

Stoichiometric flexibility regulates the co-metabolism effect during organic carbon mineralization in eutrophic lacustrine sediments*

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Abstract Several studies have suggested the pivotal roles of eutrophic lakes in carbon (C) cycling at regional and global scales. However, how the co-metabolism effect on lake sediment organic carbon (OC) mineralization changes in response to integrated inputs of labile OC and nutrients is poorly understood. This knowledge gap hinders our ability to predict the carbon sequestration potential in eutrophic lakes. Therefore, a 45-day microcosm experiment was conducted to examine the dominant mechanisms that underpin the co-metabolism response to the inputs of labile C and nutrients in lacustrine sediments. Results indicate that the labile C addition caused a rapid increase in the positive co-metabolism effect during the initial stage of incubation, and the co-metabolism effect was positively correlated with the C input level. The positive co-metabolism effect was consistently higher under high C input, which was 152% higher than that under low C input. The higher β -glucosidase activity after nutrient addition, which, in turn, promoted the OC mineralization in sediments. In addition, different impacts of nutrients on the co-metabolism effect under different C inputs were observed. Compared with the low nutrient treatments, the largest co-metabolism effect under high C with high nutrient treatment was observed by the end of the incubation. In the high C treatment, the intensity of the co-metabolism effect (CE) under high nitrogen treatment was 1.88 times higher than that under low nitrogen condition. However, in the low C treatment, the amount of nitrogen had limited impact on co-metabolism effect. Our study thus proved that the microorganisms obviously regulate sediment OC turnover via stoichiometric flexibility to maintain a balance between resources and microbial requirements, which is meaningful for evaluating the OC budget and lake eutrophication management in lacustrine sediments.

Keyword: co-metabolism effect; stoichiometric; carbon cycling; eutrophic lake; decomposition; organic carbon

1 INTRODUCTION

Organic carbon (OC) burial in lacustrine sediments represent an important sink in global carbon cycling (Cole et al., 2007; Gudas et al., 2010). Although lakes cover only about 2% of Earth's surface, annual OC burial in lake sediments can amount to approximately 50% of the annual OC burial in marine sediments (Sobek et al., 2009). Aquatic macrophytes

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are one of the primary sources of OC, which deposit residues composed of cellulose, hemicellulose, lignins, tannins, and cuticular matrix onto the surface of sediments (Li et al., 2013). The relatively recalcitrant OC accumulates gradually and then increases with the lake ecosystem succession (Hanamachi et al., 2008). However, as eutrophication becomes a more widespread environmental problem, an increasing number of shallow lakes have shifted from a clear-water state dominated by macrophytes to a turbid-water state dominated by phytoplankton (i.e., “retrogressive succession”) (Scheffer et al., 1993, 2001). Compared with the slow accumulation and decomposition of macrophyte-dominated lakes, the turnover of phytoplankton-dominated lakes is more rapid (Hanamachi et al., 2008). That is, the rate of succession may decrease in phytoplankton-dominated eutrophication lakes. Clarifying the underlying response mechanism of inputting phytoplankton-derived OC into sediments is crucial for understanding the direction and magnitude of succession in eutrophication lacustrine ecosystems.

One vital mechanism driving changes in OC reserves in terrestrial ecosystems is the priming effect, wherein labile OC input affects the extent of microbial activity mediating native OC decomposition (Kuz'yakov et al., 2000; Blagodatskaya and Kuz'yakov, 2008; Fang et al., 2018). This process is sometimes referred to as the “co-metabolism effect” because similar observations have not been made under aseptic conditions (Horvath, 1972; Wakeham and Canuel, 2006; Van Nuygen et al., 2009). Labile sources of any form, including manure, plant residues, and root exudates (Dai et al., 2009; Phillips et al., 2012; Qiao et al., 2014; Zhu et al., 2018), can aid microbial community composition and enhance the decomposition of indigenous OC (Fontaine et al., 2004; De Graaff et al., 2010). Although the co-metabolism effect has been widely reported in terrestrial ecosystems, this effect has been virtually ignored in the study of aquatic ecosystems, especially lacustrine ecosystems (Guenet et al., 2010a). A few studies have mentioned that algae may stimulate the co-metabolism effect in the water column (Bianchi, 2011; Bianchi et al., 2015). In contrast, lake sediments collect a large amount of OC from a wide range of sources and of complex composition (Xu et al., 2015), consequently, the potential co-metabolism effect of phytoplankton detritus and OC in sediments may be more spatially heterogeneous. With global climate warming and eutrophication, recurrent algae blooms

have been frequently observed in freshwater lakes with continuous and considerable deposition onto the surface of sediments after their decay, which provides ideal conditions for the co-metabolism effect between detritus and OC in sediments (Yan et al., 2017; Qin et al., 2018). In addition, the input of residual phytoplankton also maintains sediment nutrient levels in the surrounding environment (Zhao et al., 2019). Despite experimental evidence showing that nitrogen addition increases carbon dioxide (CO₂) emissions and that phosphorus (P) addition inhibits methane (CH₄) emissions (Huang et al., 2019; Wang et al., 2019; Ma et al., 2020), few studies have linked the co-metabolism effect with nutrient supply and nutrient stoichiometric control in lacustrine ecosystems.

