input and carbon residence times of different carbon pools. Explicitly incorporating microbial enzyme activities notably altered the impacts of drought on mineral-associated organic carbon and dissolved organic carbon. These findings underscore the significant role of different carbon pool partitioning schemes, their constrainability, and the consideration of microbial enzyme catalytic processes in simulating the response of soil carbon to drought, enhancing our understanding of the complexity underlying drought effects on soil organic carbon decomposition.

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CRediT author contribution statement: F.D and Z.D. collected and analyzed the data and wrote the manuscript. Z.D. conceived, designed, and oversaw the study. F.D., L.F., and Z.G. conducted the statistical analysis. F.D., X.Z., and Z.D. discussed, wrote, and revised the manuscript with major contributions from L.Z. Y.Z. and G.Z. commented on the manuscript.

COMPETING INTEREST DECLARATION: Authors declare that they have no competing interests.

DATA AND MATERIALS AVAILABILITY: Data will be made available on request.

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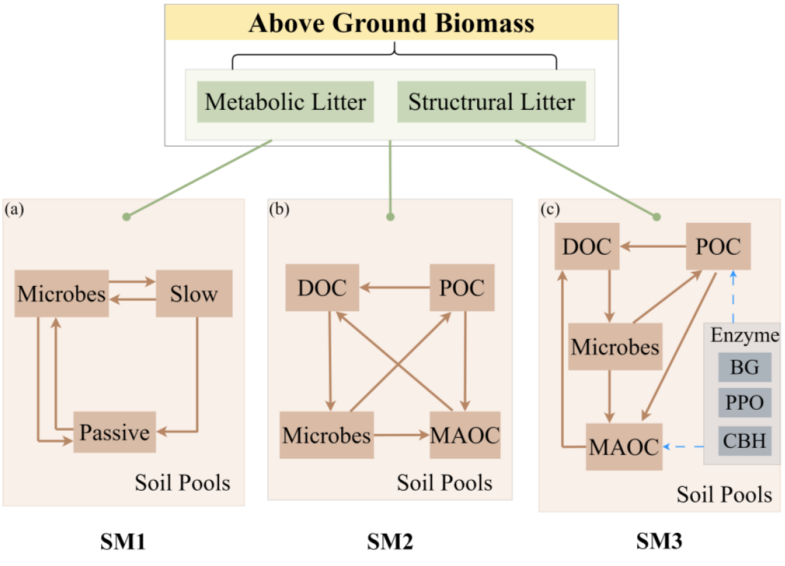

Figure 1. Conceptual diagram of the soil biogeochemical models with three schemes. **(a)** conventional three-pool partitioning scheme (SM1), **(b)** mineral and particulate-associated carbon partitioning scheme (SM2), and **(c)** Michaelis-Menten regulated carbon-stabilization scheme (SM3). All pools (boxes) and fluxes (arrows) represent C process. BG, β-1, 4-glucosidase, PPO, polyphenol oxidase, CBH, cellobiohydrolase.

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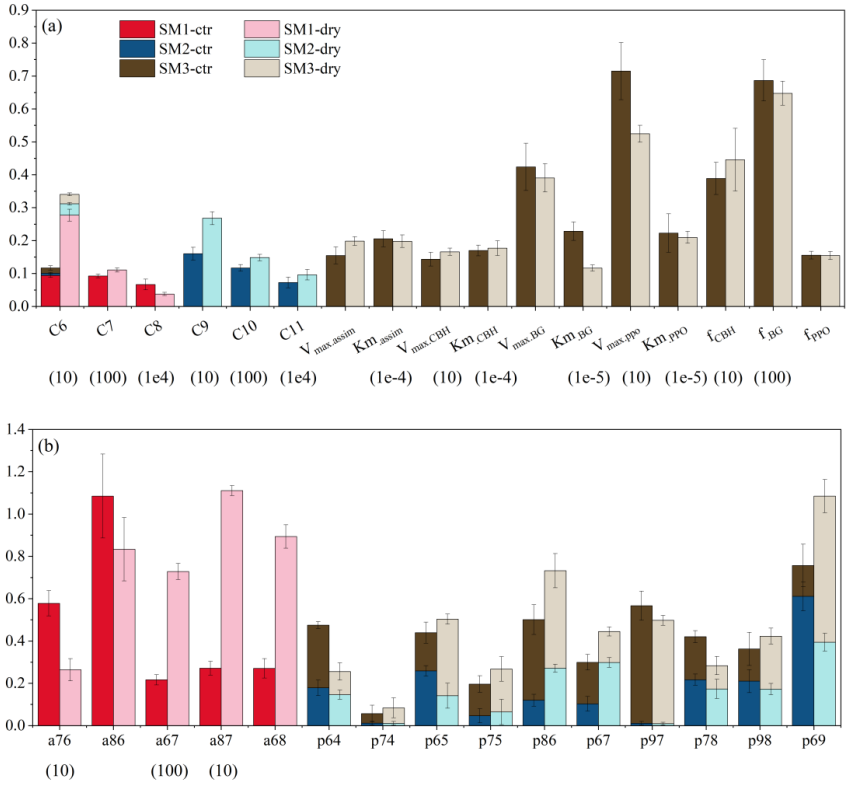

