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Biochar mitigates the mineralization of allochthonous organic matter and global warming potential of saltmarshes by influencing functional bacteria

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Abstract

Saltmarshes are suffering from severe degradation due to anthropogenic activities, leading to the loss of blue carbon and greenhouse gas (GHG) emissions. Given the significant potential of biochar in mitigating climate change, adding biochar to saltmarshes would alleviate this situation. This study investigated the effects of different biochar (made from *Spartina alterniflora*, corn straw, and *Laminaria japonica*) and their aged biochar on the carbon fraction contents, GHG emissions, and microbial community structure of saltmarsh soils with allochthonous organic matter (*Enteromorpha prolifera*) addition. After 60 days of incubation, total organic carbon (TOC) loss and global warming potential (GWP) of biochar-amended soils were reduced by 67.29–124.33% and 4.91–123.24%, respectively ($p < 0.05$). Biochar reduced the proportion of labile carbon (dissolved organic carbon (DOC) and microbial biomass carbon (MBC)) in organic carbon by 61.92–86.15% ($p < 0.05$). In addition, biochar reduced the relative abundance of specific functional bacteria (inc. cellulolysis, aromatic compound degradation, and xylanolysis) involved in organic carbon decomposition by 20.02–37.82% ($p < 0.05$). These results suggest that even in the presence of high levels of labile organic matter, the application of biochar to saltmarshes has a sustained effect in promoting carbon accumulation and reducing GHG emissions, and this effect is regulated by a decrease of functional bacteria associated with carbon metabolism. Therefore, the in situ study of biochar on restoring carbon sink function of saltmarshes is proposed for practical engineering in future.

Highlights

- Both fresh and aged biochar from different materials had promising potential in enhancing carbon sequestration and mitigating global warming potential of saltmarsh soils.
- Biochar inhibited the mineralization of allochthonous organic matter in saltmarshes.
- Biochar reduced the abundance of functional bacteria involved in organic carbon decomposition by 20.02–37.82%.

Keywords Saltmarsh, Biochar, Blue carbon, Allochthonous organic matter, Greenhouse gas, Functional bacteria

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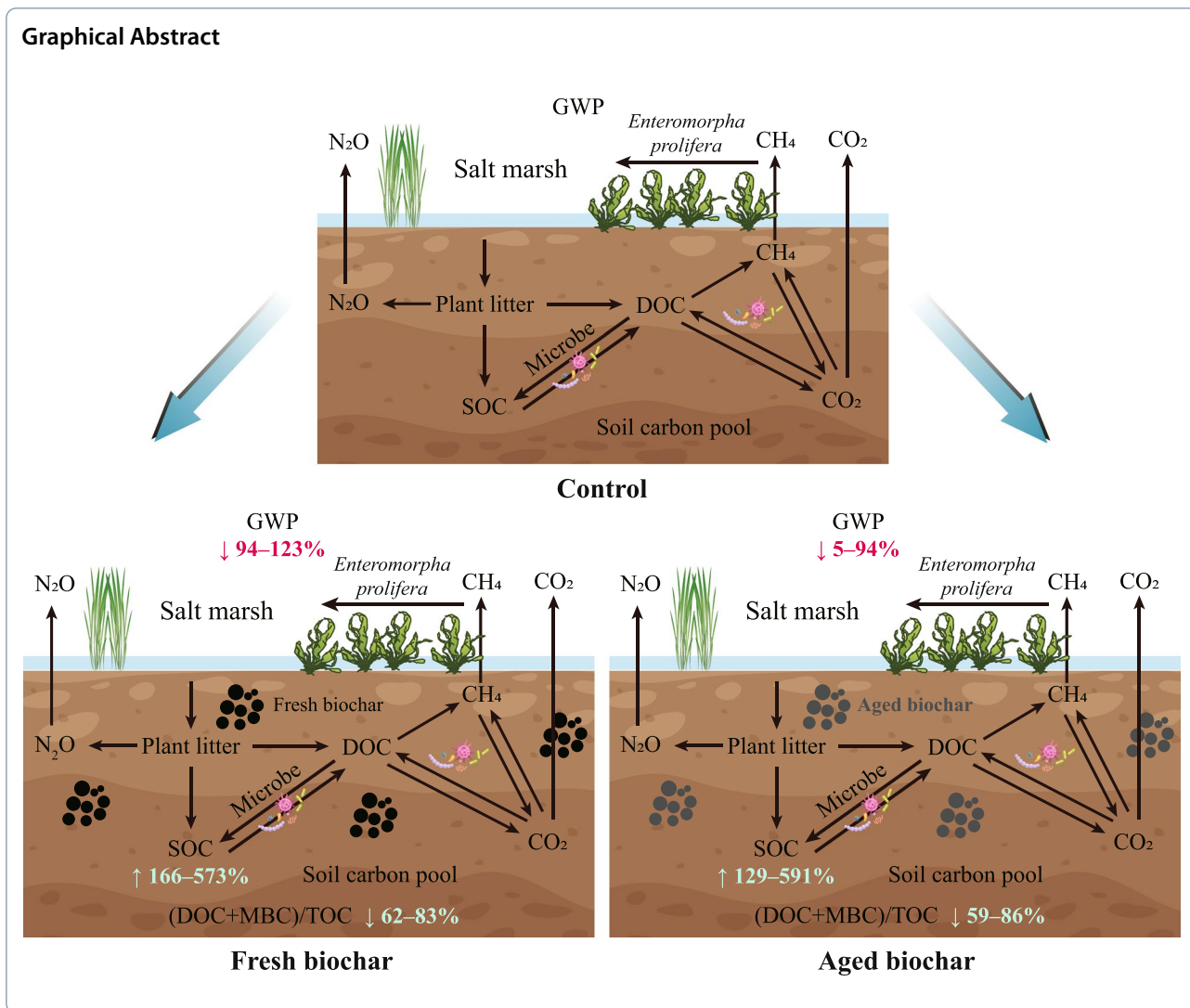
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1 Introduction

Saltmarshes, one of the blue carbon ecosystems, have a high carbon sequestration capacity of 10.1 Tg C yr⁻¹ (McLeod et al. 2011; Macreadie et al. 2019; Human et al. 2022). However, the global extent of saltmarshes has decreased by 25–50% in recent decades due to sea level rise, invasive alien species, and land reclamation (Burden et al. 2013; Ruiz-Fernandez et al. 2018; Gu et al. 2018). The degradation of saltmarshes resulted in 16.3 Tg CO₂ eq (million tons of CO₂ equivalent) emissions and a reduction in carbon sequestration of 0.045 Tg CO₂ eq per year from 2000 to 2019 (Campbell et al. 2022). Furthermore, in saltmarshes, allochthonous particulate organic matter may account for over 50% of the carbon trapped in the sediment, originating from drifting seaweed and terrestrial organic debris transported by coastal currents and tides (McLeod et al. 2011; Sasmito et al. 2020).