Two distinct mechanisms have been proposed in terrestrial ecosystems to explain the co-metabolism effect caused by nutrient availability and OC inputs: “microbial nutrient mining” and “stoichiometry decomposition” (Chen et al., 2014). In the former, the nutrient-acquiring microbes use input carbon as an energy source to enhance OC decomposition. That is, when the nutrient supply is low, microorganisms facilitate the acquisition of nutrients via native OC mineralization (Razanamalala et al., 2018). In contrast, the co-metabolism effect generated by “stoichiometric decomposition” theory predicts a correlation between stoichiometric C source and nutrient ratios. In other words, decomposition rates are maximized if C and nutrient inputs match microbial demands (Fang et al., 2018). Although many studies have focused on the mechanisms by which nutrient availability affects the co-metabolism effect in terrestrial ecosystems, these underlying mechanisms have not yet been validated in aquatic ecosystems.

This study aimed to reveal the exogenous organic C, nutrient input impact on co-metabolism effect of sediment OC in lacustrine ecosystems. Specifically, our objectives of this study were to (i) link nutrient availability and the co-metabolism effect and (ii) test the applicability of two associated but competing hypotheses of how nutrients affect the co-metabolism effect. Addressing these knowledge gaps is critical for improving the prediction of OC models in eutrophic lakes and for identifying labile OC and stoichiometric changes that can increase sediment OC.

2 MATERIAL AND METHOD

2.1 Field sampling

Taihu Lake (30°56'N–31°33'N, 119°54'E–

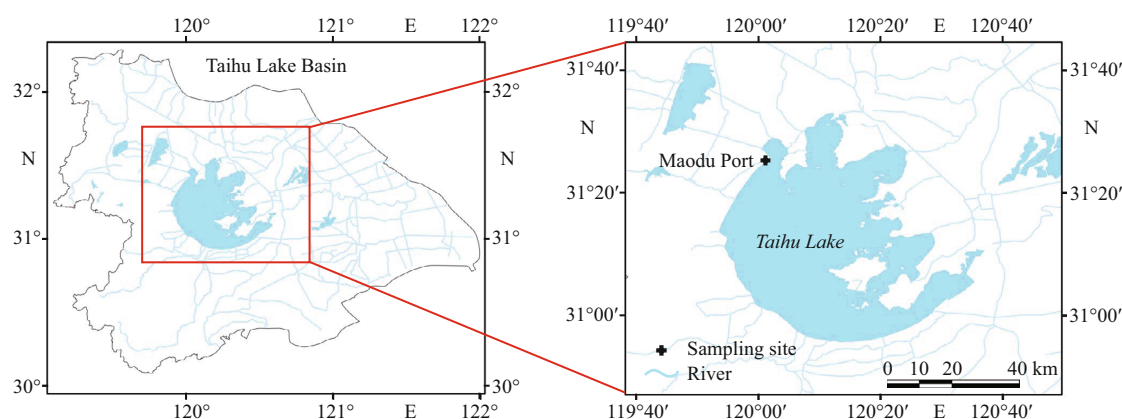


Fig.1 The sampling site in Taihu Lake

Table 1 Description of the C and nutrient (N, P) input treatments

	Treatment	C (mg/g DW)	N ($\mu\text{g/g DW}$)	P ($\mu\text{g/g DW}$)	C:N:P
No OC input	Control (Con)	0	0	0	—
	No nutrient input (L0)	0.23	0	0	—
Low OC input	Low nitrogen input (L1)	0.23	33	3.3	7:1:0.1
	High nitrogen input (L2)	0.23	167	3.3	7:5:0.1
	No nutrient input (H0)	0.93	0	0	—
High OC input	Low nitrogen input (H1)	0.93	33	3.3	28:1:0.1
	High nitrogen input (H2)	0.93	167	3.3	28:5:0.1

—: no data

120°36'E) is located in the Changjiang (Yangtze) River delta in East China. It is a typical large shallow lake with an area of 2 338 km² with a mean depth of 1.9 m (Qin et al., 2007). In recent years, large-scale cyanobacteria blooms in Taihu Lake have occurred frequently because of eutrophication, especially along the northwestern bay and shorelines, which induced a serious ecological and environmental problem (Liu et al., 2015). In September 2019, surface sediments (0–10 cm) were sampled around Maodu Port in the west of Taihu Lake (Fig.1) where the sediment has accumulated to a high degree by a steady stream of algae organic detritus. The sediments were air-dried and sieved to pass through 2-mm mesh. The values of TN, TP, and TOC in sediments were 3.39±0.24, 2.51±0.41, and 50.19±2.19 mg/g DW (dry weight), respectively. The TOC and TN in sediments were determined by an Element Analyzer (EA, VARIO EL, OSIC, Germany), and TP were measured by Inductively Coupled Plasma-Optical Emission Spectrometer (ICP-OES) (Ji et al., 2021).

