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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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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 mechanisms of microbial CUE on soil carbon stability under drought conditions are 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 9.12% (p<0.05) and 2.56% 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, 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 drought indirectly regulates the storage and transformation of SOC by affecting microbial community structure and function, which would have a profound impact on the carbon cycle of forest ecosystems.

Keywords: Drought; Microbial CUE; SOC components; Soil enzyme activity; Moso bamboo;

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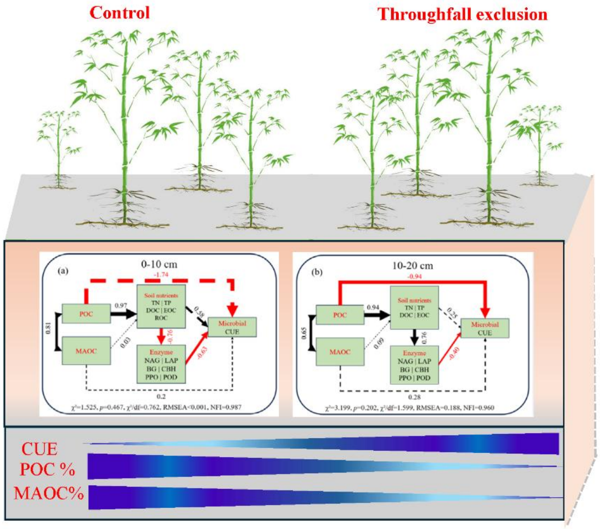

1. Introduction

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

The SOC represents a mixed pool of carbon, which varies with their turnover rates, chemical characteristics and stabilization mechanisms (Lavallee et al., 2020). Generally, SOC generally are divided into active organic carbon and inert organic carbon. Active 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% (Sun et al., 2020). This reduction leads to an increase in the accumulation of DOC in the topsoil by 30% to 60% (Deng et al., 2021; Brunn et al., 2023). Therefore, active organic carbon storage in different forests respond differently to drought intensity, and the differential mechanism could be clarified under drought.

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

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

Soil microbial carbon utilization efficiency (CUE) denotes to the fraction of carbon incorporated into microbial biomass relative to the overall carbon uptake by microorganisms (Li et al., 2021a). It reflects the carbon allocation between anabolism and catabolism processes in the soil microbial community and directly affects the soil carbon storage capacity (Sun et al., 2025). Moreover, microbial CUE may be an important parameter for determining SOC storage by controlling the proportion of SOC utilization (Geyer et al., 2016; Ullah et al., 2021). Specifically, previous studies have shown that drought may affect the activity of microbes and their CUE, which in turn affects the decomposition and accumulation of POC and MAOC (Duan et al., 2023). For example, higher CUE may accelerate the breakdown of POC, as the generation of microbial byproducts during this process facilitates the formation of MAOC, as shown by Guenet et al. (2021) and Chen et al. (2021). Further studies are needed to determine whether drought alters CUE and consequently affect soil carbon pools. Understanding how SOC fractions, particularly POC and MAOC, influence CUE could provide insights into the mechanisms through which ecosystems maintain their carbon balance during drought events. Moreover, the relationships between SOC fractions and CUE under drought is poorly understood. To address this gap, we examined the potential correlations among these variables, aiming to provide a more comprehensive perspective on how drought impacts soil carbon dynamics and plant productivity.

Phyllostachys edulis is a vital plantation in China, thriving abundantly across the subtropical regions, which is the preferred material for "replacing wood with bamboo" and "replacing plastic with bamboo" for its fast natural regeneration. In our study, a drought experiment lasting 9 years was conducted in *P. edulis* forest in southeastern China. We hypothesis that: (a) Throughfall exclusion reduced the soil microbial CUE with higher soil enzyme activities. (b) soil microbial CUE and soil carbon fractions had different responses to drought at soil vertical direction. The main objectives of this study are: (1) to evaluate the effects of throughfall exclusion on soil POC, MAOC and soil microbial CUE; and (2) to reveal how throughfall exclusion influences SOC components by changes in microbial CUE that mediates these impacts. This study helps to clarify the internal link between SOC components and CUE in *P. edulis* plantation under throughfall exclusion as identifying predictors of response to long-term drought, which would provide a reference for the optimization of carbon cycle models in terrestrial ecosystems under drought conditions (Li et al., 2021b).