Once saltmarshes are degraded, the liable organic carbon stored in the sediment is preferentially to be decomposed and released as greenhouse gases (Yang et al. 2021; Rahman et al. 2021). Currently, biochar is widely considered as an effective soil amendment for mitigating climate change (Jiang et al. 2023; Shikha et al. 2023). Therefore, we suspect that adding biochar to saltmarshes would also alleviate the increasing global warming potential of saltmarsh degradation. Biochar is a carbon-rich and porous material produced by pyrolysis or hydrothermal carbonization of biomass (Feng et al. 2022), and it contains approximately more than 50% carbon that can be stably stored in the soil (Shikha et al. 2023). Moreover, biochar has been demonstrated to alter the soil microbial community structure (Ma et al. 2023; Qiu et al. 2023), which could indirectly affect the mineralization and immobilization of soil organic carbon (SOC) (Qiu et al. 2023).

The dynamics of soil carbon pool depend on the inputs and outputs of SOC (Song et al. 2023). Soil labile organic carbon fractions, such as microbial biomass carbon (MBC) and dissolved organic carbon (DOC), are valid indicators for the ability of carbon pools to resist SOC mineralization (Ding et al. 2023). Previous studies showed that biochar induced a negative priming effect on the native SOC mineralization, which promoted SOC accumulation (Zheng et al. 2018; Yin et al. 2022; Huang and Xiao 2023). This can be explained by the following reasons: (1) biochar adsorbs carbon on its surface or forms microaggregates with soil organo-mineral, which enhances the physical protection of SOC (Weng et al. 2022); (2) toxic substances released from biochar may inhibit the microbial activity on SOC degradation (Li et al. 2018; Yin et al. 2022). However, it remains unclear whether this inhibitory effect can be sustained when large amounts of particulate organic matter are trapped in saltmarshes. The performance of biochar is mainly determined by feedstocks and production conditions (Luo et al. 2016; Yang et al. 2020; Tan et al. 2023). Furthermore, biochar aging in the soil leads to alterations in soil properties, which has either positive or negative effects on the soil (Wang et al. 2021; Yang et al. 2022b, 2022a; Qiu et al. 2023). Soil microorganisms dominate the carbon cycle (Yu et al. 2022), and their composition, structure, and characterization are interfered by biochar (Cai et al. 2021; Deshoux et al. 2023). Besides, periodic high and low tides keep the salt marshes in alternating wet and dry conditions, which affects the microbial community (Yin and Yan 2020). Compared to the flooding condition, the abundance of Gram-negative bacteria and actinobacteria increased while the abundance of fungi decreased under no flooding condition (Zhang et al. 2022b).

Several studies have shown that biochar promotes plant growth by increasing nutrient content and improving soil structure in coastal wetlands (Cai et al. 2021; Cui et al. 2021). In a 90-day laboratory experiment, biochar prepared from *Phragmites communis* and *Spartina alterniflora* reduced the GWP of the Yellow River Delta wetland soil by 27.6–87.3% (Yan et al. 2020). In addition, Zheng et al. (2018) found that biochar decreased SOC mineralization of coastal wetland soil by promoting the formation of stable agglomerates. However, few studies focused on the effects of fresh and aged biochar on carbon pools and GHG emissions of saltmarsh soil with allochthonous organic matter addition, as well as the dynamics of functional microorganisms driving the changes in carbon sequestration and emission. Therefore, to comprehensively investigate the role of biochar in restoring and improving carbon storage of saltmarshes, we prepared three types of biochar (from *Spartina alterniflora*, corn straw, and *Laminaria japonica*) and

their aged biochar. Then the prepared fresh and aged biochar was added to saltmarsh soil mixed with *Enteromorpha prolifera* as allochthonous organic matter, and these treatments were incubated for 60 days. The objectives of this study were to investigate: (1) the effects of fresh and aged biochar on soil carbon fraction contents, greenhouse gas emissions, and microbial community structure of saltmarsh soil under allochthonous organic matter addition; (2) the correlation between soil carbon content, carbon mineralization, and functional bacteria. We hypothesized that (1) both fresh and aged biochar could sequester SOC and reduce GHG emissions by protecting allochthonous organic matter from mineralization, and (2) biochar could inhibit the activity of microorganisms involved in soil carbon degradation. This study provided a theoretical basis for practical engineering about restoring and improving carbon sink capacity of saltmarshes, which is conducive to the enhancement of saltmarsh ecological function and carbon neutrality. Nevertheless, we are not capable of reproducing all the conditions of real environment in a laboratory simulation experiment, so in situ experiments will be necessary afterwards to further evaluate the effects of biochar.

2 Materials and methods

2.1 Sample preparation

The soil samples were collected from the intertidal high tide zone of the saltmarsh (*Scirpus mariqueter*) located in Hangzhou Bay, Ningbo City (30°20′55″N, 121°08′11″E). The seawater is about 100 m from the sampling area. Soil samples were first collected randomly from the topsoil (0–20 cm), then stored in boxes and transported to the laboratory. The collected soil was sieved to pass through a 2 mm mesh, and then oven-dried (2 days, 40 °C). Biochar was produced by pyrolysis of *Spartina alterniflora*, corn straw and *Laminaria japonica* at 600 °C for 2 h (labeled as SBC, CBC, and ABC, respectively) (Yang et al. 2018). To investigate the effect of biochar on the saltmarshes after 100 years, 5% H₂O₂ was used to accelerate the aging of biochar according to the method described by Jing et al. (2018). The aged biochar was labeled as OSBC, OCBC and OABC, respectively. Air-dried *Enteromorpha prolifera* was ground, passed through a 0.25 mm sieve, and added to the soil to simulate fresh allochthonous matter that accumulates in saltmarshes. The properties of saltmarsh soil, biochar, and *Enteromorpha prolifera* are presented in Table 1.