2.2 Incubation experiment

Thirty grams of dry sediment were weighed in 500-mL Schott bottles. Water was added to 2 cm above the sediment surface. All treatments were pre-

incubated at 25 °C. Thereafter, water or ¹³C-labeled glucose (10.5 atom% ¹³C) solution was evenly added dropwise to the sediment surface using an injector. Before the incubation, the labeled glucose was gently and uniformly mixed, and added to the sediment at two levels. This is equivalent to adding 0.23 and 0.93 mg/g DW carbon to the sediment. There were seven treatments: low and high input levels of the labeled glucose with and without two levels of nutrients and a control without nutrient and glucose inputs (Table 1). Each treatment had three replicates. All treatments were incubated at 25 °C. The headspace gas was collected at Days 3, 7, 13, 21, 32, and 45 for total CO₂-C and $\delta^{13}\text{C}$ -CO₂ analyses.

2.3 CO₂ analysis

Headspace samples were collected using a 25-mL gas-tight syringe and stored in pre-evacuated 35-mL glass bottles (Yan et al., 2017). The CO₂ concentrations were measured using an Agilent 7890B gas chromatograph (Agilent Technologies, Alto Palo, California, USA) equipped with flame ionization, flame photometric, electron capture detectors, and a nickel catalyst methanizer. The CO₂ emission was expressed as cumulative production. In addition, the stable C isotope composition in the headspace samples

was analyzed using a Picarro G2101-i CO₂ cavity ring-down isotope spectroscope (Picarro Inc., Sunnyvale, California, USA).

2.4 Extracellular enzyme activities

Extracellular enzyme activities reflect the functions of decomposer communities. Three enzymes: β -glucosidase (AG), chitinase (CH), and phosphatase (PHOS), were determined using a modified 96-well plate assay method (Bell et al., 2013). β -glucosidase is a commonly measured enzyme responsible for degrading cellulose. Chitinase is a common enzyme involved in degrading organic N compounds. Artificial substrates labeled with the methylumbelliferone fluorophore were used to estimate the activities of three enzymes involved in sediment organic C, N, and P degradation.

2.5 Sediment microbial community abundance analysis

Total genomic DNA of each sediment sample was used for DNA extraction using a soil DNA isolation kit (OMEGA Bio-tek, Inc.). DNA concentrations were measured with a spectrophotometer (Nanodrop ND-2000; NanoDrop Technologies). The extracted DNA was stored at -20 °C until further analysis.

PCR amplification was conducted for Illumina MiSeq sequencing using bacterial primers. The forward primer 5'-ACTCCTACGGGAGGCA-GCA-3' and the universal reverse primer 3'-GGACTACHVGG-GTWTCTAAT-5' targeted the V3V4 hypervariable regions of bacterial 16S rRNA genes. PCR amplification was performed in triplicate using an ABI 2720 PCR System. The 25- μ L PCR mixture contained 5 μ L of 5 \times buffer, 5 μ L of 5 \times GC buffer, 2 μ L of dNTP (2.5 mmol/L), 1 μ L of forward primer (10 μ mol/L), 1 μ L of reverse primer (10 μ mol/L), 2 μ L of DNA template, 8.75 μ L of ddH₂O, and 0.25 μ L of Q5 DNA polymerase. Cycling parameters were as follows: initial denaturation 98 °C for 2 min, denaturation 98 °C for 15 s, annealing 55 °C for 30 s, extension 72 °C for 30 s, with a final extension of 10 min at 72 °C. For each sample, the products of three parallel PCRs were mixed. The PCR amplicons were pooled together and purified using a PCR purification kit. The purified amplicons were merged at equal concentrations for all samples with a KAPA Library Quantification Kit. The purified amplicons were sequenced on the Illumina MiSeq platform.

2.6 Calculations and statistics

Because of the different $\delta^{13}\text{C}$ signatures between sediment and labeled glucose, the total CO₂ emissions can be separated into sediment-derived CO₂ emissions (C_{sed}) and glucose-derived CO₂ emissions (C_{glu}) using the following equations (Grasset et al., 2018):

$$C_{\text{sed}} = C_{\text{total}} \times \frac{\delta^{13}\text{C}_{\text{total}} - \delta^{13}\text{C}_{\text{glu}}}{\delta^{13}\text{C}_{\text{sed}} - \delta^{13}\text{C}_{\text{glu}}},$$

$$C_{\text{glu}} = C_{\text{total}} - C_{\text{sed}},$$

where C_{sed} represent the CO₂ derived from the glucose-treated sediment, C_{glu} represent the CO₂ derived from added glucose, and C_{total} represent the total CO₂ produced. Values of $\delta^{13}\text{C}_{\text{glu}}$ in equations are $\delta^{13}\text{C}$ values of glucose. $\delta^{13}\text{C}_{\text{sed}}$ in the equations was obtained from control treatment.

$$\text{CE} = C_{\text{sed}} - C_{\text{con}},$$

where CE is the intensity of the co-metabolism effect. C_{con} represent the total CO₂ derived from control treatment.

