

Long-term throughfall exclusion reduced soil organic carbon towards higher soil microbial carbon use efficiency and lower microbial enzyme activities on *Phyllostachys edulis* plantations

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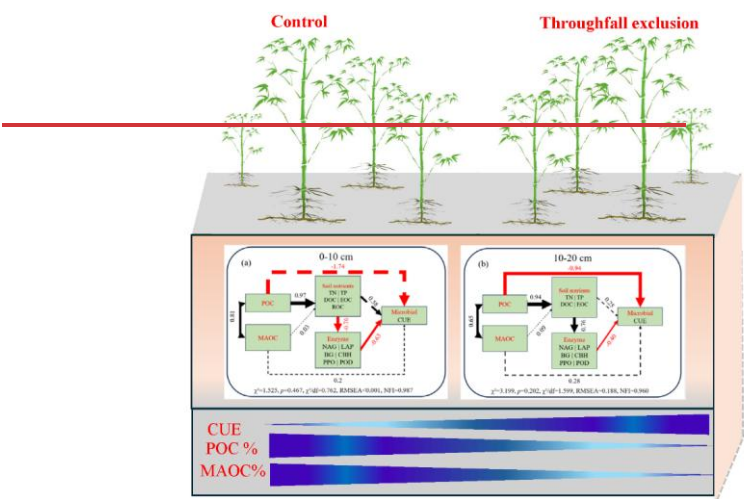
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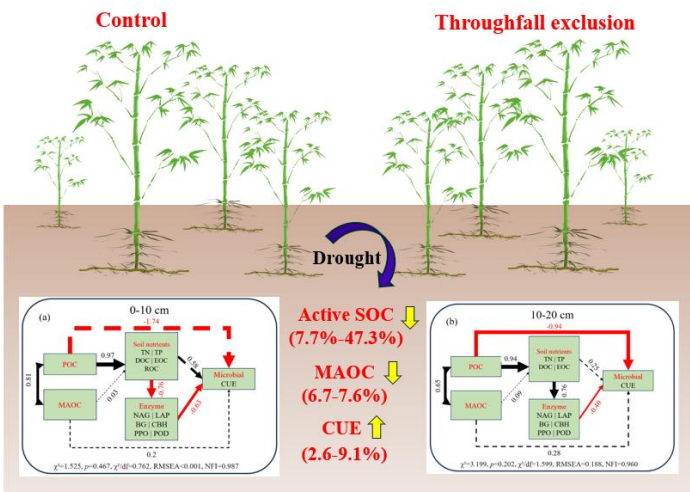
Abstract: Soil microbial carbon utilization efficiency (CUE) serves as a crucial metric for evaluating the effectiveness with which microbes assimilate organic carbon, acting as a vital benchmark for assessing the potential of soil carbon sequestration. Previous studies have shown that drought can significantly affect microbial CUE, which is crucial for the carbon cycle in forest ecosystems. However, the effect mechanisms of microbial CUE on soil carbon fractionsstability under drought conditions ~~are-is~~ not well understood. In this study, a throughfall exclusion experiment was conducted in subtropical *Phyllostachys edulis* plantations (The control, CK; throughfall exclusion, T). The results showed that drought increased microbial CUE by 9.1~~2~~% ($p<0.05$) and 2.~~5~~6% in 0-10 cm and 10-20 cm soil layers, respectively. Soil organic carbon (SOC), soil particulate organic carbon (POC), soluble organic carbon (DOC), and easily oxidized organic carbon (EOC) all significantly decreased by 7.7%–47.3%, while the proportion of mineral-associated organic carbon (MAOC) in SOC increased by 4.1% and 6.3% ($p<0.05$) at two layers, respectively. Microbial CUE was positively correlated with POC/SOC ratio and MAOC/SOC ratio, indicating that variation of SOC components substrate quality was an important factor driving microbial physiological changes. Structural equation model (SEM) further showed that soil polyphenol oxidase (PPO) and cellobiohydrolase (CBH) enzymes were the main factors driving changes in microbial CUE. Our results suggested that long-term drought indirectly regulates the storage and transformation of SOC by affecting microbial ~~community structure~~activities and function, which would have a profound impact on the carbon cycle of forest ecosystems.

Keywords: Long-term Droughtdrought; Microbial CUE; SOC components; Soil enzyme activity; Moso bamboo;

45 **Graphical Abstract**



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48

49 1. Introduction

50 Rising global average air temperature and shifting precipitation patterns, both attributable to
51 human-induced greenhouse gas emissions, will inevitably ~~extend the drought season~~ get drier
52 or wetter in ~~most regions of the world~~ some regions (Peng et al., 2025). This ~~prolongation~~
53 change of the drought season has a profound impact on various aspects, such as vegetation
54 ~~and community~~ composition and ~~soil organic soil~~ carbon (SOC) utilization, which ultimately
55 affect ~~the the interaction process of plant and soil carbon cycling processes~~ in terrestrial
56 ecosystems (Miao et al., 2020; Spinoni et al., 2021). Soil represents the most extensive
57 carbon pool within terrestrial ecosystems, playing a crucial role in the regulation of carbon
58 cycle processes and the dynamics of climate change (Crowther et al., 2019). Meanwhile,
59 long-term drought may lead to a continuous reduction of forest soil organic carbon
60 (SOC) ~~SOC~~ (Peng et al., 2025), which in turn strongly affected the global soil carbon cycle
61 and carbon storage processes (Müchael and Bahn, 2022). In forest ecosystems, the effects of
62 drought on SOC accumulation were mostly negative (Zhou et al., 2019; Kabir et al., 2024). A
63 meta-analysis of the effects of drought (precipitation reduction experiments) on soil carbon
64 cycling in natural ecosystems, particularly forests, showed that prolonged drought led to a
65 -3.3% reduction in SOC content (based on 148 drought-manipulation studies) (Deng et al.,
66 2021).

67 The SOC represents a mixed pool of carbon, which varies with ~~their carbon components~~
68 formation, turnover rates, chemical characteristics and stabilization mechanisms (Lavallee et
69 al., 2020). Generally, SOC generally ~~are~~ is divided into active organic carbon and inert
70 organic carbon according to the complexity of chemical structure (Zhou et al., 2025). Active
71 organic carbon is readily broken down by microorganisms and directly participates in the

chemical transformation processes involving soil organisms (Sun et al., 2023). It quickly reflected changes in soil organic matter, with the research concentrated on SOC components (Zhao et al., 2018). Specifically, dissolved organic carbon (DOC), easily oxidizable organic carbon (EOC), and microbial biomass carbon (MBC) all belong to the active carbon components with fast turnover in SOC. However, the impacts of drought on SOC components vary across regions around the world (Deng et al., 2021; Soares et al., 2023). Specifically, drought reduced MBC reservoir size by 2% to 30% in subtropical natural forest of China (Sun et al., 2020). This reduction ~~leads~~ led to an increase in the accumulation of DOC in the topsoil by 30% to 60% from meta-analysis synthesizing data and temperate mature forest of Southwestern Germany (Deng et al., 2021; Brunn et al., 2023). Therefore, active organic carbon storage ~~in across~~ different forests ecosystems exhibited divergent respond-responses ~~differently~~ to drought ~~intensity severity, and the mechanistic disparity that differential mechanism~~ could be clarified under drought conditions.