2.2 Incubation experiment

The incubation experiment consisted of seven treatments: (1) soil with 0.5 wt% *Enteromorpha prolifera*, (2) soil amended with 3 wt% SBC and 0.5 wt% *Enteromorpha prolifera*, (3) soil amended with 3 wt% CBC and 0.5

Table 1 Properties (mean \pm standard error, $n = 3$) of the saltmarsh soil, biochar and *Enteromorpha prolifera*

Samples ^a	pH	EC (mS/cm)	Total C (g/kg)	Total N (g/kg)	DOC (dissolved organic carbon) (mg/kg)
Soil	8.55 \pm 0.02	2.03 \pm 0.04	10.46 \pm 0.31	0.35 \pm 0.03	20.67 \pm 1.44
<i>Enteromorpha prolifera</i>	6.53 \pm 0.00	13.69 \pm 0.04	296.98 \pm 0.31	37.20 \pm 0.08	38,991.67 \pm 1282.17
SBC	10.77 \pm 0.01	11.18 \pm 0.68	636.59 \pm 20.07	11.08 \pm 0.55	137.47 \pm 10.55
CBC	10.75 \pm 0.01	8.53 \pm 0.11	701.38 \pm 24.42	10.00 \pm 0.43	640.95 \pm 63.71
ABC	10.64 \pm 0.01	43.73 \pm 1.36	187.42 \pm 11.19	12.44 \pm 0.75	251.63 \pm 11.47
OSBC	9.95 \pm 0.01	9.17 \pm 0.68	614.73 \pm 8.18	9.59 \pm 1.39	449.45 \pm 55.08
OCBC	9.46 \pm 0.01	3.34 \pm 0.80	678 \pm 7.83	7.50 \pm 0.87	2016.33 \pm 521.88
OABC	10.57 \pm 0.01	39.45 \pm 0.35	159.38 \pm 8.03	10.64 \pm 0.76	346.20 \pm 13.52

^a SBC: *Spartina alterniflora* derived biochar, CBC: corn straw derived biochar, ABC *Laminaria japonica* derived biochar, OSBC: aged *Spartina alterniflora* derived biochar, OCBC: aged corn straw derived biochar, OABC: aged *Laminaria japonica* derived biochar

wt% *Enteromorpha prolifera*, (4) soil amended with 3 wt% ABC and 0.5 wt% *Enteromorpha prolifera*, (5) soil amended with 3 wt% OSBC and 0.5 wt% *Enteromorpha prolifera*, (6) soil amended with 3 wt% OCBC and 0.5 wt% *Enteromorpha prolifera*, (7) soil amended with 3 wt% OABC and 0.5 wt% *Enteromorpha prolifera*.

To revive the soil microbial activity, the soil was pre-incubated at 25 °C for 7 days at 70% water holding capacity (WHC) before starting the experiment (You et al. 2023). Biochar and *Enteromorpha prolifera* powder were then mixed with the pre-incubated soil. Subsequently, each sample (150 g dry soil, 0.5% *Enteromorpha prolifera* powder with/without 3 wt% biochar) was placed in an uncapped 1 L glass bottle and incubated at 25 °C for 60 days in a climatic incubator (4800 lx illumination intensity on a 12/12-h light/dark cycle). A rubber stopper was used to seal each bottle for 24 h on days 1, 4, 7, 10, 15, 20, 30, 40, and 60. Gas samples with four replicates were taken from the headspace of the bottle with a syringe throughout the entire incubation. Soil moisture content of all the treatments was maintained at 32%, consistent with that of collected soils in Hangzhou Bay. Water evaporation was compensated by weighing the bottle every two days. Soil samples were destructively sampled on days 1, 7, 15, 30, and 60 in three replicates. In general, there are seven bottles for each treatment, with four bottles for gas emission monitoring and three bottles for the analysis of soil properties.

2.3 GHG and soil properties analysis

Soil total carbon (TC) and total nitrogen (TN) contents were measured by elemental analyzer (Vario Macro Cube, Elementar, Germany) (Cui et al. 2021). After acid-washing soil samples with 12 M HCl (10 mL/g soil) to remove carbonates, total organic carbon content (TOC)

of soil was determined using an elemental analyzer according to the method from Gross et al. (2022). Dissolved organic carbon (DOC) content in the solution was determined in 0.5 M K₂SO₄ (5 mL/g soil) with an organic carbon autoanalyzer (TOC-V_{CPH}, Shimadzu, Japan) (Luo et al. 2016). Microbial biomass carbon (MBC) was measured using the fumigation extraction method (Cui et al. 2021).

Greenhouse gas concentration was measured using a gas chromatograph (Agilent 7890B, USA). The emission flux (F) of CO₂, CH₄, or N₂O was estimated by Eq. (1) (Han et al. 2022b):

$$F = \frac{\rho \frac{dc}{dt} V \frac{273}{273+T}}{M} \quad (1)$$

where ρ is the density of each greenhouse gas under standard conditions; dc/dt is the change in concentration of the gas per unit time; T is the incubation temperature; and M is the weight of the soil.

The cumulative emission amounts of three gases throughout the entire incubation period were calculated based on the following equation (You et al. 2023):

$$S = \sum \left[24 \frac{(F_{i+1} + F_i)}{2} (t_{i+1} - t_i) \right] \quad (2)$$

where S is the cumulative emission of CO₂, CH₄ or N₂O, F_i is the emission flux described in Eq. (1), and t_i is the incubation days of collected gas sample.

The global warming potential (GWP) of the cumulative emission of CO₂, CH₄, and N₂O in 100-year time series was calculated by Eq. (3) (Han et al. 2022b):

$$GWP = S(CO_2) + 265 \times S(N_2O) + 28 \times S(CH_4) \quad (3)$$

where S is the cumulative emission described in Eq. (2).