The repeated measures Anova test method was used to identify the differences for cumulative CO₂ emissions and CE in different treatment groups by R language, version 3.5.1. Moreover, One-way ANOVAs test method was used to compare the accumulated sediment-derived CO₂ emissions and glucose-derived CO₂ emissions in different treatment groups at final stage. The multifactorial analysis was used to explain time, C, N, and P inputs to cumulative CE. The criteria of $P < 0.05$ and $P < 0.01$ were used to determine statistical significance at the 0.05 and 0.01 levels, respectively.

3 RESULT

3.1 Cumulative CO₂ emissions

CO₂ emissions from the background sediments gradually increased to 2112.82 $\mu\text{g/g DW}$ during the 45-day incubation period (Fig.2a). The repeated measures Anova test showed that the glucose addition led to a significant increase in CO₂ emissions relative to background levels ($P < 0.05$). High-C treatments caused 40.52% higher CO₂ emissions than low-C treatments during incubation. Glucose with high nitrogen treatments led to higher CO₂ emissions compared with the no nutrient treatments. By the end of incubation, both high nitrogen input treatments led to higher cumulative CO₂ emissions than low nitrogen treatments. The CO₂ released from each treatment increased rapidly at the beginning of the incubation and then increased slowly after 13 days. The

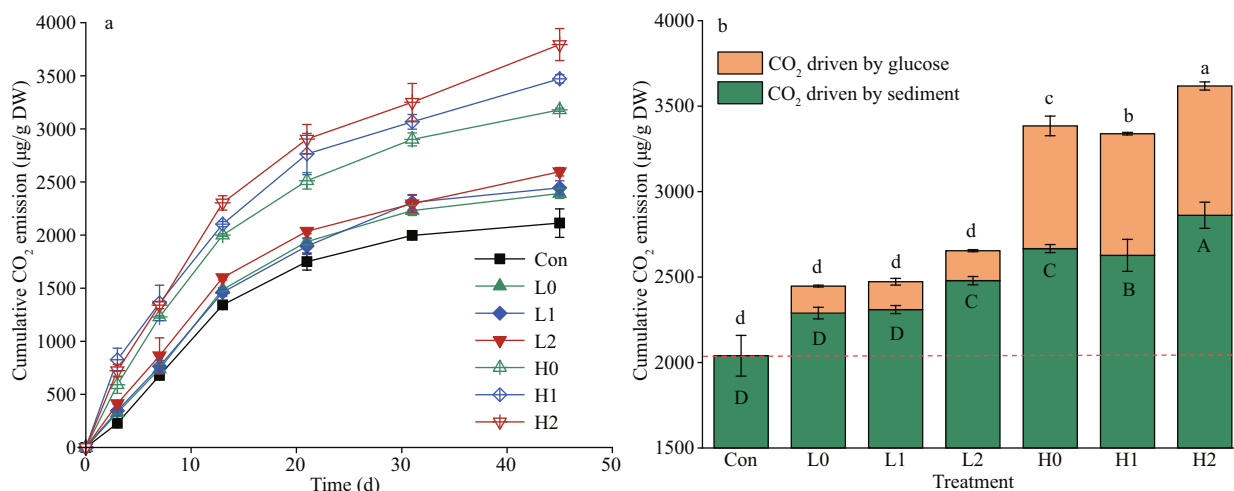


Fig.2 The cumulative CO₂ emissions in each treatment over time (a) and the cumulative CO₂ emissions at the end of the experiment (b)

Data are means of 3 replicates \pm SE ($n=3$). Bars contained the same letter are not significantly different ($P<0.05$); uppercase letters are for sediment-derived CO₂ and lowercase letters for glucose-derived CO₂. The orange dotted line represents the CO₂ emission in the control group without glucose added.