Despite some progress in understanding the general trends in SOC dynamics under drought conditions, several challenges remain (Brunn et al., 2023). Specifically, one key issue is the lack of a comprehensive understanding of the mechanisms in regulating soil particulate organic carbon (POC) and mineral-associated organic carbon (MAOC) dynamics during drought (Lai et al., 2024). POC was influenced directly by the plant-derived inputs and the functional genes of carbon-degrading fungi with modulated by DOC and total nitrogen (TN). In contrast, MAOC was shaped by the increasing inputs of labile-active carbon, such as DOC (Gao et al., 2024). Therefore, there were more research complex relationships among is

93 ~~necessary to explore SOC fractions stability the role of additional factors including by soil~~
94 ~~microorganisms, enzyme activities, and other biological factors in mediating SOC~~
95 ~~decomposition and stability~~. For example, ~~in surface soil~~, MAOC in surface soil increased
96 proportionally with microbial biomass and POC, fungal necromass carbon ~~had a more~~
97 ~~contributed to MAOC~~ in Qinling Mountains (Lai et al., 2024). Oppositely, some study
98 reported that the impact of drought on POC and MAOC was limited, but POC exhibited
99 greater vulnerability to drought compared to MAOC (Shi et al., 2024). Therefore, these
100 inconsistent results were verified differently response to drought.

101 Soil microbial carbon utilization efficiency (CUE) denotes to the fraction of carbon
102 incorporated into microbial biomass relative to the overall carbon uptake by microorganisms
103 (Li et al., 2021a). It reflects the carbon allocation between anabolism and catabolism
104 processes in the soil microbial community and directly affects the soil carbon storage
105 capacity (Sun et al., 2025). Moreover, microbial CUE may be an important parameter for
106 determining SOC storage by controlling the proportion of SOC utilization (Geyer et al., 2016;
107 Ullah et al., 2021). Specifically, previous studies have shown that drought may affect the
108 activity of microbes and their CUE, which in turn affects the decomposition and
109 accumulation of POC and MAOC (Duan et al., 2023). For example, higher CUE may
110 accelerate the breakdown of POC, as the generation of microbial byproducts during this
111 process facilitates the formation of MAOC, as shown by Guenet et al. (2021) and Chen et al.
112 (2021). Further studies are needed to determine whether drought alters CUE and
113 consequently affect soil carbon pools. ~~Understanding-Elucidating the impact of how~~ SOC
114 fractions, particularly POC and MAOC, ~~on influence~~ CUE ~~could may~~ provide insights into the

115 mechanisms ~~through by~~ which ecosystems ~~maintain preserve~~ their carbon balance ~~during~~
116 ~~under~~ drought ~~events stress~~. Moreover, the relationships between SOC fractions and CUE
117 under drought is poorly understood. To address this gap, we examined the potential
118 correlations among these variables, aiming to provide a more comprehensive perspective on
119 how drought impacts soil carbon dynamics and plant productivity.

120 *Phyllostachys edulis* is a vital plantation in China, thriving abundantly across the
121 subtropical regions ~~with excellent carbon sink function~~, which is the preferred material for
122 “replacing wood with bamboo” and “replacing plastic with bamboo” for its fast natural
123 regeneration. ~~Under the background of increased drought frequency and intensity, drought-~~
124 ~~induced changes in soil environmental, nutrients input and microbial activities may~~
125 ~~considerably influence SOC pool and microbial CUE (Huang et al., 2026).~~ In our study, a
126 drought experiment lasting 9-8 years was conducted in *P. edulis* ~~forest plantation~~ in
127 southeastern China, ~~while it is still unknown how long-term drought affected the SOC~~
128 ~~fractions by microbial CUE~~. We hypothesis that: (a) Throughfall exclusion reduced ~~the~~ soil
129 microbial CUE with higher soil enzyme activities ~~and active SOC~~. (b) ~~soil-Soil~~ microbial
130 CUE and soil carbon fractions had different responses to drought at soil vertical direction ~~by~~
131 ~~soil enzyme activities~~. The main objectives of this study are: (1) to evaluate the effects of
132 throughfall exclusion on soil POC, MAOC and soil microbial CUE; and (2) to reveal how
133 throughfall exclusion influences SOC ~~components fractions~~ by changes in microbial CUE
134 that mediates these impacts. This study helps to clarify the internal link between SOC
135 components and CUE in *P. edulis* plantation under throughfall exclusion as identifying
136 predictors of response to long-term drought, which would provide a reference for the

137 optimization of carbon cycle models in terrestrial ecosystems under drought conditions (Li et
138 al., 2021b).

139

140 **2. Materials and methods**

141 *2.1 Study area*

142 The study area locates in Huanggongwang Forest Park (119 56 '~120 02' E, 30 03 '~30 06'
143 N), Hangzhou, Zhejiang Province, which is 10 km away from the city. It exhibits a
144 characteristic subtropical humid monsoon climate, with an average annual temperature of
145 16.1°C, abundant rainfall and annual average rainfall of 1441.9 mm. The soil type in the
146 forest area ~~is belongs to red soil according to WRB classificationslightly acidic red soil, pH~~
147 ~~value was 4.95–5.72, soil texture includes clay 8.6%–13.2%, sand 46.1%–54.3%, silt 38.5%–~~
148 ~~43.6%.~~ The bamboo ~~forestplantations~~ in experimental areas were planted in the 1960s, which
149 have been used for special experimental areas without agricultural implementations and
150 management such as fertilization, tillage, bamboo shoots harvest or thinning. The physical
151 and chemical properties of soil ~~were are first delineatedpresented~~ in Table 1.

152 **Table caption**

153 Table 1 General information of the experimental *P. edulis* stands (mean±SD, n=9)

Factors	Stand 1		Stand 2		Stand 3	
	CK	TE	CK	TE	CK	TE
Altitude /m	136	136	141	141	146	146
Slope / °	15	15	20	20	22	22
Slope aspect	S	S	S	S	S	S
Soil depth /cm	60	60	60	60	60	60
SOC /g·kg ⁻¹	34.37±9.06	36.11±7.03	36.74±8.04	39.78±7.39	37.82±8.21	37.42±9.64

TN/g·kg ⁻¹	2.72±0.79	2.34±0.27	2.72±0.48	2.91±0.52	2.56±0.29	2.52±0.41
SAP / mg·kg ⁻¹	4.25±0.93	4.64±0.81	5.50±1.03	5.94±1.23	6.48±1.09	6.45±2.04
DBH /cm	13.42±2.17	14.72±1.55	14.44±2.14	14.30±1.93	12.99±2.53	14.60±1.26
Height / m	17.28±0.90	16.32±2.28	16.97±1.50	15.97±2.04	15.80±2.41	16.64±0.86
Density/ n·ha ⁻¹	3800	3600	3400	3000	3250	2800

Note: TN: Total nitrogen; SAP: Soil available phosphorus; DBH: Diameter at breast height; CK: Control treatment; T: Throughfall exclusion treatment.

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2.2 The design of throughfall exclusion experiment

In July 2014, three *P. edulis* stands with similar sites, altitude and growth conditions were selected as the experimental plots. To guarantee the scientific rigor and precision of the experiment, two plots, each measuring 10 m×10 m (excluding boundary effect), were designated for the control (CK) and throughfall exclusion (T) treatments, with a completely random allocation. Among them, each stand included CK and T treatment ~~s~~ were with three repetitions in three stands.