2. Materials and methods

2.1 Study area

The study area locates in Huanggongwang Forest Park (119 56 '~120 02' E, 30 03 '~30 06' N), Hangzhou, Zhejiang Province, which is 10 km away from the city. It exhibits a characteristic subtropical humid monsoon climate, with an average annual temperature of 16.1℃, abundant rainfall and annual average rainfall of 1441.9 mm. The soil type in the forest area is slightly acidic red soil. The bamboo forests in experimental areas were planted in the 1960s, which have been used for special experimental areas without agricultural implementations and management such as fertilization, tillage, bamboo shoots harvest or thinning. The physical and chemical properties of soil were first delineated in Table 1.

Table caption

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

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, CK and T treatments were three repetitions. The PVC waterproof plates were systematically placed at a height of 1.5 m above the experimental plots to mitigate throughfall, supported by frameworks constructed from galvanized steel pipes with an area of 11 m×11 m. The PVC material had good 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 were buried to further cut off the entry water from outside plots. Since August 2014, these samples have officially entered the experimental stage of rain interception. Litter from the exclusion shelters were gathered bi-weekly and allocated to the respective plots, thus mitigating the effects of variability in litter input.

2.3 Soil sampling and analysis

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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 by 5-point sampling and mixed into one sample with 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℃) with soil β-glucosidase (BG), N-acetyl aminoglycosidase (NAG), leucine aminopeptidase (LAP), microbial carbon (MBC) measurement; one was put in laboratory natural with air drying to screen soil organic carbon (SOC), and total soil nitrogen (TN), etc. Soil samples were promptly returned to the laboratory, where they were sifted through 2-mm sieve and subsequently preserved at 4°C or dried in natural condition for 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 Vario MAX, Germany). The concentrations of dissolved organic carbon (DOC) and dissolved organic nitrogen (DON) within the soil were quantified employing a TOC analyzer (Shimadzu, Japan) alongside a continuous flow analytic system (Skalar, Netherlands), maintaining the ratio of soil:water as 1:4. Mineral N levels were ascertained through extraction with 2 M KCl solution, utilizing a continuous flow analytical system (Netherlands). Soil microbial biomass C (MBC) and microbial biomass N (MBN) were quantified from freshly collected soil samples through the chloroform fumigation extraction technique utilizing a 0.5 M K_2SO_4 solution (Vance et al., 1987). The extractable C and N were assessed via a TOC analyzer (Shimadzu, Japan) and continuous flow analytical system

(Breda, Netherlands). The MBC and MBN were calculated as the difference in C and N between fumigated and non-fumigated samples and divided by 0.45 and 0.54 (Vance et al., 1987).

2.3.2 Soil fractions separation

The measurement of SOC fractionation was according to Degryze et al. (2004). A 60 g sample, air-dried and measuring less than <2 mm, was introduced into 100 mL of a 5% sodium hexametaphosphate solution and agitated for 15 h. Following this, the resulting soil suspension was transferred into a sieve with an aperture of 0.053 mm, the material retained on the sieve (particles larger than 53 μm) was utilized for the assessment of POC quality, while the fractions pasted through the sieve (particles smaller than 53 μm) 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℃ 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.

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 phenol oxidase: POX, and peroxidase: PER),

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following the methodologies outlined by German (2011) and Saiya-Cork et al. (2002). In summary, 100 µM methylumbelliferone (MUB)-labeled substrates of α-D-glucopyranoside and β-D-glucopyranoside were utilized for AG and BG, 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 µl sample suspension and 50 µl of the corresponding enzyme substrates were dispensed into wells of the substrate plate, followed by the addition of suitable standards. In the case of POX and PER, each assay well was filled with 50 µl of 25 mM L-DOPA complemented by 200 µl sample suspension. The fluorescence of hydrolytic enzymes was measured using 365 nm excitation and 450 nm for emission with a microplate reader (BMG LABTECH GmbH, Germany). The activities of hydrolytic and oxidative enzyme were quantified as nmol·g^{-1}soil·h^{-1}.