Figure 2. Maximum likelihood value (MLEs) (or means for unconstrained parameters) of the target parameters in both control and drought treatments among the three schemes. Error bars represent standard deviations (SDs). See Table S1 for parameter abbreviations and units.

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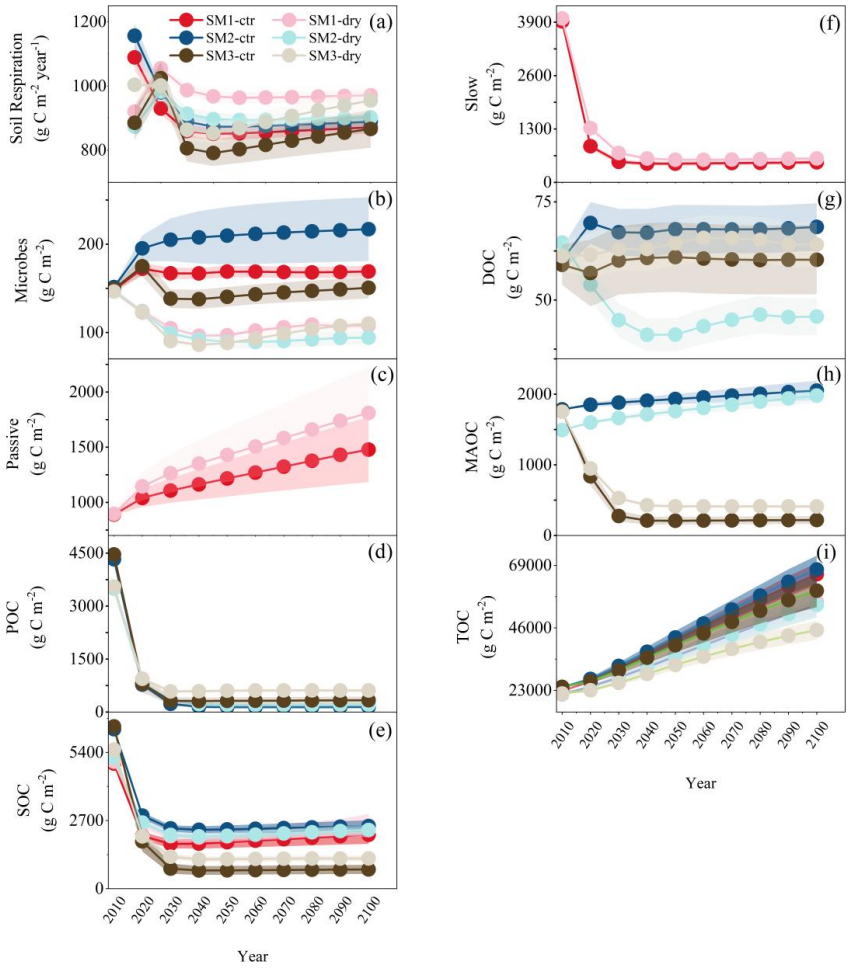

Figure 3. Predicted soil respiration **(a)**, microbial C **(b)**, passive SOM **(c)**, POC **(d)**, SOC **(e)**, slow SOM **(f)**, DOC **(g)**, MAOC **(h)**, total organic C **(i)** from 2014 – 2100 under dry and control conditions for three schemes.