2.4 Soil bacterial community analysis

Total genomic DNA was extracted from the samples using the TGuide S96 Magnetic Soil /Stool DNA Kit (Tiangen Biotech (Beijing) Co., Ltd.) according to the manufacturer's instructions. The V3 and V4 hyper-variable region of the bacterial 16S rRNA gene was amplified using primer pairs 338F: 5'-ACTCCTACG GGAGGCAGCA-3' and 806R: 5'-GGACTACHVGGG TWTCTAAT-3' (You et al. 2023). High-throughput sequencing analysis of bacterial 16S rRNA genes was performed based on the Illumina HiSeq 6000 platform (2×250 paired ends) at Biomarker Technologies Corporation (Beijing, China). The raw data were quality filtered, trimmed, merged, and clustered into operational taxonomic units (OTUs) at 97% similarity. The OTUs were used for bioinformatics analysis. Alpha diversity (Chao1 and Shannon index) was calculated and plotted by QIIME2 software (version 2020.6.0) and R software (version 4.1.2) to assess the richness and diversity of microbial communities (Zhu et al. 2019). Beta diversity was determined to evaluate the degree of similarity of microbial communities from different samples using QIIME2 (Ibáñez et al. 2024). Principal coordinate analysis (PCoA) was used to analyze the beta diversity based on Bray–Curtis dissimilarity (Yang et al. 2022b). The function of bacteria was predicted by FAPROTAX (version 1.2.6) (Tong et al. 2023).

2.5 Statistical analysis

SPSS 26.0 (SPSS Inc., Chicago, IL, USA) statistical analysis software was used to process the measured data, and Origin 2022 (OriginLab Corp., Northern, MA, USA) software was used for graphing. The data were shown as mean values and error bars represented standard error. Significant differences between the treatments were analyzed by one-way analysis of variance (ANOVA) with a Duncan's multiple range test ($p=0.05$), and were marked by different lowercase letters. The correlations between soil carbon fraction, greenhouse gases and microbial community were analyzed by Pearson's test.

3 Results

3.1 Soil carbon pool

The addition of biochar ($p<0.05$) increased the soil TC and TOC content by 30.02–193.85% and 87.33–684.28%, respectively ($p<0.05$, Table 2 and Fig. 1a and b). Throughout the incubation period, biochar reduced the loss of soil TOC by 67.29–124.33% ($p<0.05$). The soil TC and TOC contents of all the treatments followed the descending order of CBC/OCBC-amended soil (TC: 29.07–33.16 g/kg; TOC: 23.15–26.06 g/kg) > SBC/OSBC-amended soil (TC: 27.04–30.62 g/kg; TOC: 21.53–25.56 g/kg) > ABC/OABC-amended soil (TC: 14.12–17.94 g/kg; TOC: 7.01–9.79 g/kg) > the control (TC: 10.40–11.92 g/kg; TOC: 3.32–4.76 g/kg).

Table 2 TC (total carbon) content (g/kg soil) of different treatments on day 1, 7, 15, 30 and 60

Treatments ^a	Day 1	Day 7	Day 15	Day 30	Day 60
Fresh biochar					
CK	11.92±0.10d	10.40±0.40d	10.69±0.64c	10.86±0.20c	11.03±0.32d
SBC	30.62±0.72b	27.65±1.09b	29.82±0.81a	29.57±1.57a	28.37±0.55b
CBC	33.16±0.63a	30.15±0.47a	30.87±1.07a	30.14±0.98a	30.99±0.21a
ABC	17.94±1.10c	15.23±0.98c	14.92±0.58b	15.99±0.21b	16.37±0.59c
Aged biochar					
CK	11.92±0.10d	10.40±0.40d	10.69±0.64c	10.86±0.20d	11.03±0.32d
OSBC	29.76±1.08b	27.69±0.48b	27.73±1.59a	27.04±0.76b	27.59±0.63b
OCBC	31.57±1.40a	30.56±0.92a	29.07±1.67a	29.89±0.26a	29.93±0.94a
OABC	16.38±0.81c	13.76±0.48c	14.68±1.54b	14.12±0.72c	14.84±0.52c

^a CK: soil amended with *Enteromorpha prolifera*, SBC: soil amended with SBC and *Enteromorpha prolifera*, CBC: soil amended with CBC and *Enteromorpha prolifera*, ABC: soil amended with ABC and *Enteromorpha prolifera*, OSBC: soil amended with OSBC and *Enteromorpha prolifera*, OCBC: soil amended with OCBC and *Enteromorpha prolifera*, OABC: soil amended with OABC and *Enteromorpha prolifera*. Values are means ± standard error ($n=3$). Lowercase letters indicate statistically significant differences ($p<0.05$) between treatments at the same sampling time

(See figure on next page.)

Fig. 1 TOC (total organic carbon) content (a and b), DOC (dissolved organic carbon) content (c and d) and MBC (microbial biomass carbon) content (e and f) of different treatments on day 1, 7, 15, 30 and 60. CK: soil amended with *Enteromorpha prolifera*; SBC: soil amended with SBC and *Enteromorpha prolifera*; CBC: soil amended with CBC and *Enteromorpha prolifera*; ABC: soil amended with ABC and *Enteromorpha prolifera*; OSBC: soil amended with OSBC and *Enteromorpha prolifera*; OCBC: soil amended with OCBC and *Enteromorpha prolifera*; OABC: soil amended with OABC and *Enteromorpha prolifera*. Bars with different lowercase letters indicate statistically significant differences ($p<0.05$) between treatments at the same sampling time. Error bars represent means ± standard error ($n=3$)