The PVC waterproof plates were systematically placed at a height of 1.5 m above the experimental plots to mitigate throughfall (exclusion about 70%-80% of the rainfall), supported by frameworks constructed from galvanized steel pipes with an area of 11 m×11 m. (Ge et al., 2024). The PVC material had ~~good~~ excellent light transmittance, ensuring that the light conditions in the throughfall exclusion treatments were as consistent as possible with the counterpart. At the same time, to prevent the horizontal transport of water from the surrounding soil to the throughfall exclusion treatments plots, trenches (about 50 cm deep and 20 cm wide) were dug in all around of throughfall exclusion plots, cut off the bamboo whip connected to the throughfall exclusion plots. In the trench, PVC waterproof ~~plates~~ panels

were ~~buried-put in inside the trenches~~ to further cut off ~~the external the entry~~ water from outside plots. Since August 2014, ~~these samples have officially entered the experimental stage of rain interception. Litter-litter~~ from the exclusion shelters were gathered ~~about~~ bi-weekly ~~on sunny days~~ and ~~then returned~~ allocated to the ~~respective plots~~ corresponding sample plots, ~~thus mitigating the effects of variability in litter input after weighing to minimize nutrient input interference.~~

2.3 Soil sampling and analysis

Soil samplings were collected in August 2022 with 0–10 cm and 10–20 cm soil depth from all 6 plots. Each sample was collected ~~using a soil auger with a diameter of 5 cm along an S-shaped path by-with~~ 5-point sampling ~~and~~ mixed into one sample ~~with-at~~ the same soil layer. The fresh soil samples after 2 mm soil sieve were divided into two parts, one was stored in a refrigerator (–20°C) with soil β -glucosidase (BG), N-acetyl aminoglycosidase (NAG), leucine aminopeptidase (LAP), microbial carbon (MBC) measurement; ~~another one~~ was put in laboratory naturally ~~ly with air-air-drying dried~~ to ~~screen-measure~~ soil organic carbon (SOC), and ~~total~~ soil ~~total~~ nitrogen (TN), ~~soil total phosphorus (TP)~~, etc. Soil ~~air-dried~~ samples were ~~promptly returned to the laboratory, where they were~~ sifted through 2-mm sieve and ~~0.15 mm sieve subsequently preserved at 4°C or dried in natural condition forbefore~~ future analysis.

2.3.1 Soil properties measurement

Moisture content was determined gravimetrically by utilizing samples dried in an oven for 48 h at 105°C. SOC and TN were evaluated utilizing a soil CN elemental analyzer (Elementar

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195 Vario MAX, Germany). The concentrations of dissolved organic carbon (DOC) and dissolved
196 organic nitrogen (DON) within the soil were quantified employing a TOC analyzer
197 (Shimadzu, Japan) alongside a continuous flow analytic system (Skalar, Netherlands),
198 maintaining the ratio of soil:water as 1:4 (Xu et al., 2022). Mineral N levels were ascertained
199 through extraction with 2 M KCl solution, utilizing a continuous flow analytical system
200 (Netherlands). Soil microbial biomass C (MBC) and microbial biomass N (MBN) were
201 quantified from freshly collected soil samples through the chloroform fumigation extraction
202 technique utilizing a 0.5 M K₂SO₄ solution (Vance et al., 1987). The extractable C and N
203 were assessed via a TOC analyzer (Shimadzu, Japan) and continuous flow analytical system
204 (Breda, Netherlands). The MBC and MBN were calculated as the difference in C and N
205 between fumigated and non-fumigated samples and divided by 0.45 and 0.54 (Vance et al.,
206 1987).

208 2.3.2 Soil fractions separation

209 The measurement of SOC fraction~~sation~~ was according to Xu et al. (2022) and Degryze et al.
210 (2004). The measurement of easily oxidizable organic C (EOC) was using KMnO₄ oxidation
211 method, recalcitrant organic C (ROC) was assessed using the acid hydrolysis K₂Cr₂O₇
212 oxidation method. A 60 g sample, air-dried and measuring less than <2 mm, was introduced
213 into 100 mL of a 5% sodium hexametaphosphate solution and agitated for 15 h. Following
214 this, the resulting soil suspension was transferred into a sieve with an aperture of 0.053 mm,
215 the material retained on the sieve (particles larger than 53 µm) was utilized for the assessment
216 of POC quality, while the fractions passed through the sieve (particles smaller than 53 µm)

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was allocated for the evaluation of MAOC quality. The upper and lower sections of the sieve were gathered separately and placed in a thermostatic oven set at 65°C for drying, after which their respective masses were recorded, and then the total soil mass percentage was calculated. Subsequently, the desiccated soil in the beaker was collected and pulverized through a 0.15 mm sieve, with the organic C content determined utilizing the external heating method involving potassium dichromate-concentrated sulfuric acid.

223

2.3.3 Soil enzyme activities measurement

Four soil enzyme activities were assessed in the decomposition of relatively labile C compounds (hydrolytic enzymes such as β -glucosidase, BG), and more resistant C compounds (oxidative enzymes including polyphenol oxidase: ~~POX~~PPO, ~~and~~ peroxidase: ~~PER~~POX, cellobiohydrolase: CBH), following the methodologies outlined by German (2011) and Saiya-Cork et al. (2002). In summary, 100 μ M methylumbelliferone (MUB)-labeled substrates of β -D-glucopyranoside and β -D-cellobioside were utilized for BG and CBH, respectively, while a 25 mM 3, 4-dihydroxyphenylalanine (DOPA) substrate was employed for oxidative enzymes. For each soil sample, 2 g of freshly collected soil were measured and subsequently immersed in 2 L of 50 mM sodium acetate buffer solution at a pH of 5. For the hydrolytic enzymes (BG), a volume of 200 μ l sample suspension and 50 μ l of the corresponding enzyme substrates were dispensed into wells of the substrate plate, followed by the addition of suitable standards. In the case of PPO and POX~~and~~ PER, each assay well was filled with 50 μ l of 25 mM L-DOPA complemented by 200 μ l sample suspension. The fluorescence of hydrolytic enzymes was measured using 365 nm excitation and 450 nm for

239 emission with a microplate reader (BMG LABTECH GmbH, Germany). The activities of
240 hydrolytic and oxidative enzyme were quantified as nmol·g⁻¹soil·h⁻¹.

241 The enzymatic activities of β-1,4-N-acetyl-glucosaminidase (NAG) and leucine
242 aminopeptidase (LAP) were evaluated utilizing microplate-based fluorometric methodologies
243 (Sinsabaugh et al., 1997). BG, NAG, and LAP possessed the ability to extract assimilable
244 nutrients from fundamental organic sources of C (e.g., β-linked glucans) and N (e.g., protein
245 and amino polysaccharides) (Sinsabaugh et al., 2013). The microplates were analyzed
246 through an automated fluorometer (Winooski, VT), employing an excitation wavelength of
247 365 nm and an emission wavelength of 450 nm (Saiya-Cork et al., 2002).