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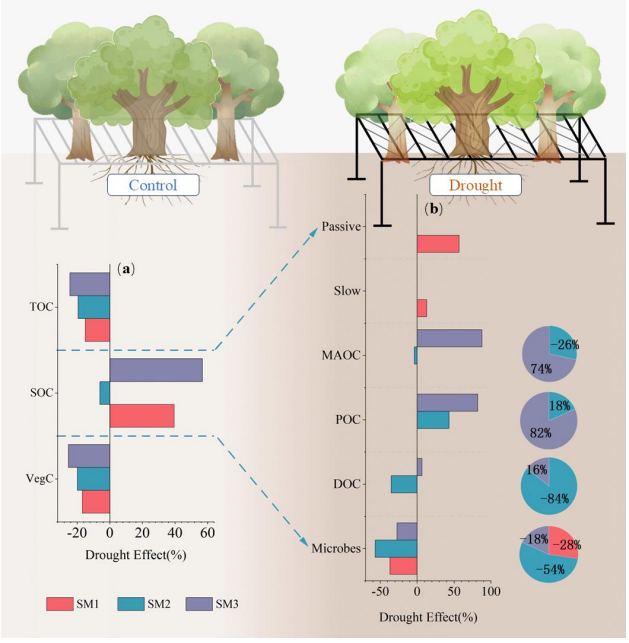

Figure 4. Conceptual figure of the effects of drought simulated by three schemes on carbon stocks. The histogram represents the drought effects on carbon pools (percentage change of the carbon pools from 2022 to 2100), and corresponding pie charts represent the proportion of the drought effects simulated by each of the three schemes for the same carbon pool, relative to the sum of the drought effects from all three schemes. TOC, soil total organic carbon. VegC, vegetation carbon.

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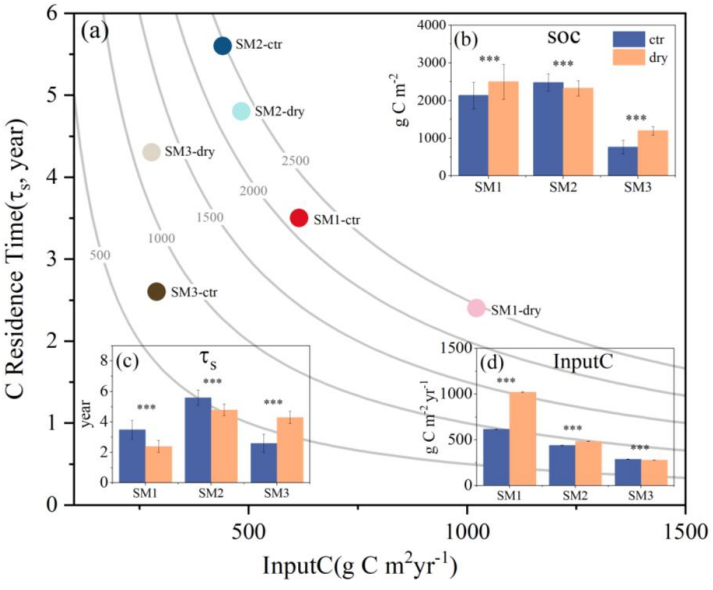

Figure 5. Predicted soil C storage capacity in 2100 by C influx (InputC, x axis) and soil carbon residence time (τ_s, y axis) between control and drought treatments in three model schemes. ***, represents $p < 0.01$.