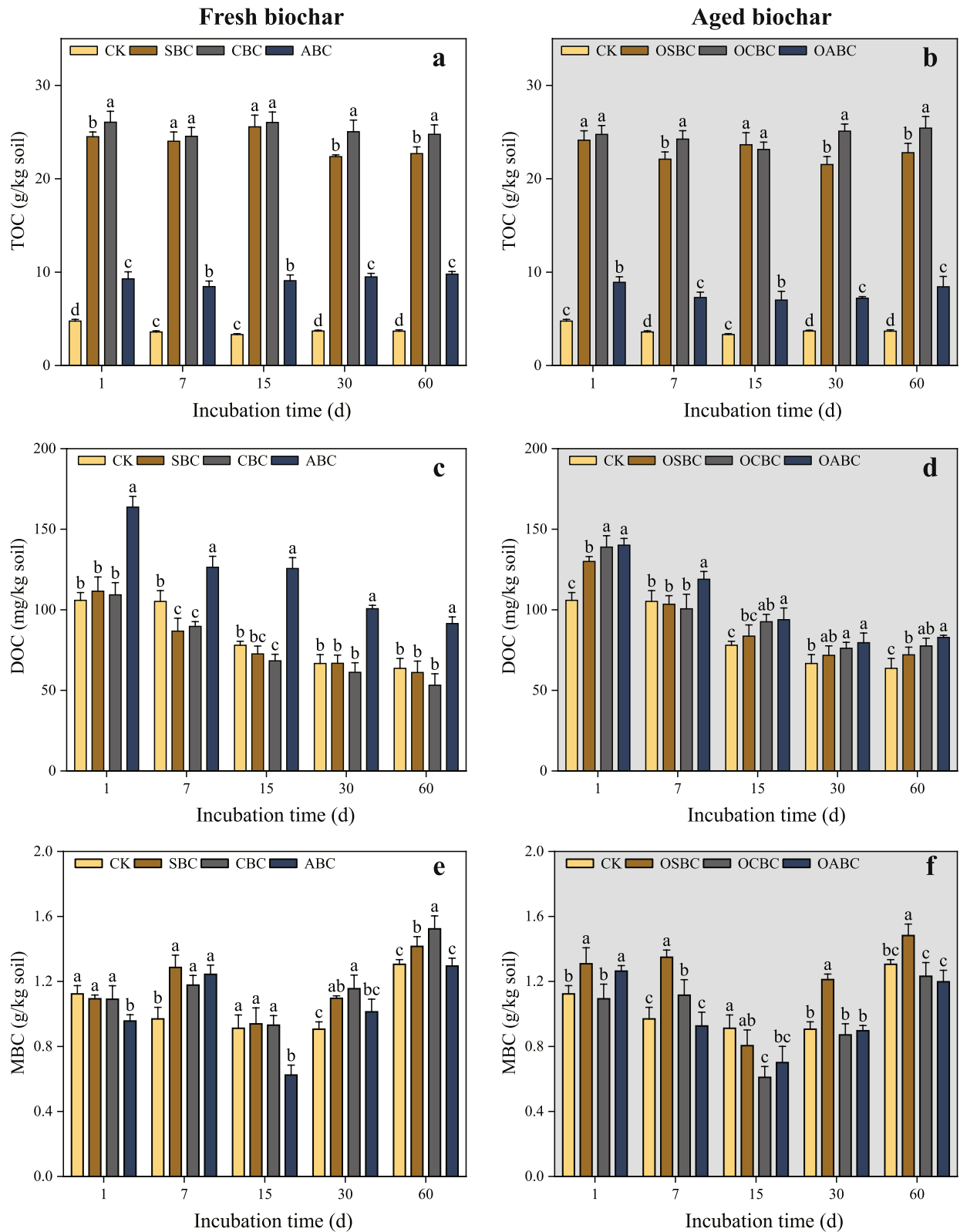


Fig. 1 (See legend on previous page.)

The addition of aged biochar and ABC increased the DOC (dissolved organic carbon) content by 13.16–43.65% on day 60 ($p < 0.05$, Fig. 1c and d). In addition, the DOC content was higher in the ABC/OABC treatments (82.84–163.72 mg/kg) compared to the other treatments. As shown in Fig. 1e and f, the SBC/CBC/OSBC treatment increased the MBC content by 8.42–16.72% ($p < 0.05$). The lowest MBC content (0.61–0.94 g/kg) occurred on day 15. Compared to the control, the percentage of DOC and MBC content in the TOC content was reduced by 61.92–86.15% after biochar application ($p < 0.05$, Fig. S1).

3.2 GHG emissions

As shown in Fig. 2a and b, all biochar except OSBC increased soil cumulative CH_4 emissions by 17.98–36.27% compared to the control at the end of the incubation ($p < 0.05$). The soil cumulative CH_4 emissions of the OSBC treatment (6.16 $\mu\text{g}/\text{kg}$ soil) were the lowest among all the treatments. Biochar decreased the soil cumulative CO_2 emissions by 25.42–153.70% (Fig. 2c and d, $p < 0.05$). Compared to fresh biochar, OSBC and OABC reduced the soil cumulative CO_2 emissions by 60.72–80.49%, while OCBC promoted the soil cumulative CO_2 emissions. Except for the OSBC treatment, the soil cumulative N_2O emissions of the biochar treatments were 42.26–91.05% lower than the control (Fig. 2e and f, $p < 0.05$). The soil cumulative N_2O emissions of fresh biochar treatments were decreased by 25.52–119.02% compared to aged biochar treatments.

Fresh and aged biochar decreased soil global warming potential (GWP) by 94.27–123.24% and 4.91–93.93%, respectively (Fig. 2g and h, $p < 0.05$). The GWP for all the treatments followed the order of ABC-amended soil (–38.88 mg/kg soil) < SBC-amended soil (–17.46 mg/kg soil) < CBC-amended soil (9.59 mg/kg soil) \approx OCBC-amended soil (10.16 mg/kg soil) < OABC-amended soil (81.11 mg/kg soil) < OSBC-amended soil (159.12 mg/kg soil) < the control (167.34 mg/kg soil).

3.3 Soil bacterial community and functions

On day 60, after biochar addition, the abundance of *Chloroflexi*, *Acidobacteriota*, and *Myxococcota* was decreased by 23.75–38.58%, 43.00–45.76%, and 39.27–47.47%, respectively, while the abundance of *Proteobacteria* and *Desulfobacterota* was increased by 6.19–9.85%

and 46.63–131.07%, respectively (Fig. 3a–f). Overall, biochar decreased bacterial richness (Chao1 index) and diversity (Shannon index) by 3.30–3.55% and 7.68–11.60%, respectively (Fig. 3g and h). The PCoA analysis showed that the SBC/OSBC treatment changed bacterial composition (Fig. 3i).