248

249 2.3.4 CUE and CA estimation

250 We employed soil enzyme activity, readily organic matter, and the C:N ratio of microbial
251 biomass to determine the CUE based on stoichiometric modelling (Geyer et al., 2019;
252 Sinsabaugh et al., 2016). Labile organic matter was assessed through the measurement of
253 DOC and N extracted from non-fumigated samples (Geyer et al., 2019). The CUE was
254 derived from stoichiometric models based on the growth and respiration of bacteria[†] and
255 fungal (Sinsabaugh et al., 2016). We determined microbial efficiency in utilizing C and N
256 through the lens of ecological stoichiometry. The method was described as follows:

$$257 \quad CUE = CUE_{max} \left[S_{C:N} / (S_{C:N} + K_N) \right]$$

258 Where S_{C:N} indicates the enzyme activity allocation offset the difference between the
259 existing available resource element composition (DOC/DN ratio) and the microbial biomass
260 composition (MBC/MBN ratio). The half-saturation constant K_N was established at 0.5. The

maximum ~~efficiency of~~ carbon utilization ~~efficiency denoted generally refers to the upper~~
~~limit of pinnae of~~ C that could be ~~harnessed-utilized for by~~ microbial proliferation, ~~which is~~
~~determined to beset at~~ 0.6 ~~in accordance with~~ based on the thermodynamic constraints. The
ratio of the C: N enzyme (i. e. EEAC: N) activity was calculated using BG / (NAG + LAP).
L_{C: N} is the carbon to nitrogen ratio of unstable organic matter.

Carbon pool activity (CA, %) was estimated according to Yuan et al. (2023):

CA=100%×sample active organic carbon content (EOC)/inert organic carbon content

Within the formula, the inert organic carbon is defined as the residual value obtained by
subtracting active organic carbon from the total soil organic carbon content pool.

2.4 Statistical analysis

All statistical evaluations were performed utilizing SPSS 20 or Origin version 12.0. Normal
distribution of data and homogeneity of variance were checked using Shapiro-Wilk and
Levene's tests, respectively. ~~One-way ANOVA was employed to examine the influence of soil~~
~~depth and drought treatments on soil indicators.~~ To evaluate the effect of a singular variable,
one-way ANOVA was employed for the data that followed a normal distribution, while the
Kruskal–Wallis tests was utilized for those that did not conform to normally. Two-way
ANOVA was employed to examine the interaction influence of soil depth and drought
treatments on soil indicators and enzyme activities. To investigate the impact of
environmental factors on microbial-related parameters, ~~Pearson and Spearman~~
~~correlations~~ canonical correspondence analysis (CCA) ~~were was~~ used for ~~data that followed a~~
~~ascertaining the relationships between SOC fraction and soil enzyme activities normal~~
~~distribution and those that deviated from it, respectively.~~ Differences and correlations

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considered at a significant level of $p < 0.05$. Within the structural equation models, the acceptable fit was established when the Chi-square p-value exceeded 0.05, Chi-square-to-degrees-of freedom ratio remained below 5, RMSEA fell under 0.08, and NFI surpassed 0.90 (Kline et al., 2011).

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3. Results

3.1 Effect of the throughfall exclusion on SOC fractions

Throughfall exclusion significantly reduced SOC, POC, DOC and ROC both for two soil layers ($p < 0.05$), but did not affect MAOC and EOC at 10–20 cm soil layer ($p > 0.05$) (Fig. 1).

SOC and soil carbon fractions varied significantly across soil layers (Fig. 1). Compared to the control, EOC and MBC in throughfall exclusion treatments were significantly reduced by 53.5% and 61.6% at the 0–10 cm soil layer, respectively, but they had no significant change at the 10–20 cm soil layer. In vertical direction, SOC, MAOC, EOC, and ROC content in control treatment decreased by 21.8%, 23.7%, 26.7% and 51.1% with depth increased ($p < 0.05$), respectively. In vertical direction, SOC, MAOC, EOC, and ROC in throughfall exclusion treatment decreased by 18.2%, 25.1%, 21.3% and 34.1% with soil depth increased ($p < 0.05$), respectively.

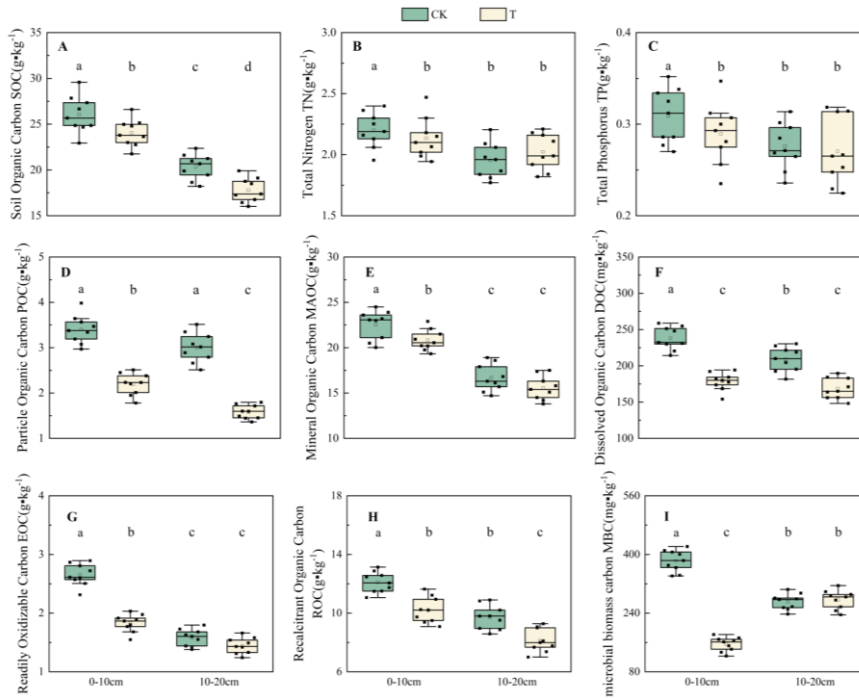


Fig. 1 Effect of throughfall exclusion on soil organic carbon fractions. Different lowercase letters indicate significant differences across treatments ($p < 0.05$).

3.2 Effect of throughfall exclusion on the proportion of POC and MAOC

The throughfall exclusion treatments had a significant impact on the proportion of POC and MAOC in SOC for both soil layers ($p < 0.05$) (Fig.2 and Table S1). Throughfall exclusion treatments, in contrast to CK, led to a 4.0% reduction in POC, which in turn caused a significant increase of MAOC within SOC. Specifically, the POC/SOC ratio diminished by 4.1% in the 0–10 cm soil layers and by 6.3% in the 10–20 cm soil layer. The vertical distribution of POC/SOC exhibited a slight increase of 2.6% with depth in the control

treatments ($p<0.05$), while throughfall exclusion treatments showed a negligible effect of merely 0.4%. ~~The one-way ANOVA revealed that~~ The throughfall exclusion treatment had a significant impact on the interaction of the soil depth and the proportion of POC and MAOC in SOC ($p<0.01$) (Table S1), whereas the soil depth remained unaffected.