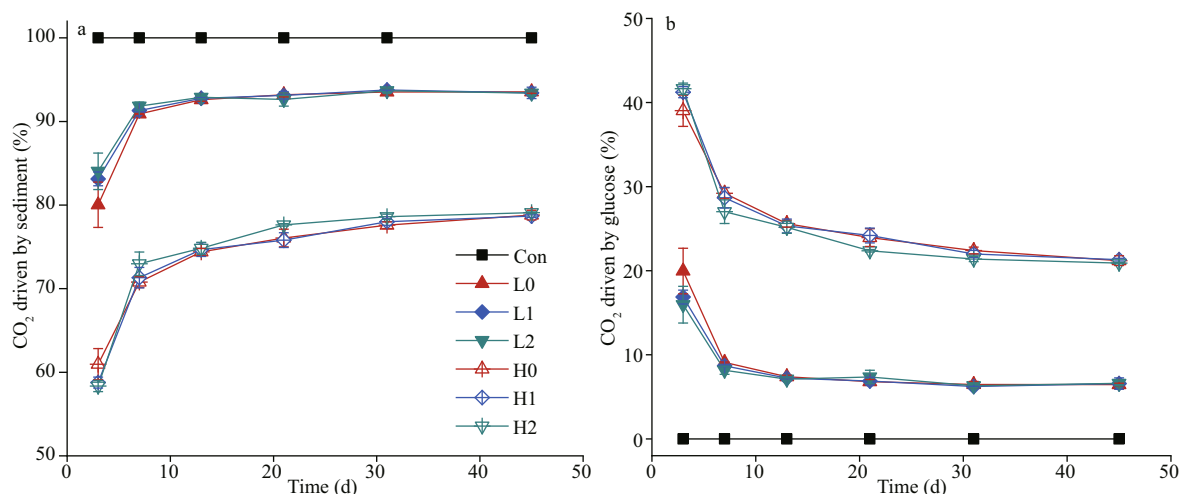


Fig.3 The percentage of CO₂ driven by sediment (a) and CO₂ driven by glucose (b) in each treatment

cumulative CO₂ emissions ranged from 2 112.82–3 794.23 µg/g DW. However, nutrient input significantly increased glucose-C mineralization at the high-C input level relative to the no nutrient treatment but not at low-glucose input. The cumulative CO₂ driven by glucose ranged from 154.47–793.27 µg/g DW, which was equivalent to adding 4.33%–17.70% of CO₂ emissions across all treatments (Fig.2b).

The percentage of CO₂ emission driven by sediment and glucose during the decomposition was shown in Fig.3a & b, respectively. The percentage of CO₂ driven by glucose in each treatment continually decline over time, while the percentage of CO₂ driven by sediment showed an opposite direction (Fig.3). Noteworthy, the proportion of CO₂ emission in low C treatment driven by sediment and glucose reached

dynamic equilibrium around Day 13. As a contrast, similar dynamic equilibrium in high C treatment was reached in about 30 days.

3.2 Cumulative CE of labile C addition on CO₂ production

All treatments with added glucose with or without nutrients had a significantly positive co-metabolism effect of sediment OC mineralization over the 45-day period ($P<0.05$). The co-metabolism effect generally remained positive until the end of the experiment (except for the occurrence of negative rates on Days 7 and 13) (Fig.4). During the first three days, the positive co-metabolism effect increased rapidly in all treatment groups and reached 34.12–258.17 µg/g DW. All treatments except for the high C and high nitrogen treatment (H2) declined to varying degrees (i.e., the

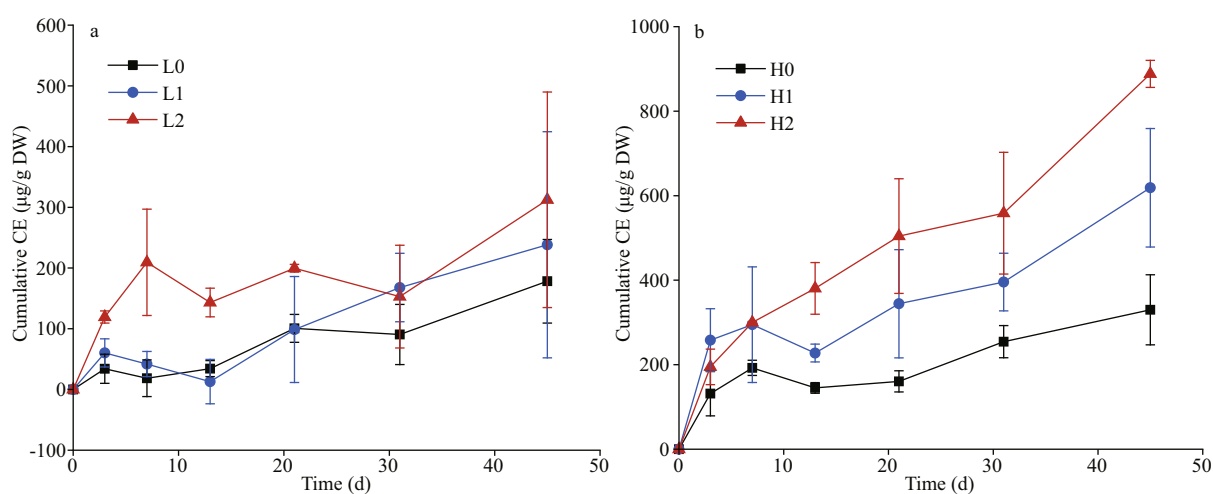


Fig.4 The cumulative co-metabolism effect in the low glucose treatment (a) and high glucose treatment (b)

rate of OC decomposition in sediments reduced). However, the positive co-metabolism effect of each group increased gradually after Day 13. By the end of incubation, the cumulative co-metabolism effect reached 178.25–888.14 $\mu\text{g/g DW}$. The positive co-metabolism effect was consistently higher at high C inputs, which was 152% more than low C inputs across the nutrient treatments. The multifactorial analysis showed that C input and time are significant positive correlation with the co-metabolism effect ($P < 0.05$).