On day 60, biochar increased functional bacteria involved in carbon cycle by 4.91–6.02 (Fig. 4a and c, $p < 0.05$). The carbon cycle was mainly driven by aerobic chemoheterotrophy (32.23–42.84%) and chemoheterotrophy (18.61–36.63%) for all the treatments. The relative abundance of cellulolysis bacteria, aromatic compound degradation bacteria, and xylanolysis bacteria were significantly reduced by 20.02–37.82% with biochar addition throughout the experiment ($p < 0.05$). The addition of SBC increased functional bacteria involved in nitrogen cycle by 76.01–181.99%, while OSBC had the opposite effect (decreased by 64.4–80.85%) ($p < 0.05$, Fig. 4b and d).

3.4 Correlation analysis

As shown in Fig. 5a, there was a positive correlation between DOC content and soil CO_2 emission rate ($r = 0.45$, $p < 0.001$). There was a significant positive correlation between soil CO_2 emission rate and the abundance of *Actinobacteriota* ($r = 0.79$, $p < 0.001$), *Chloroflexi* ($r = 0.84$, $p < 0.001$), *Acidobacteria* ($r = 0.97$, $p < 0.001$) and *Myxococcota* ($r = 0.96$, $p < 0.001$), and the abundance of *Proteobacteria* was negatively correlated with soil CO_2 emission rate ($r = -0.83$, $p < 0.001$, Fig. 5b). The soil CO_2 emission rate was positively correlated with the abundance of cellulolysis bacteria ($r = 0.69$, $p < 0.01$), aromatic compound degradation bacteria ($r = 0.64$, $p < 0.01$) and xylanolysis bacteria ($r = 0.67$, $p < 0.01$, Fig. 5c).

4 Discussion

4.1 The role of biochar in protecting allochthonous organic matter

In our study, the addition of biochar reduced the soil cumulative CO_2 emissions and TOC loss, which was attributed to the negative priming effect on the mineralization of SOC (Zheng et al. 2018, 2021). Both fresh and aged biochar inhibited SOC mineralization, indicating that the negative priming effect induced by biochar could persist for a long time and promote the accumulation of

(See figure on next page.)

Fig. 2 The cumulative CH_4 (a and b), CO_2 (c and d), N_2O (e and f) and GWP (global warming potential) (g and h) emissions of different treatments. CK: soil amended with *Enteromorpha prolifera*; SBC: soil amended with SBC and *Enteromorpha prolifera*; CBC: soil amended with CBC and *Enteromorpha prolifera*; ABC: soil amended with ABC and *Enteromorpha prolifera*; OSBC: soil amended with OSBC and *Enteromorpha prolifera*; OCBC: soil amended with OCBC and *Enteromorpha prolifera*; OABC: soil amended with OABC and *Enteromorpha prolifera*. Error bars represent means \pm standard error ($n = 4$)