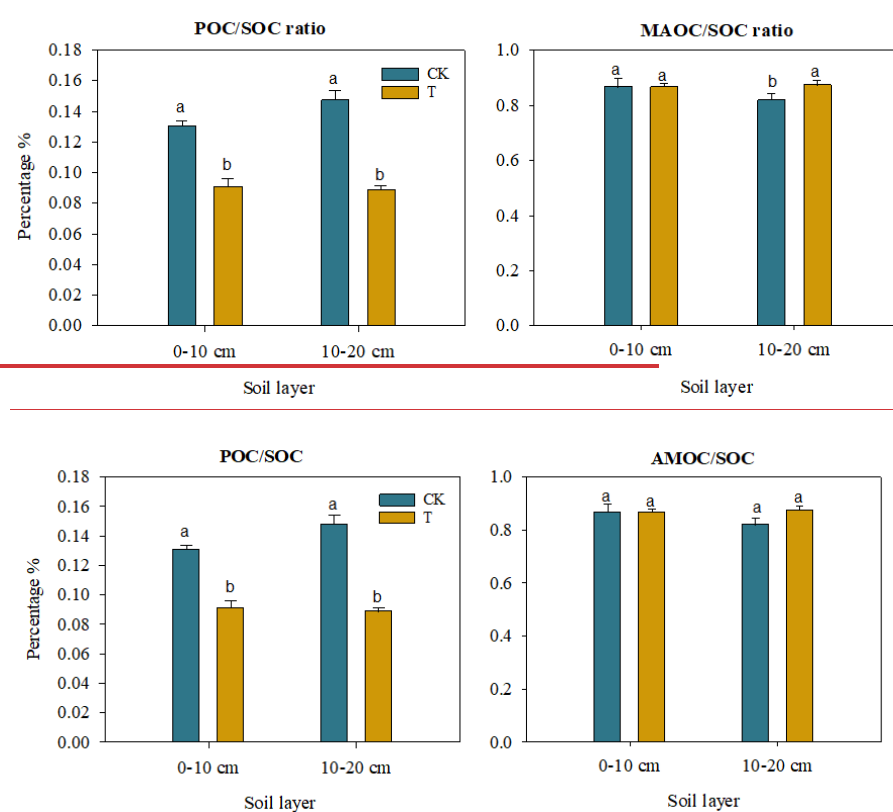


Fig. 2 Effect of throughfall exclusion on the proportion of POC and MAOC in SOC.

Note: POC: Soil particulate organic carbon; MAOC: Mineral-associated organic carbon;

SOC: Soil organic carbon. Different lowercase letters indicate significant differences across

treatments ($p<0.05$).

3.3 Effect of throughfall exclusion on soil enzyme activities and CUE

Compared with the control, PPO activities in throughfall exclusion treatments were significantly reduced by 30.1% and 27.9% ~~in-at~~ the two soil layers, respectively (Fig.3). The activities of BG and CBH in the 10–20 cm soil layer decreased by 34.6% and 38.1%, respectively, whereas no significant differences were detected in the 0–10 cm soil layer ~~for~~ BG and NAG. On the contrary, throughfall exclusion treatments significantly increased the activities of ~~NAG-LAP~~ and POX by 14.9% and 29.4% in 0–10 cm soil layers, ~~NAG and~~ POX by 18.3% and 29.1% in 10–20 cm soil layers ($p<0.05$), respectively. Additionally, the activities of PPO exhibited a notable decline ($p<0.05$) as the increase of soil depth, whereas the activities of CBH and NAG remained no significant change with the increase of soil ~~deep~~ depth (Fig.3).

Throughfall exclusion treatments significantly decreased carbon pool activity (CA) by 31.0% at 0–10 cm (Fig.4), however, no significant change was observed at 10–20 cm (Fig.4a). Conversely, throughfall exclusion treatments significantly enhanced microbial CUE by 9.1% at 0–10 cm ($p<0.05$), ~~and~~ by 2.6% at 10–20 cm, ~~and affected the interaction of~~ drought treatment and soil layer ($p<0.05$) (Fig.4 and Table S1).

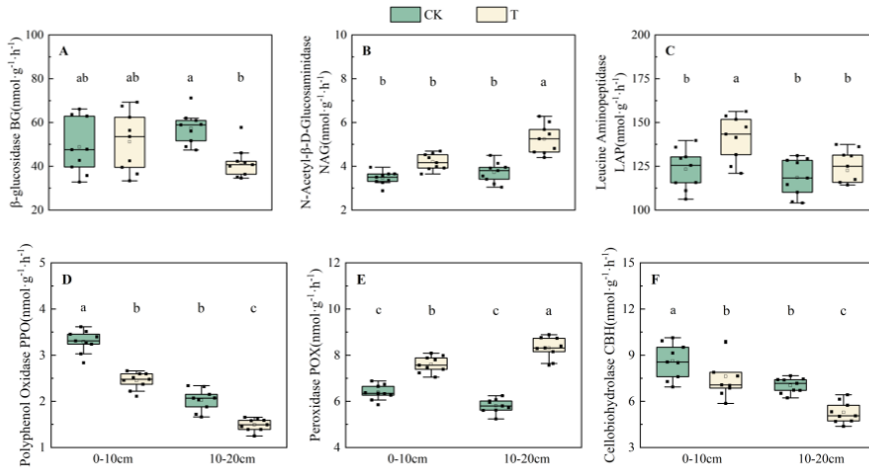


Fig.3 Effect of throughfall exclusion on soil enzyme activity at 0–20 cm soil layer. Different lowercase letters indicate significant differences across treatments ($p < 0.05$).

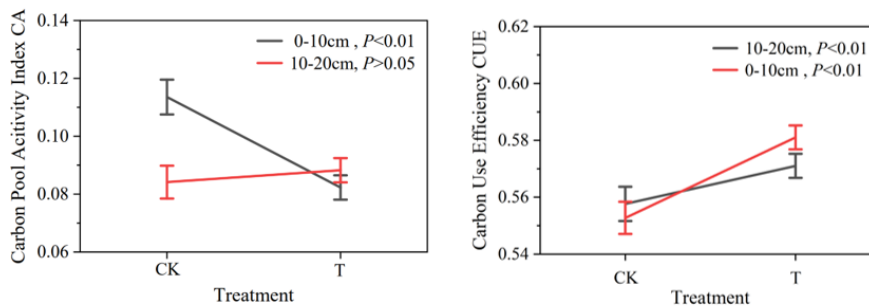
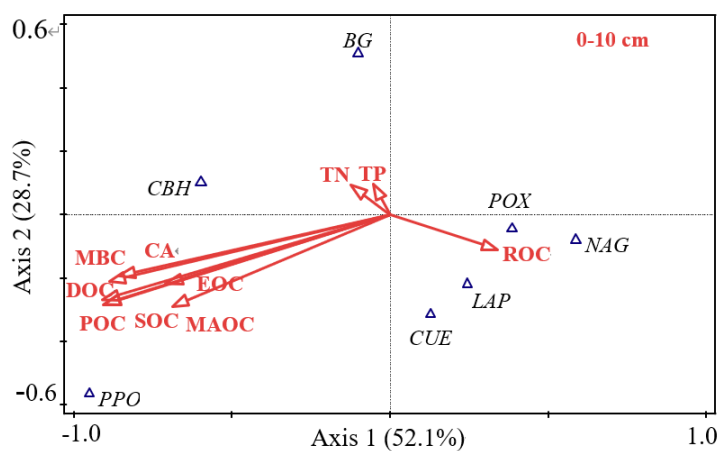


Fig.4 Effect of throughfall exclusion on carbon pool activity index (CA) and soil microbial carbon use efficiency (CUE) across 0–20 cm soil layer.