3.3 Extracellular enzyme activities

All treatments with added labile C at both low and high levels led to increases in the activities of all measured enzymes on Days 3, 10, and 45 (Fig.5). The activity of β -glucosidase has no significant differences between treatments on Day 3. However, treatments with the addition of N and P were higher with the only glucose treatments on Days 10 and 45 ($P < 0.05$). In both high C and low C addition treatments, increasing nutrient input levels generally increased the activity of phosphatase on Day 3, but no significant differences were observed among treatments. The activity of chitinase almost continuously decreased over time, which was significantly higher in C input treatment than control treatment on Day 3 ($P < 0.05$).

3.4 Gene abundance

The dominant phyla in this study were Proteobacteria, Firmicutes, Actinobacteria, Bacteroidetes, and Armatimonadete (Fig.6). In treatments with low C input, Proteobacteria generally increased, especially on Day 3, and then decreased to the same level as in the high C input treatments. Furthermore, almost no Acidobacteria were observed

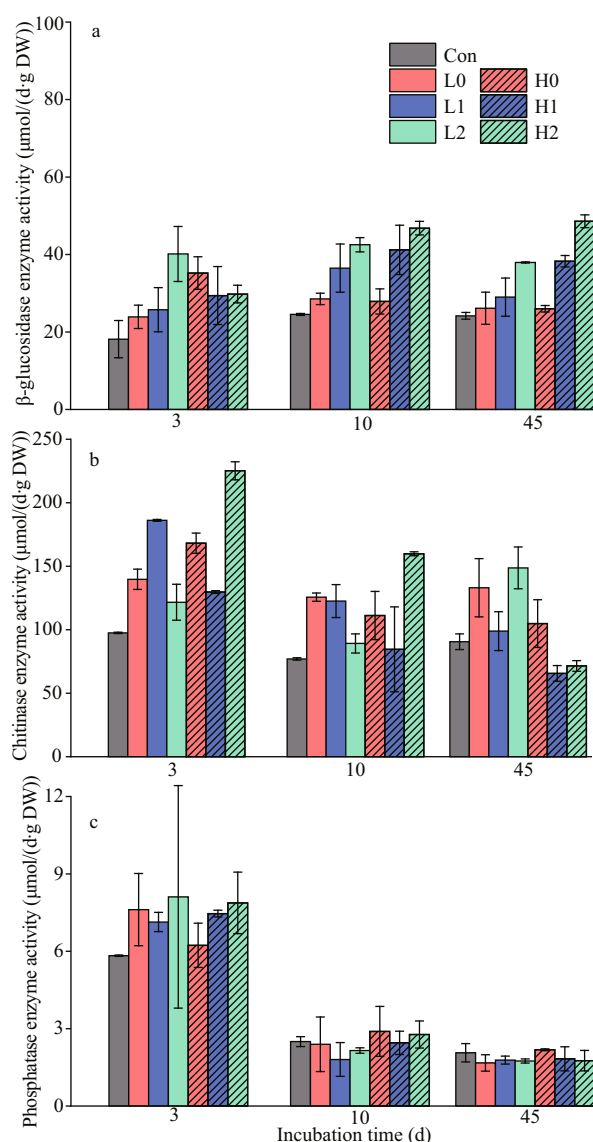


Fig.5 Activity of the extracellular enzymes β -glucosidase (a), chitinase (b), and phosphatase (c) in sediments on days 3, 10, and 45