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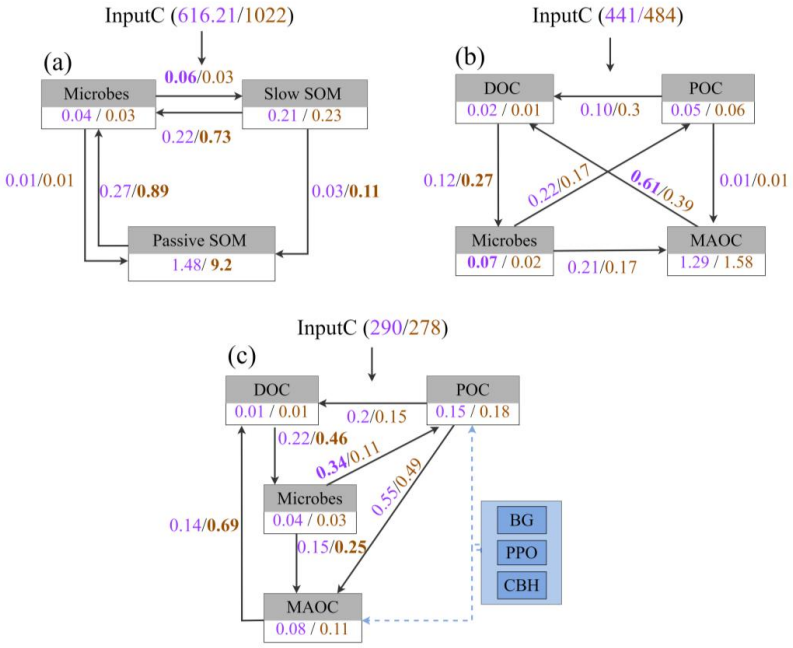

Figure 6. The carbon residence time of each soil carbon pool in the drought and control conditions simulated by three schemes and the allocative proportion of carbon turnover among some pools. The numbers in the box represents the carbon residence time, and the carbon near the arrow represents the carbon allocation proportion. Purple represents the control and brown represents the drought.

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Appendix

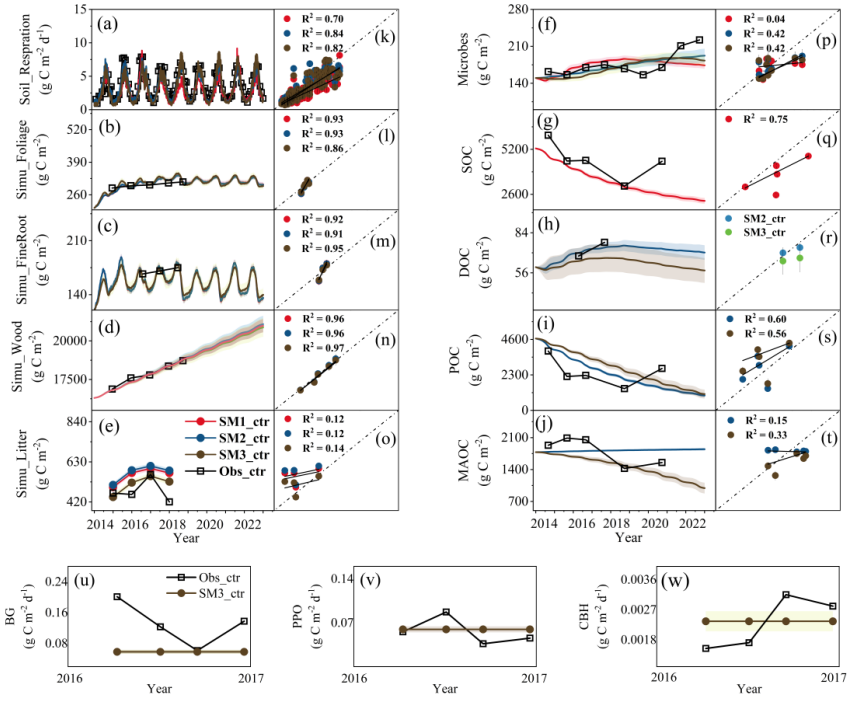

Figure A1. Comparison of the measured values (black squares) and simulated values (lines) in the control conditions of three schemes from 2014 to 2022, $p < 0.05$.