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

2.3.4 CUE estimation

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

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

Where $S_{C:N}$ indicates the enzyme activity allocation offset the difference between the existing available resource element composition (DOC/DN ratio) and the microbial biomass composition (MBC/MBN ratio). The half-saturation constant K_N was established at 0.5. The maximum efficiency of carbon utilization denoted the pinnacle of C that could be harnessed for microbial proliferation, which is determined to be 0.6 in accordance with 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.

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. To investigate the impact of environmental factors on microbial-related parameters, Pearson and Spearman correlations were used for data that followed a normal distribution and those that deviated from it, respectively. Differences and correlations considered at a significant level of $p < 0.05$.

3. Results

3.1 Effect of the throughfall exclusion on SOC fractions

Throughfall exclusion significantly reduced SOC, POC, DOC and ROC (p<0.05), but did not affect MAOC (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%, and 34.1% with soil depth increased (p<0.05), respectively.

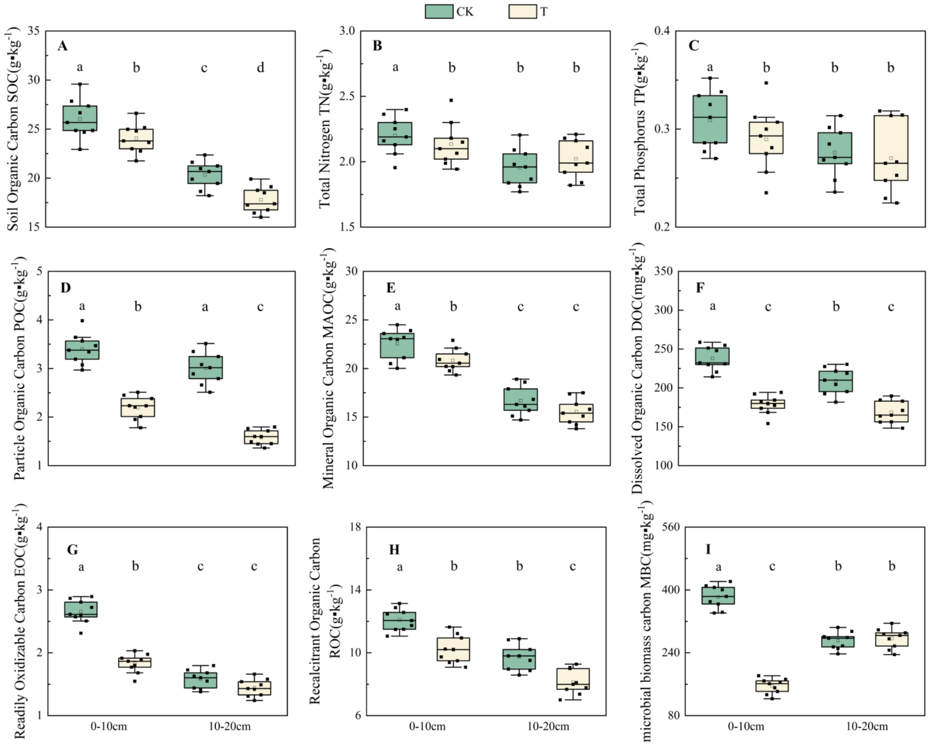

Fig. 1 Effect of throughfall exclusion on soil organic carbon fractions. Different lowercase letters indicate significant differences across treatments (p<0.05).

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 (p<0.05) (Fig.2). 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 proportion of POC and MAOC in SOC (p<0.01), whereas the soil depth remained unaffected.