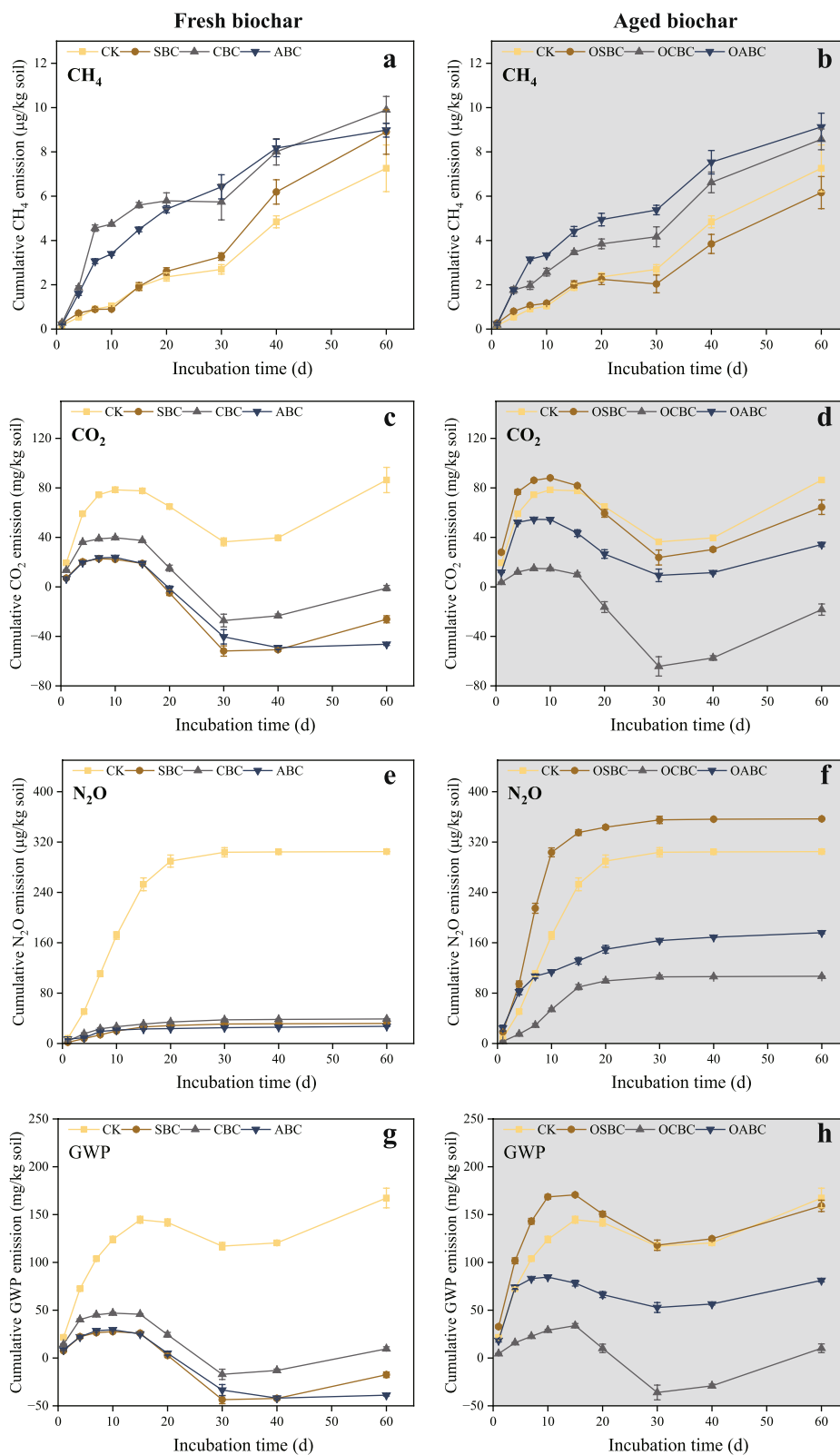


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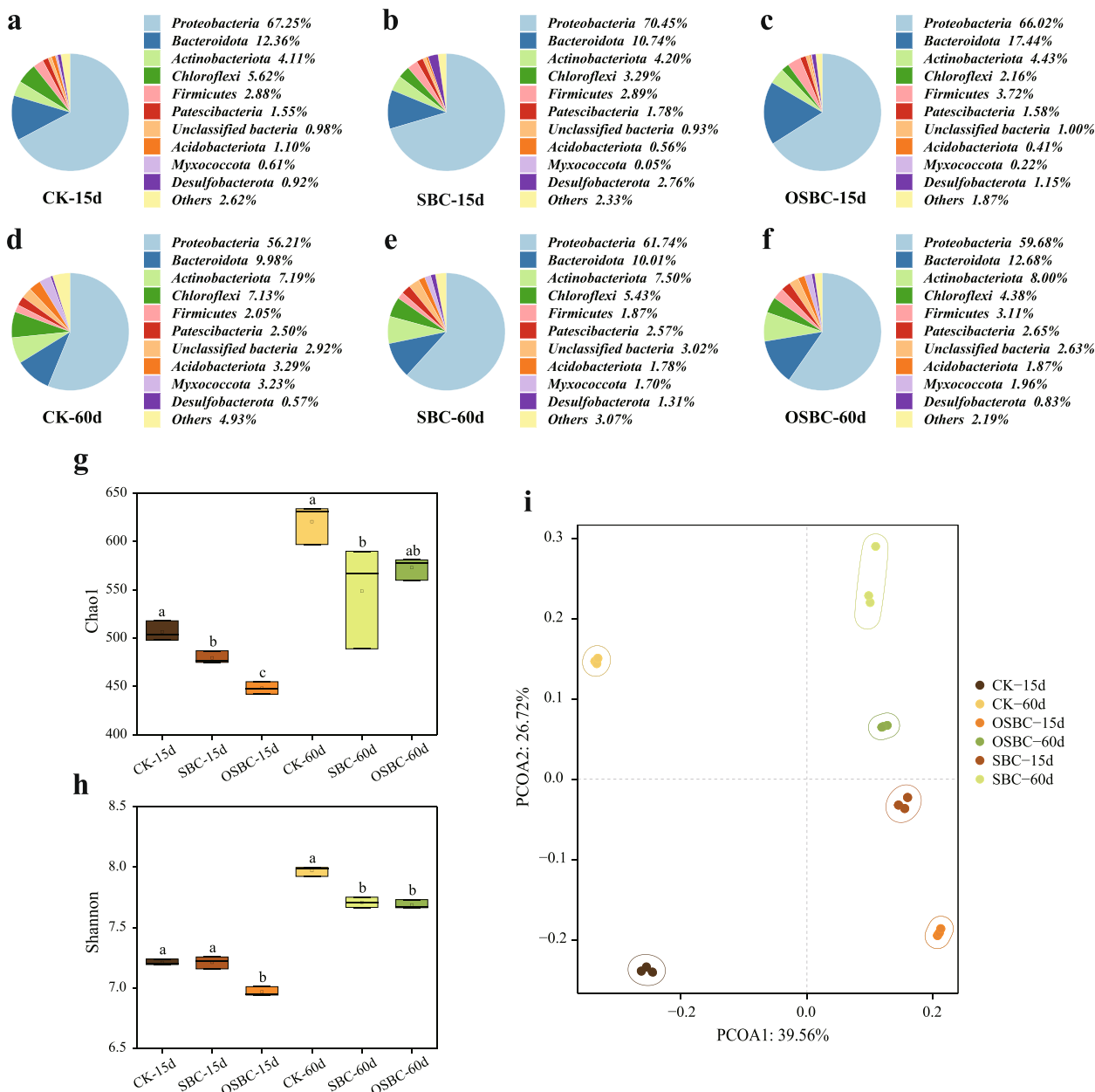


Fig. 3 Relative abundance of bacterial community at phyla level in samples on day 15 (**a**, **b** and **c**) and day 60 (**d**, **e** and **f**). The value of Chao1 (**g**) and Shannon (**h**) of bacteria in soils under different treatments. Unconstrained principal coordinate analysis (PCoA) of the soil bacterial communities based on Bray–Curtis difference (**i**). CK-15d: soil amended with *Enteromorpha prolifera* on day 15; SBC-15d: soil amended with SBC and *Enteromorpha prolifera* on day 15; OSBC-15d: soil amended with OSBC and *Enteromorpha prolifera* on day 15; CK-60d: soil amended with *Enteromorpha prolifera* on day 60; SBC-60d: soil amended with SBC and *Enteromorpha prolifera* on day 60; OSBC-60d: soil amended with OSBC and *Enteromorpha prolifera* on day 60. Bars with different lowercase letters indicate statistically significant differences ($p < 0.05$) between treatments at the same sampling time

SOC. However, contrary to our results, the addition of walnut shell biochar increased cumulative CO₂ emissions by 50.7–73.4% in a field experiment (Sial et al. 2022). A possible reason is that saltmarshes soils contain more iron minerals than terrestrial soils (Zhao et al. 2023), and these minerals promote the formation of organic–mineral

and organic coatings on the surface and in the pores of biochar, mainly through the attraction of negatively charged organic molecules by mineral cations adsorbed on the biochar (Wang et al. 2022; Weng et al. 2022), thus protecting SOM from decomposition. Similarly, biochar modified with iron minerals promoted the stability