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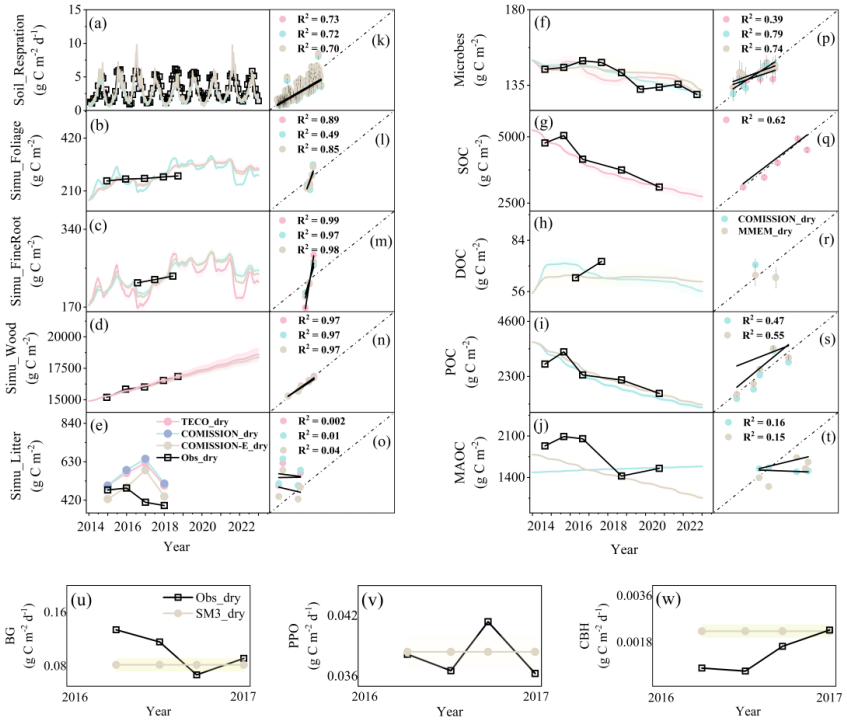

Figure A2. Comparison of the measured values (black squares) and simulated values (lines) in the drought conditions of three schemes from 2014 to 2022, $p < 0.05$.

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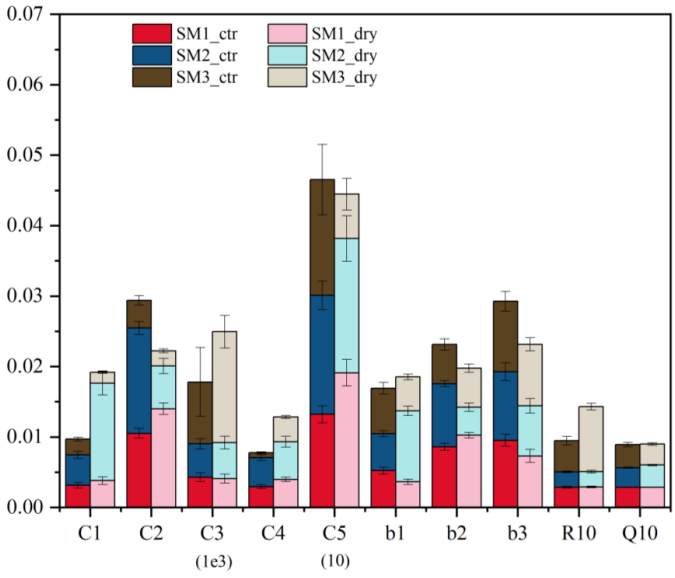

Figure A3. Maximum likelihood value (MLEs) (or means for unconstrained parameters) of the target parameters of vegetations in various models and treatments. Error bars represent standard deviations (SDs). See Table S1 for parameter abbreviations and units.

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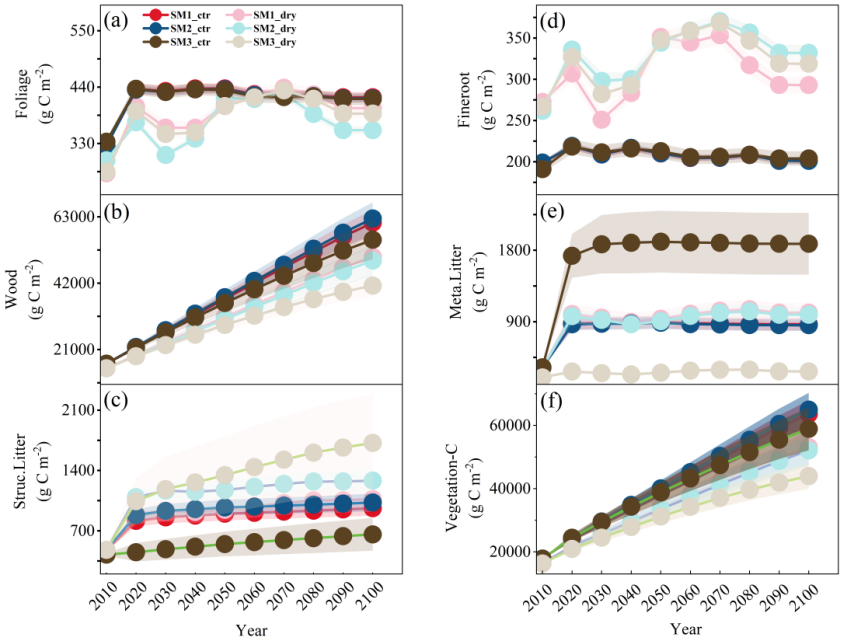