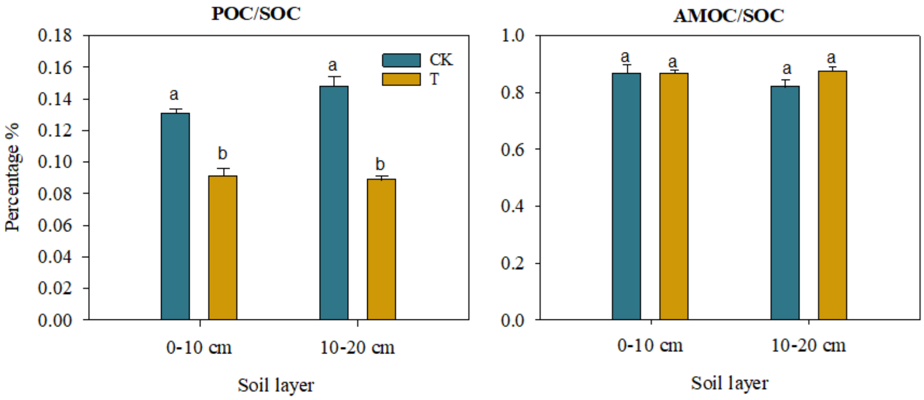

Fig. 2 Effect of throughfall exclusion on the proportion of POC and MAOC in SOC.

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 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. On the contrary, throughfall exclusion treatments significantly increased the activities of NAG and POX by 14.9% and 29.4% in 0-10 cm soil layers, 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 (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 (Fig.4).

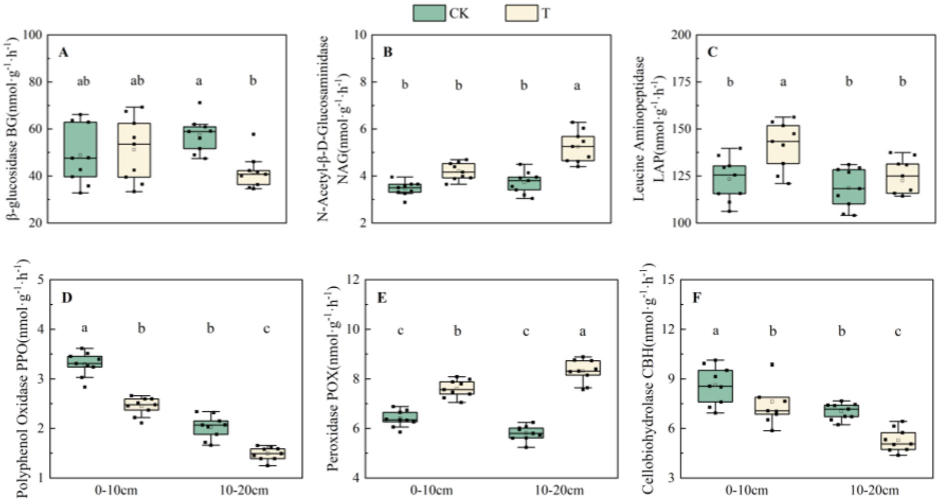

Fig.3 Effect of throughfall exclusion on soil enzyme activity at 0-20 cm soil layer. Different lowercase letters indicate significant differences across treatments (p<0.05).

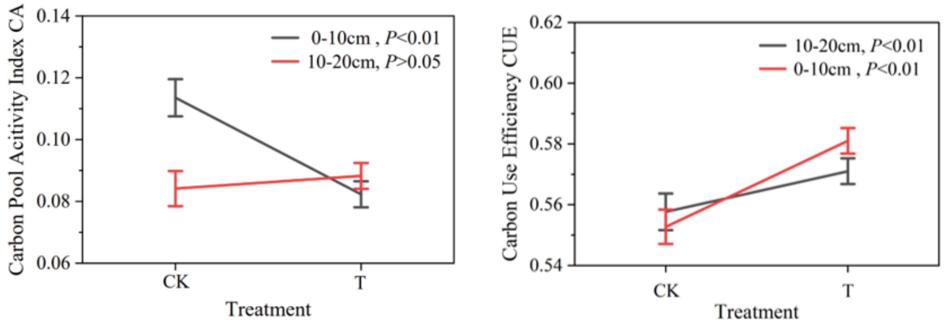

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Fig.4 Effect of throughfall exclusion on soil microbial CUE across 0-20 cm soil layer.

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

CUE was significantly correlated with POC and DOC across both two soil layers (Fig.5 and Fig. 6). 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 (Fig. 5), and a significant negative correlation with LAP (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).