3.4 Effect of throughfall exclusion on the relationships between CUE and SOC fractions

CUE was significantly negatively correlated with SOC fractions POC and DOC across both

two soil layers (Fig.5 and Fig. 6). CCA showed that the first and second components of the principal coordinate accounted for the total CUE variance of 52.1% and 28.7%, 71.2% and 7.3% across both two soil layers. CUE significantly affected by POC, DOC, EOC, MBC, MBN in 0–10 cm soil layer ($p<0.05$), CUE extremely significantly affected by POC, DOC, MBN, BG in 10–20 cm soil layer ($p<0.01$) and significantly affected by SOC, NAG and PPO ($p<0.05$). POC showed a highly significant positive correlation with CBH, PPO as well as soil nutrients TP (Fig. 5), and a significant negative correlation with LAP, NAG (0–10 cm) and POX (10–20 cm). There was significantly difference relationships between CUE and POC across two soil layers, as well as soil nutrients and soil enzyme (Fig.6).



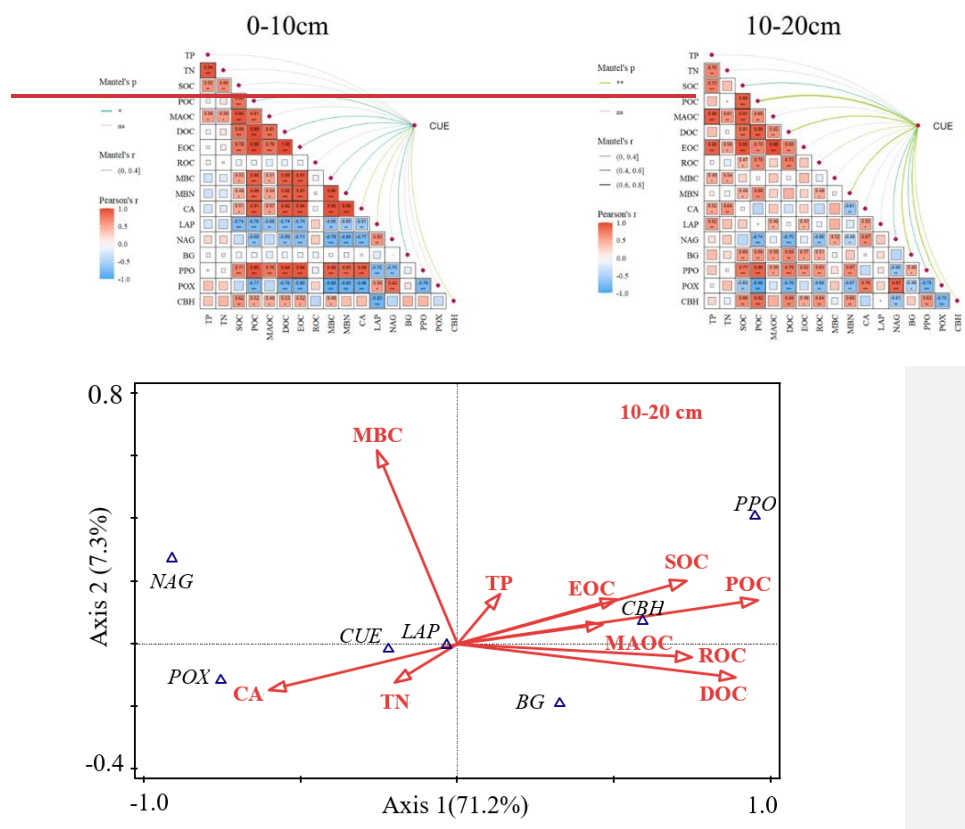


Fig.5 ~~Correlation~~ Canonical correspondence analysis (CCA) between CUE and soil chemical properties as well as soil enzymes across two soil layers. CUE: ~~Soil-soil~~ microbial carbon utilization efficiency; CA: ~~Carbon-carbon~~ Pool Activity Index; SOC: ~~Soil-soil~~ organic carbon-~~(SOC)~~; ~~TN~~: soil total nitrogen; TP: soil total phosphorus; POC: soil particulate organic carbon; MAOC: mineral-associated organic carbon; DOC: soluble organic carbon; ROC: easily oxidized organic carbon; EOC: MBC: microbial carbon; PPO: polyphenol oxidase; PER: peroxidase CBH: cellobiohydrolase; BG: β -glucosidase; NAG: N-acetyl aminoglycosidase; LAP: leucine aminopeptidase.

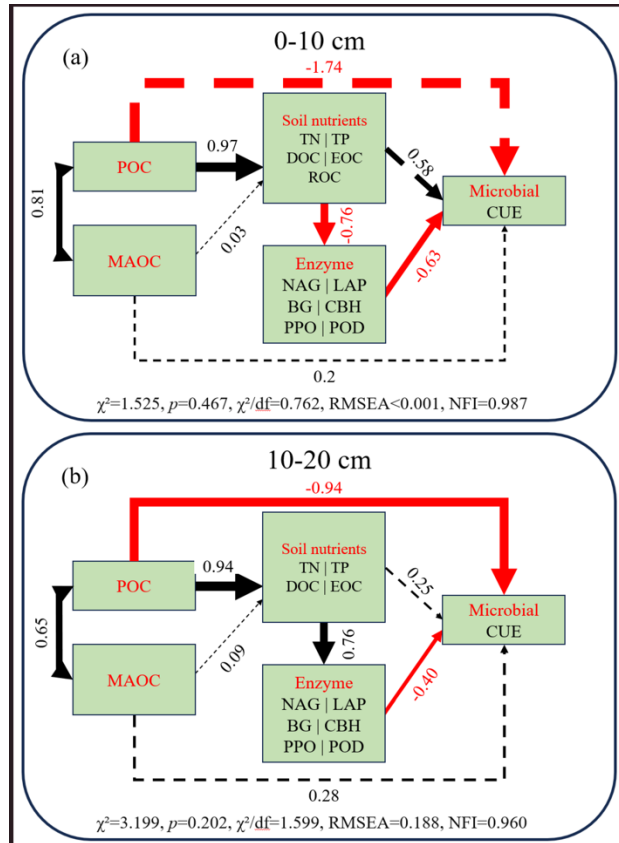


Fig. 6 The structural equation model (SEM) depicts the direct and indirect effects of CUE, soil microorganisms and soil nutrients under two treatments at 0–10 cm and 10–20 cm.

Notes: Principal component analysis was conducted for soil enzyme data from DOC, EOC, ROC, TN, TP; Principal component analysis was conducted for soil enzyme data from NAG, LAP, NG, CBH, PPO, POD. DOC: soluble organic carbon, EOC: readily oxidizable organic carbon, ROC: recalcitrant organic carbon, TN: soil total nitrogen, TP: soil total phosphorus. PPO: polyphenol oxidase; PER: peroxidase CBH: cellobiohydrolase; BG: β -glucosidase; NAG: N-acetyl aminoglycosidase; LAP: leucine aminopeptidase. The black arrows signify a

positive effect, while the red lines denote a negative effect. The thickness of the arrow is directly proportional to the magnitude of the effect.