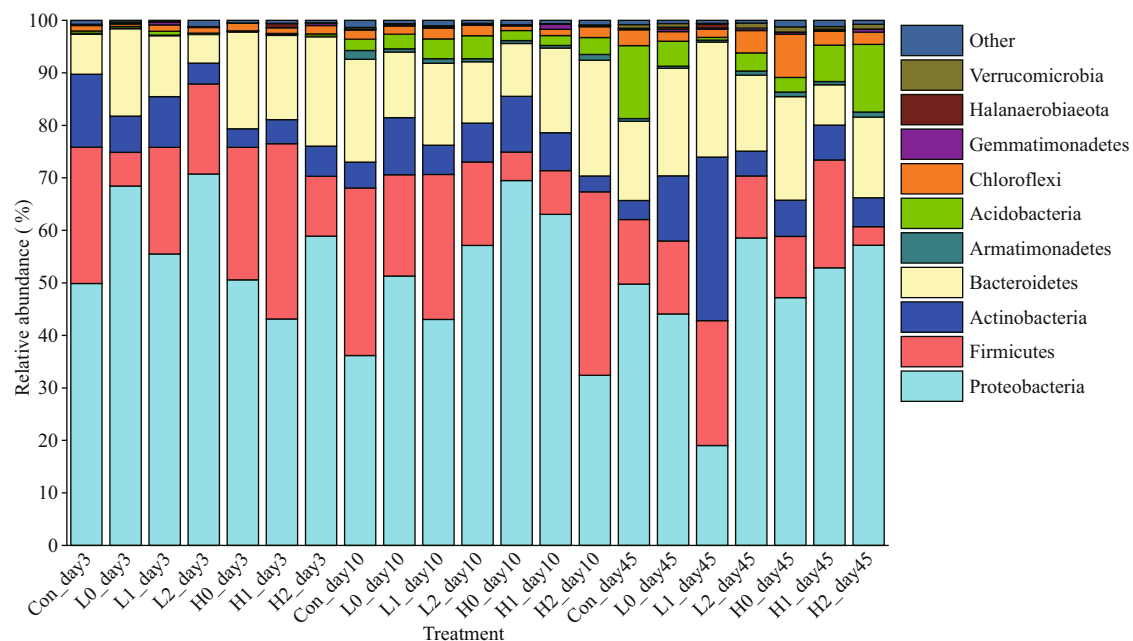


Fig.6 Bacterial community composition of the sediment layers at the phylum level

in each treatment group on Day 3. However, the relative abundance of Acidobacteria increased over time. Although the relative abundance changed, there was no significant difference at the phylum level in each treatment.

4 DISCUSSION

4.1 Co-metabolism effect in response to labile C addition

Increases and decreases in OC decomposition upon labile C input (a readily available energy source) have been commonly observed (Löhnis, 1926; Kuzyakov et al., 2000). The recent renewed interest in this phenomenon—the priming effect—has still not penetrated many disciplines. However, it has been virtually ignored in aquatic ecosystems. As a subcomponent of priming (Bianchi, 2011), the co-metabolism effect primarily emphasized the role of microorganisms in OC decomposition, and excluded other bioprocess such as biodigestion, biodisturbance, etc. (Dai et al., 2009; Ma et al., 2020). Here, we proposed a method to evaluate the co-metabolism effect based on the end-member mixing model to calculate the fraction of CO₂ from labile C added and refractory OC derived from sediment in shallow lake ecosystems.

The labile C addition caused a rapid increase in the positive co-metabolism effect at the first 7 days of incubation (Fig.4). This increase is generally attributed to the activation of microorganisms from starvation

states to active states by labile OC (Blagodatskaya and Kuzyakov, 2008). We observed enzyme production rapidly increasing during the initial stage, which caused the microbial switch from dormancy to activity (Fig.5). Especially on Day 10, the higher β -glucosidase activity after nutrient addition, which, in turn, promoted the OC mineralization in sediments (Figs.2 & 5a). On a time scale, the sediment OC mineralization was inhibited by glucose addition during early incubation (the first 3–13 days) (Fig.4). This inhibition likely stems from the fact that the preference of microorganisms for substrate switched from the relatively recalcitrant OC in sediments to the available energy source, thus causing a negative co-metabolism effect (Kuzyakov and Bol, 2006; Zhu et al., 2018). Moreover, the proportion of CO₂ emissions from glucose in the total emissions decreased gradually, which was attributable to microorganisms preferentially utilizing glucose (Fig.3). However, as more glucose was consumed, the microorganisms had to utilize sediment OC, which then enhanced the co-metabolism effect (Fang et al., 2018).

Generally, the co-metabolism effect is positively correlated with OC input level (Guenet et al., 2010b; Di Lonardo et al., 2019; Lyu et al., 2019). This finding may result from the alleviation of energy limitation, thus leading to increased microbial activities and nutrient demand (Fang et al., 2018). By the end of incubation, the co-metabolism effect with high C input was almost double that at low C input, which was not proportional to the applied dose of glucose

(4 times higher in the high glucose compared with the low glucose treatment) (Fig.4). Nevertheless, several studies indicate that the occurrence of the positive co-metabolism effect requires the amount of labile OC to reach a threshold, but this threshold differs between substrates (Bastida et al., 2013; Qiao et al., 2014). In addition, if the threshold is exceeded, further addition may not lead to increases in mineralization (Bremer and Kuikman, 1994). Microbial growth has been shown to strongly depend on the quality and size of available substrates (Wang et al., 2015); however, the underlying mechanisms need to be clarified for our understanding of sediment OC decomposition and turnover in eutrophic lakes to be enhanced.

4.2 Co-metabolism effect in response to N and P addition

There is an interactive effect between labile C and nutrient input on the co-metabolism effect. We observed different impacts of nutrients on the co-metabolism effect under different C inputs, which were supported by previous study in paddy soil ecosystem (Wang et al., 2019). Under high C treatments, a significant impact of nutrients on the magnitude of the co-metabolism effect was observed. However, there was no obvious impact of nutrients on co-metabolism under low C input treatments (Fig.4). In general, nutrient addition may induce shifts in the abundance and diversity of bacteria, extracellular enzyme activities with increasing C turnover and sediment OC mineralization (Luo et al., 2019). A study showed that nutrient input did not increase the co-metabolism effect of maize straw after a 9-day incubation period (Chen et al., 2014). This result implies that microbial growth was constrained by C availability more than by nutrient availability (Heuck et al., 2018), which is supported by the changes in enzyme activities observed in this study, especially during the initial phase (Fig.5). Similarly, another study reported that nutrient inputs did not affect the co-metabolism effect under low-residue input levels (Fang et al., 2018).