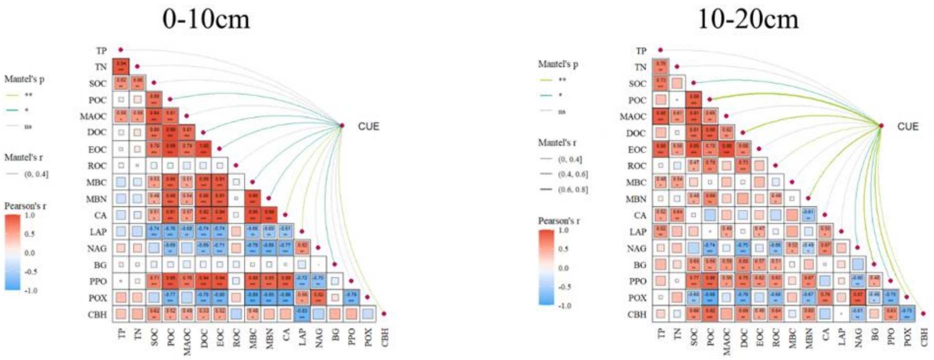

Fig.5 Correlation between CUE and soil chemical properties as well as soil enzymes across two soil layers. CUE: Soil microbial carbon utilization efficiency; CA: Carbon Pool Activity Index; SOC: Soil organic carbon (SOC); POC: soil particulate organic carbon; MAOC: mineral-associated organic carbon; 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.

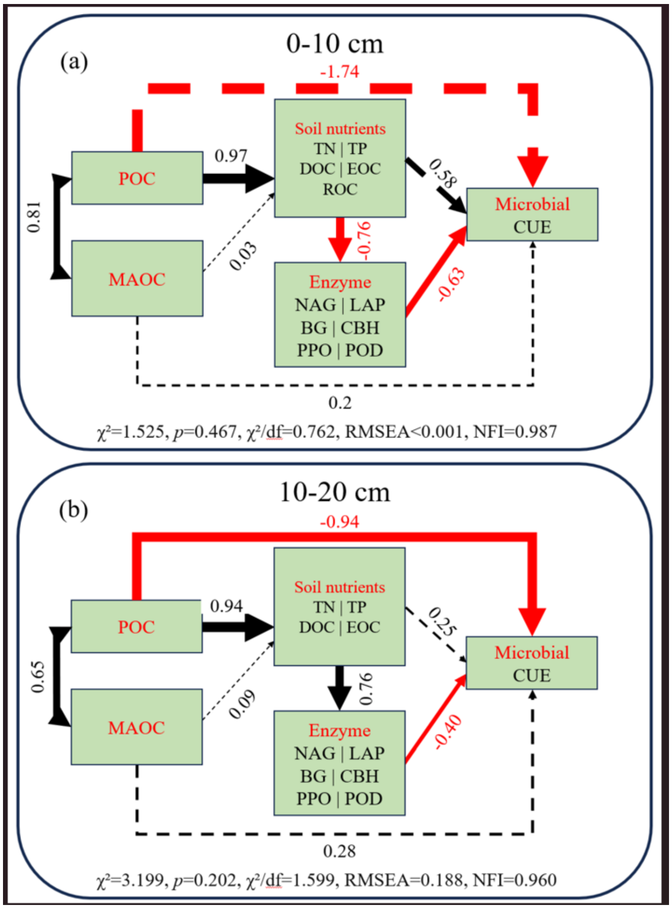

Fig. 6 The structural equation model (SEM) depicts the direct and indirect effects of CUE, soil microorganisms and soil nutrients under two treatments at 0-10 cm and 10-20 cm.

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: total nitrogen, TP: 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

4.1The influence of throughfall exclusion on soil POC and MAOC

These findings indicated that drought resulted in a decline in soil organic carbon reserves, and the volatile carbon pools experienced a more pronounced impact compared with the stable 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 the response of SOC to climate change, 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. The significant increase of stable soil carbon pools under drought conditions may reflect an adaptive adjustment response, while soil microorganisms tent 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 diminish throughfall exhibited significant differences.

The distinctions in SOC components between topsoil and subsoil may be intricately

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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 carbon supply when compared to topsoil microorganisms (Fontaine et al., 2007; Jones et al., 2019). According to microbial economic theory, when labile 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 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 throughfall exclusion treatment (Burns et al., 2013; Mcdaniel et al, 2013; Sardans & Penuelas, 2005).