Figure A4. Predicted foliage (a), wood (b), structural litter (c), fineroot (d), Metabolic litter (e), Vegetation C (f) from 2014 – 2100 under dry and control conditions for three schemes.

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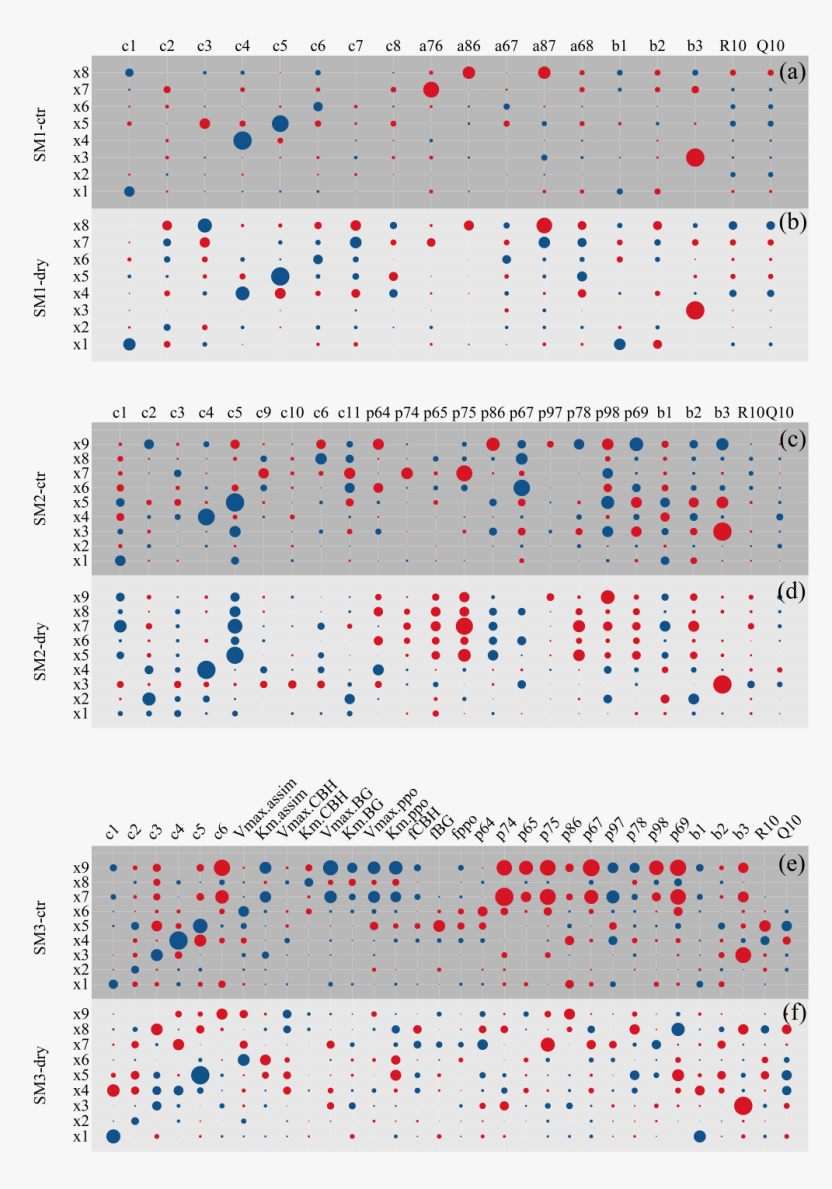

Figure A5. The correlation between carbon pools and model parameters under control and drought conditions of three schemes. Red represents positive correlation and blue represents negative correlation. The *x1, x2, x3, x4, x5* represent the carbon content of foliage, fineroot, wood, metabolic litter, structural litter. *x6, x7, x8* represent microbes slow SOM and passive SOM for SM1. *x6, x7, x8, x9* represent DOC, POC, microbes and MAOC for SM2 and SM3.