4. Discussion

4.1 The influence of throughfall exclusion on soil POC and MAOC

These findings indicated that drought resulted in a decline in ~~soil organic carbon~~ SOC reserves, and the ~~volatile-active~~ carbon pools experienced a more pronounced impact compared with the ~~stable~~ inert carbon pools (Fig.1). The proportion increase of stable soil carbon pools may reflect an adaptive adjustment to drought conditions. In this context, soil microorganisms were inclined to utilize more resilient carbon sources to maintain their biological functions (Jones et al., 2019). ~~Analyzing-Disregarding the POC and MAOC reservoirs,~~ the response of SOC to climate change ~~risks accuracy, as the responses of topsoil and subsoil carbon pools to diminish throughfall exhibited significant differences, without taking account the POC and MAOC pools, may be misleading.~~ In this study, eight years of throughfall exclusion significantly decreased soil POC and had a limited impact on MAOC (Fig.2), indicating that ~~as the percentage of MAOC in SOC escalated, the proportion of stable SOC components increased~~ MAOC accrual in subsoil depended on microbial maintenance demands and more chemically complex substrate inputs (Zhang et al., 2026). The significant increase of ~~stable~~ inert soil carbon pools under drought conditions may reflect an adaptive adjustment response, while soil microorganisms ~~tent-tended~~ to use more stable carbon sources to maintain their metabolic activities (Jones et al., 2017). ~~If the POC and MAOC pools were omitted from consideration, examining the response of SOC to climate change in isolation could be misleading, as the responses of both surface and subsurface carbon pools to~~

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~~diminish throughfall exhibited significant differences.~~

The distinctions in SOC components between topsoil and subsoil may be intricately linked to (i) the diverse environmental and microbial properties inherent to different soil layers and (ii) the diminished nitrogen availability in the subsoil under drought conditions, in contrast to the topsoil. Subsoil microorganisms were recognized for their susceptibility to deficiencies in accessible carbon or energy (Jones et al., 2018), exhibiting a more sensitive to fluctuations in ~~labile-active~~ carbon supply when compared to topsoil microorganisms (Fontaine et al., 2007; Jones et al., 2019). According to microbial economic theory, when ~~labile-active~~ carbon is available, microorganisms can minimize their metabolic energy expenditure and reduce extracellular enzyme production (Bradford, 2013). Thus, increased root deposition and unstable carbon supply may inhibit the microbial production of hydrolytic enzymes in subsoil (Wei et al., 2019). The elevated root density of moso bamboo may exacerbate the nutrient competition between the plant and microbes for nutrients located in the subsoil (Hill & Jones, 2019; Liu et al., 2018). This may further limit the metabolism of subsoil microorganisms and the synthesis of extracellular enzymes (Schimel & Weintraub, 2003), and the drought stress caused by the long-term throughfall exclusion treatment (Burns et al., 2013; Mcdaniel et al, 2013; Sardans & Penuelas, 2005).

~~As-In soil vertical directiondepth increased, there was a subtle-significant reduction in the soil POCEOC, ROC and MAOC, which could be attributed to the implementation of the throughfall exclusion treatments, which involved the installation of shelters beneath the forest canopythe lower litter input and decomposition rate with less nutrients migrating downward – and microbial depolymerization by lower SOC decomposition rates in the topsoil (Pallandt et~~

424 al., 2025). The decrease of SOC in topsoil was primarily driven by reduction in POC, ROC,
425 EOC, DOC, MAOC (Fig.1 and Fig. 6), which resulted in smaller total SOC losses from the
426 topsoil than the subsoil with less drought sensitive for MAOC (Sun et al., 2023). While these
427 structures diminished the amount of rainfall reaching the soil, they permitted both the canopy
428 and trunk of the *P. edulis* forest to continue absorbing precipitation. Furthermore, throughfall
429 exclusion treatments in this study were relatively moderate compared to methods employed
430 in previous studies. Forest ecosystems were resilient to throughfall exclusion, therefore,
431 detecting significant alterations in POC content, In addition, the decline of POC content at
432 both soil layers under drought conditions, as highlighted by Canarini et al. (2017), could be
433 attributed to less litter input, loss of aggregate stabilization caused by mycorrhizal activity
434 and decouple the relationship of POC with MBC (Huang et al., 2026). Therefore, long-term
435 drought may favor the stabilization of MAOC on subsoil instead of topsoil, protecting it from
436 microbial depolymerization with higher microbial CUE on subtropical plantation.

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438 4.2 Effect throughfall exclusion on soil enzyme and microbial CUE

439 Soil enzymes play an indispensable role in nutrient mineralization, functioning as a distinct
440 indicator for forecasting the available nutrient of plants (Aon and Colaneri, 2001; Baum et
441 al., 2003). In this study, soil enzyme activity exhibited different sensitivity to drought
442 conditions, throughfall exclusion significantly reduced PPO activities (27.9% to 68.4%)
443 ($p < 0.05$), CBH activity activities (16.2% to 38.6%) ($p < 0.05$) and POX enzyme activity
444 activities (18.2% to 51.0%) ($p < 0.05$), respectively. These changes indicated soil moisture
445 played a critical role in regulating microbial enzyme activity in subtropical forest soils. In the

446 long run, alterations in the activity of soil enzymes involved in carbon and nitrogen cycles
447 ~~will~~would affect soil available nutrients, ~~thereby affecting and~~ the nutrient supply to plants
448 (Roldán et al., 2025). In this study, drought reduced the activity of carbon-related enzymes
449 (BG, CBH) and increased the activity of nitrogen-related enzymes (NAG, LAP), which could
450 be explained by the limiting effect of nitrogen in subtropical forest soils, as reported in
451 previous studies (Mayo et al., 1994). ~~The limitation of nitrogen implied a higher sensitivity to~~
452 ~~throughfall exclusion conditions.~~ The most pronounced impact of drought in our study was
453 observed in oxidases (POX, PPO), which were produced by microorganisms ~~that function as~~
454 essential decomposers ~~of in the~~ substrates oxidation ~~breakdown of substrate, such as like~~
455 lignin (Tian et al., 2025). This result indicated microorganisms played a crucial role in the
456 decomposition of organic carbon in soil, with POX involved in humus transformation and
457 PPO promoting lignin and humus degradation (Wang et al., 2008).

458 In this study, drought reduced ~~the activity of polyphenol oxidase~~ PPO activity; and
459 slowed organic matter decomposition, ~~and concomitant with the accumulation of SOC~~
460 accumulation, indicating that drought may become ~~the a~~ limiting factor for microbial
461 community nutrients availability, thereby affecting the growth of related microorganisms and
462 reducing MBC content (Tian et al., 2014). Hydrolytic enzymes, exemplified by BG, can
463 facilitate the breakdown of macroglycemic sugars and active organic matter, transforming
464 them into nutrients available to both plants and microorganisms (Grandy et al., 2007). In this
465 study, we found that drought improved the activity of nitrogen-related hydrolase and reduced
466 the DOC content, enhanced hydrolase activity promoted the decomposition of active organic
467 matter, expediting the microbial utilization of DOC (Fan et al., 2015). The activity of the six

enzymes decreased with soil depth, consistent with [Chen \(2003\)](#), due to ground litter and better soil ventilation leading to higher soil enzyme activity in the 0-10 cm layer compared to the 10-20 cm lower.