As soil depth increased, there was a subtle reduction in the soil POC, which could be attributed to the implementation of the throughfall exclusion treatments, which involved the installation of shelters beneath the forest canopy. While these structures diminished the amount of rainfall reaching the soil, they permitted both the canopy and trunk of the *P. edulis* forest to continue absorbing precipitation. Furthermore, throughfall exclusion treatments in this study were relatively moderate compared to methods employed in previous studies. Forest ecosystems were resilient to throughfall exclusion, therefore, detecting significant alterations in POC content, as highlighted by Canarini et al. (2017).

4.2 Effect throughfall exclusion on soil enzyme and microbial CUE

Soil enzymes play an indispensable role in nutrient mineralization, functioning as a distinct indicator for forecasting the available nutrient of plants (Aon and Colaneri, 2001; Baum et al., 2003). In this study, soil enzyme activity exhibited different sensitivity to drought conditions, throughfall exclusion significantly reduced PPO activities (27.9% to 68.4%) (p<0.05), CBH activity (16.2% to 38.6%) (p<0.05) and POX enzyme activity (18.2% to 51.0%) (p<0.05), respectively. These changes indicated soil moisture played a critical role in regulating microbial enzyme activity in subtropical forest soils. In the long run, alterations in the activity of soil enzymes involved in carbon and nitrogen cycles will affect soil available nutrients, thereby affecting the nutrient supply to plants (Roldán et al., 2025). In this study, drought reduced the activity of carbon-related enzymes (BG, CBH) and increased the activity of nitrogen-related enzymes (NAG, LAP), which could be explained by the limiting effect of nitrogen in subtropical forest soils, as reported in previous studies (Mayo et al., 1994). The limitation of nitrogen implied a higher sensitivity to throughfall exclusion conditions. The most pronounced impact of drought in our study was observed in oxidases (POX, PPO), which were produced by microorganisms that function as essential decomposers of substrates oxidation, such as lignin (Tian et al., 2025). This resulted indicated microorganisms played a crucial role in the decomposition of organic carbon in soil, with POX involved in humus transformation and PPO promoting lignin and humus degradation (Wang et al., 2008).

In this study, drought reduced the activity of polyphenol oxidase, slowed organic matter decomposition and with the accumulation of SOC, indicating that drought may become the limiting factor for microbial community nutrients, affecting the growth of related microorganisms and reducing MBC content (Tian et al., 2014). Hydrolytic enzymes, exemplified by BG, can facilitate the breakdown of macroglycemic sugars and active organic matter, transforming them into nutrients available to both plants and microorganisms (Grandy et al., 2007). In this study, we found that drought improved the activity of nitrogen-related hydrolase and reduced the DOC content, enhanced hydrolase activity promoted the decomposition of active organic 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. It was possible that the microbial community was carbon-limited and thus secreted less extracellular enzymes with higher CUE (Ullah et al., 2021). This secretion accelerated the decomposition, absorption and utilization of organic carbon, thereby increasing CUE and enhancing microbial carbon sequestration. 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 microbial residues, including aminoglycans, were nitrogen-rich organic substrates, they played a crucial role in soil nitrogen cycling (Heuck et al., 2015), microorganisms may recover or decompose them, especially under nitrogen-limiting conditions (Cui et al., 2020).

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 correlation with SOC, DOC and POC (Fig. 5), 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, 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 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 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 enzymatic response also contributed 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 further quantify the effects of drought on long-term C sequestration and the microbial mechanisms underlying this process. The drought duration of our study was 9 years, to better understand how SOC components respond to droughts of varying durations, further studies should observe the long-term effects of drought over different time scales. The increase of CUE with SOC reduction mainly depended on scenarios such as forest vegetation restoration under global change (Shi et al., 2025).

5. Conclusion

We found that throughfall exclusion significantly decreased POC and MAOC and increased soil microbial CUE. Furthermore, the proportion reduction of POC/SOC under drought was mainly due to the improvement of CUE. POC subjected to fewer soil aggregate protection mechanisms was more variable under drought, which reflected the 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 CUE leads to changes in soil carbon components. This change provides an important explanation for SOC dynamics. The results showed that soil microbial CUE primarily influenced 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 processes, along with the microbial mechanisms underpin these processes.

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Declaration of interests

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

Availability of data and materials

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

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