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Table A1. Target parameters of this study and their prior ranges.

Parameters	Intervals	Unit	Description
C1	0.176-9.95	mg C g^{-1} d^{-1}	exit rate of C from foliage
C2	0.176-17.9	mg C g^{-1} d^{-1}	exit rate of C from fineroot
C3	0.00176-0.01	mg C g^{-1} d^{-1}	exit rate of C from wood
C4	0.274-8.22	mg C g^{-1} d^{-1}	exit rate of C from metabolic litter
C5	0.0548-1.64	mg C g^{-1} d^{-1}	exit rate of C from structural litter
C6	2.74-13.7	mg C g^{-1} d^{-1}	exit rate of C from microbes
C7	0.027-1.37	mg C g^{-1} d^{-1}	exit rate of C from slow SOM
C8	0.00137-0.00913	mg C g^{-1} d^{-1}	exit rate of C from passive SOM
C9	2.74-68.5	mg C g^{-1} d^{-1}	exit rate of C from DOC
C10	0.1-1	mg C g^{-1} d^{-1}	exit rate of C from POC
C11	0.00137-0.013	mg C g^{-1} d^{-1}	exit rate of C from MAOC
b1	0-0.315	-	allocation of GPP to foliage
b2	0-0.3	-	allocation of GPP to fineroot
b3	0-0.3	-	allocation of GPP to wood
R10	0-1	g C m^{-2} d^{-1}	basic respiration rate
Q10	2-5	-	temperature sensitivity of respiration
a76	0-0.5	-	allocation of microbes to slow SOM
a86	0-0.5	-	allocation of microbes to passive SOM
a67	0-0.5	-	allocation of slow SOM to microbes
a87	0-0.5	-	allocation of slow SOM to passive SOM
a68	0-1	-	allocation of passive SOM to microbes
p64	0-0.3	-	allocation of metabolic litter to DOC
p74	0-0.7	-	allocation of metabolic litter to POC
p65	0-0.6	-	allocation of structural litter to DOC
p75	0-0.4	-	allocation of structural litter to POC
p86	0-0.7	-	allocation of DOC to microbes

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p67	0-0.8	-	allocation of POC to DOC
p97	0-0.2	-	allocation of POC to MAOC
p78	0-0.7	-	allocation of microbes to POC
p98	0-0.3	-	allocation of microbes to MAOC
p69	0-0.8	-	allocation of MAOC to DOC
$V_{max.assim}$	0.001-0.4	mg C mg^{-1} MBC d^{-1}	microbe maximum assimilation rate
$Km_{.assim}$	300-3000	g C m^{-3}	half-saturation for assimilation
$V_{max.CBH}$	0.0001-0.01	mg C mg^{-1} CBH d^{-1}	maximum reaction rate of CBH
$Km_{.CBH}$	300-3000	g C m^{-3}	half-saturation for reaction of CBH
$V_{max.PPO}$	0.0001-0.2	mg C mg^{-1} PPO d^{-1}	maximum reaction rate of PPO
$Km_{.PPO}$	300-6000	g C m^{-3}	half-saturation for reaction of PPO
$V_{max.BG}$	0.0001-0.2	mg C mg^{-1} BG d^{-1}	maximum reaction rate of BG
$Km_{.BG}$	300-3000	g C m^{-3}	half-saturation for reaction of BG
f_{CBH}	0-0.01	-	CBH-to-microbial carbon ratio
f_{PPO}	0-0.2	-	PPO-to-microbial carbon ratio
f_{BG}	0-0.1	-	BG-to-microbial carbon ratio

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