Drought altered soil carbon and nitrogen cycling and reduced the nutrient utilization efficiency of soil microorganisms ([Guo et al., 2020](#)). In this study, drought improved soil microbial CUE, but significantly decreased CA, suggesting CUE was negatively associated with some enzyme activities under drought conditions, which was inconsistent with our hypotheses. It was possible that the microbial community under drought conditions was carbon resource-limited and thus secreted less extracellular enzymes with higher CUE to increase microbial physiological investment with higher stress tolerance ([Ullah et al., 2021](#); [Jones et al., 2025](#)). This secretion accelerated the decomposition, absorption and utilization of organic carbon, thereby increasing CUE and enhancing microbial carbon sequestration by microbial strategy shifts ([Huang et al., 2026](#)). However, CA decreased with SOC, DOC, POC and MBC, indicating a threat posed by drought to soil carbon sequestration. The intensification of nitrogen limitation and its effects on soil enzyme activity most likely underlay the changes in CUE under drought conditions ([Allison & Vitousek, 2005](#); [Bicharanloo et al., 2020](#)). This conclusion was supported by the strong positive correlation between CUE and leucine aminopeptidase activity in soil. ~~Furthermore, although CUE increased as LAP rose in the subsoil, NAG did not exhibit similar change. Since since~~ microbial residues, ~~including aminoglycans, were with~~ nitrogen-rich organic substrates, ~~they~~ played a crucial role in ~~soil nitrogen cycling~~ maintaining microbial community-level efficiency by shifting microbial strategies even under drought and nitrogen-limiting

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conditions (Heuck et al., 2015; Cui et al., 2020; Huang et al., 2026), microorganisms may
recover or decompose them, especially under nitrogen limiting conditions (Cui et al., 2020).
In addition, the similar change of CUE across two soil layers in this study were both
dependent on the decreased substrate availability, POC, and the change of microbial resource
utilization strategies and resource acquisition with group drought resistance for moso bamboo
(Ge et al., 2024; Huang et al., 2026).

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4.3 The influence of microbial CUE on soil carbon fractions

POC is a functional soil component that contributes to the stabilization of SOC (Witzgall et al., 2021) and has weaker physical and chemical protection than MAOC, making it more susceptible to microbial utilization and mineralization (Tang et al., 2023). Higher CUE could potentially expedite the breakdown of the POC (Averill et al., 2018). In this study, soil microbial CUE demonstrated a significant ~~and positive~~negative correlation with SOC, DOC and POC at 10–20 cm (Fig. 5 and 6), indicated that CUE was responsible for the most alteration in both the quantity and composition of SOC (Shi et al., 2025). The study of Liu et al (2018) concluded that CUE mediated carbon loss via microbial respiration and strongly influenced the rate of SOC formation. In this study, the diminished accessibility of POC to microorganisms may foster an enhancement in CUE for survival (Fig. 6), elucidating the favorable correlation observed between CUE and POC in our findings (Fig. 5). Furthermore, the study by Stone et al (2023) showed that drought could reduce CUE by declining the NH_4^+ -N and NO_3^- -N, thereby decreasing nitrogen use efficiency and consequently reducing CUE. In this study, TN and MBC both decreased (Fig. 1), because lower microbial CUE resulted in

less accumulation of MBC and ~~microbial residues, thereby reducing the~~ MAOC repertoire. ~~Thus, changes in MAOC concentrations may result from alterations in~~for microbial N cycling in response to drought. These findings did not support our observation that drought decreased CUE and promoted MAOC reduction, but demonstrated the microbial CUE was affected by SOC fractions with substrate available C.

In addition, studies have shown that long-term drought reduced soil available N, which may cause a significant increase in soil C/N ratio, resulting in microorganisms experiencing N limitation with a decrease in microbial biomass (Chen et al., 2020). When soil microorganisms were relatively limited by a specific element, which were induced to synthesize the corresponding element acquisition enzymes (Wang et al., 2009). This response of enzymatic ~~response to drought also was contributed attributed~~ to the rapid improvement of LAP activity observed in our study (Fig. 3). However, Koyama et al. (2025) showed microbial CUE significantly decreased by the increase of C availability. Ullah et al. (2021) showed that drought caused small increases in CUE across season on grassland in Australia. Fuchslueger et al. (2019) showed microbial CUE decreased with temperature change independent of drought by substrate respiration. Therefore, drought may affect microbial CUE ~~differently~~ over different time scales, substrate quantity and quality change of C availability (Koyama et al., 2025) and temperature sensitivity (Fuchslueger et al., 2019).

~~There is a need to f~~urther ~~quantify quantification the effects~~ of drought on long-term C sequestration and the microbial mechanisms ~~underlying this process is needed. As our study lasted~~ The drought duration of our study was 9 ~~eight~~ years, ~~to better understand further~~ research should observe drought's how long-term impacts on SOC components ~~respond to~~

~~droughts of varying durations, further studies should observe the long-term effects of drought~~
over ~~different-varying~~ time scales and soil depth. The increase of CUE with SOC reduction
mainly depended on scenarios such as forest vegetation restoration and disrupted the
interactions of soil-microbe-minerals under ~~global-further drought change scenario~~ (Shi et al.,
2025; Zhou et al., 2026).

5. Conclusion

We found that throughfall exclusion significantly decreased SOC driven mainly by DOC,
EOC, ROC, POC and MAOC in surface soil layer and increased soil microbial CUE at both
soil layers. Furthermore, the proportion reduction of POC/SOC ratio under drought was
mainly due to the improvement of CUE. POC₁ ~~subjected to fewer being less shielded by~~ soil
aggregate protection mechanisms, exhibited was more-greater variable-variability under
drought, which reflected the drought adaptive adjustment of the soil carbon pools ~~under-~~
~~drought stress~~. Under drought conditions, changes in enzyme activity played a key role in
understanding how ~~the increase of elevated~~ CUE ~~leads-reshaped to changes in the mosaic of~~
soil carbon ~~components constituents~~. This change provides an important explanation for SOC
dynamics. ~~The results showed that soil- and the influence of~~ microbial CUE ~~primarily-~~
~~influenced on~~ –soil microbial biomass, which in turn affected SOC components. ~~These-~~
~~findings helped to better understand how throughfall exclusion impacts on SOC in P. edulis~~
plantations. Drought may have variable effects on CUE over different time periods and
substrate C quality. To gain a deeper understanding of this complex relationship, it is
imperative to assess the precise impacts of drought on long-term carbon sequestration

556 processes, along with the microbial mechanisms underpin these processes.

557

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563

564 **Declaration of interests**

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

567

568 **Availability of data and materials**

569 The data that support the findings of this study are available from the corresponding author
570 upon reasonable request.

571

572 Author Contributions:

573 Xiaogai Ge and Hongwen Yao conceived the ideas and designed the methodology; Xiaogai
574 Ge, Yilian Mao and Xupeng Xue collected the data; Yilian Mao and Xiaogai Ge analysed the
575 data; Yilian Mao and Xupeng Xue led the writing of the manuscript; Tida Ge and Benzhi
576 Zhou contributed critically to revising the drafts. All authors gave final approval for
577 publication.

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