In this study, no increase in the co-metabolism effect during the first 3–13 days was observed in all treatments except for the high C with high nitrogen treatment (Fig.4). This finding may stem from the fact that the initial nutrients were not limited, which increased the decomposition of glucose during the early period (Kuzakov and Bol, 2006). As available nutrients were depleted, nutrient limitation might lead to a shift in microorganisms when they degrade

recalcitrant compounds in sediment OC in later stages (Kuzakov et al., 2000). The microorganisms could then decompose more stable OC for nutrient acquisition and induce a higher mineralization of OC (positive co-metabolism effect), which is explained by the domination of “microbial nutrient mining” theory (Blagodatskaya et al., 2009). We also observed that the co-metabolism effect increased continuously in the high C with high nitrogen treatment and induced the largest co-metabolism effect by the end of the incubation period (Fig.4), which contradicts microbial “nutrient mining” predicting a lower co-metabolism effect at higher nutrient availability (Chen et al., 2014). Another mechanism called “stoichiometric decomposition” (Craine et al., 2007) might explain the co-metabolism effect under high C levels and nutrient availability in the substrate. Differing from the “microbial nutrient mining” theory, the “stoichiometry decomposition” theory suggests that native OC decomposition can be enhanced as nutrient limitation is alleviated. Due to sufficient amount of nutrients and labile C may promote the growth of microbial communities. That is, decomposition rates are increased if C and nutrient inputs match microbial demands. In our study, chitinase activity in high nitrogen with high C treatment was significantly higher than other groups during early incubation (Fig.5), which may stimulate the growth and activity of microbial communities.

4.3 Implications for eutrophic lacustrine ecosystems

In this study, we tested the occurrence of the co-metabolism effect in lake sediments. The availability of nutrients may lead to different co-metabolism effect mechanisms, even though decomposers can degrade sediment OC by using labile C substrate as a source of energy. The microorganisms maintained their stoichiometric responses to labile C input, indicating that the acquisition of nutrients may be constrained by the environment. Thus, the nutrient requirements of microorganisms are likely beneficial for sediment OC decomposition. In this study, a positive co-metabolism effect was also observed without nutrient addition (Fig.4). Alternatively, the sediment microbes may be flexible and shift their elemental balance in response to such labile C input (Kuzakov et al., 2000). Hence, the highest co-metabolism effect was observed in the high C with high nitrogen treatment.

In lacustrine ecosystems, the dramatic increase in nutrient inputs has accelerated eutrophication (Qin et

al., 2019). An increase in nutrient availability further stimulates the primary production of algae in shallow lakes, making the large algae blooms during summer months increasingly severe (Shi et al., 2015; Ma et al., 2016) and resulting in the deposition of massive amounts of algae detritus (Yan et al., 2017). In this case, algae detritus may be a preferred energy source for sediment microorganisms given that it is better suited to their requirements. Such an energy source also contributes to the decomposition of recalcitrant OC (mainly macrophyte residue and humus) in sediments. This finding could also be explained by an increase in microorganism production because of labile C and the nutrient supply (Guenet et al., 2014). This positive co-metabolism effect might be common in most shallow lakes, where phytoplankton is primarily dominated by algae blooms. In addition, massive algae decomposition has also led to increases in nutrients, which may be one of the important factors underlying the self-maintenance of eutrophic lakes, such as Taihu Lake in China, especially at the northwestern shorelines. The algal blooms accumulate, decay, and release nitrogen and phosphorus (Otten et al., 2012), which might further affect the metabolism of OC in sediments. For example, with sufficient C sources and nutrients, the stoichiometric ratio can be adjusted according to microbial demands, maintain activity and further facilitate OC mineralization in sediments (Fang et al., 2018). The co-metabolism effect of algae detritus and sediment OC further weakened the function of the lake sediment carbon sink. The amount of glucose added in this study was based on the accumulation of algae in the context of eutrophication lakes (Liu et al., 2017; Yan et al., 2017).

5 CONCLUSION

New evidence indicating that different dominant mechanisms can co-exist in the same system and co-influence the strength of the co-metabolism effect, probably because the availability of labile C and nutrients in sediments can be explained by the correlation of the co-metabolism effect with key microbial variables. Compared with the low nutrient treatments, larger co-metabolism effect under high C with high nutrient treatment was observed by the end of the incubation. And in the low C treatment, the amount of nitrogen had limited impact on co-metabolism effect. Higher nutrition further promotes the decomposition of sediment OC, which should be considered in the future management of aquatic

ecosystems. Considering that the occurrence intensity, frequency, and duration of algae blooms were still enhanced, this study may underestimate the co-metabolism effect in eutrophic lacustrine ecosystems.

6 DATA AVAILABILITY STATEMENT

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

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