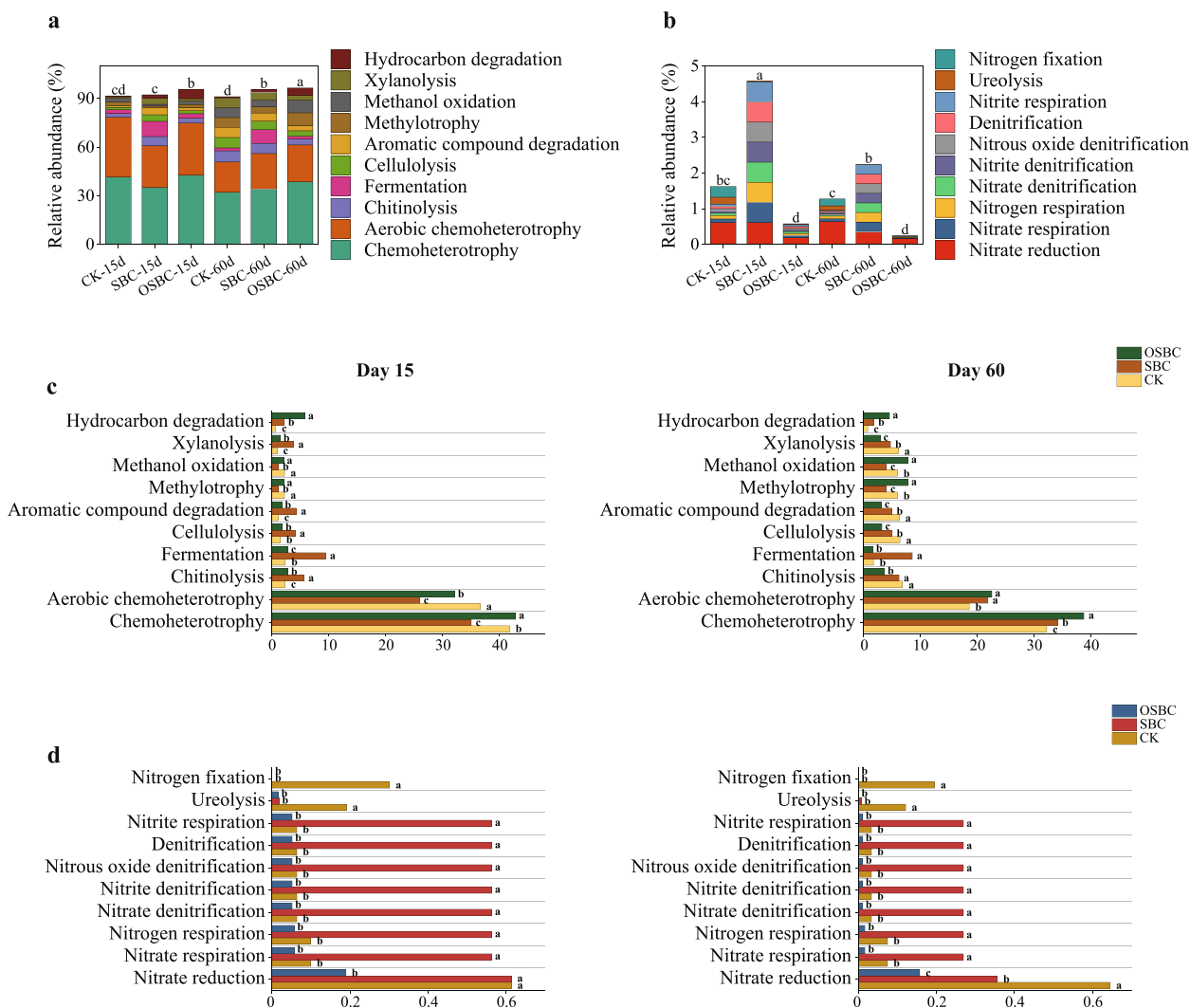


Fig. 4 Relative abundance of functional bacteria associated with the carbon (a and c) and nitrogen (b and d) cycles. CK-15d: soil amended with *Enteromorpha prolifera* at day 15; SBC-15d: soil amended with SBC and *Enteromorpha prolifera* at day 15; OSBC-15d: soil amended with OSBC and *Enteromorpha prolifera* at day 15; CK-60d: soil amended with *Enteromorpha prolifera* at day 60; SBC-60d: soil amended with SBC and *Enteromorpha prolifera* at day 60; OSBC-60d: soil amended with OSBC and *Enteromorpha prolifera* at day 60. Bars with different lowercase letters indicate statistically significant differences ($p < 0.05$) between treatments

of soil aggregate and inhibited SOC mineralization (Liu et al. 2020). Hence, it can be inferred that iron minerals in saltmarshes are a major factor in improving the performance of biochar in sequestering carbon and reducing GHG emissions. Liu et al. (2019) proposed that biochar reduced the activity of enzymes involved in SOM degradation. However, our results showed no reduction in the MBC content of biochar-amended soils (Fig. 2e and f). The reason may be that biochar selectively adsorbs the aliphatic carbon component of SOC and reduces the accessibility of the liable carbon to microorganisms (Zhu et al. 2019), which increases the proportion of recalcitrant carbon in the soil carbon pool and thus facilitates

carbon sequestration. In addition, microbial necromass is preserved by the organic-mineral complexes of biochar (Weng et al. 2022). After biochar addition, the proportion of labile carbon in total organic carbon was reduced by 61.92–86.15%. Biochar contains 60–80% stable aromatic carbon (Brassard et al. 2016) and is much less mineralized than biomass (*Enteromorpha prolifera*) with abundant aliphatic and ester carbon structures (Zhu et al. 2019). Therefore, the addition of biochar dilutes some SOM that is sensitive to microbial activities, thereby enhancing the stability of the carbon pool (Yang et al. 2022b).

The aging of SBC and ABC weakened their ability to mitigate CO₂ emissions. Similarly, Feng et al. (2022)

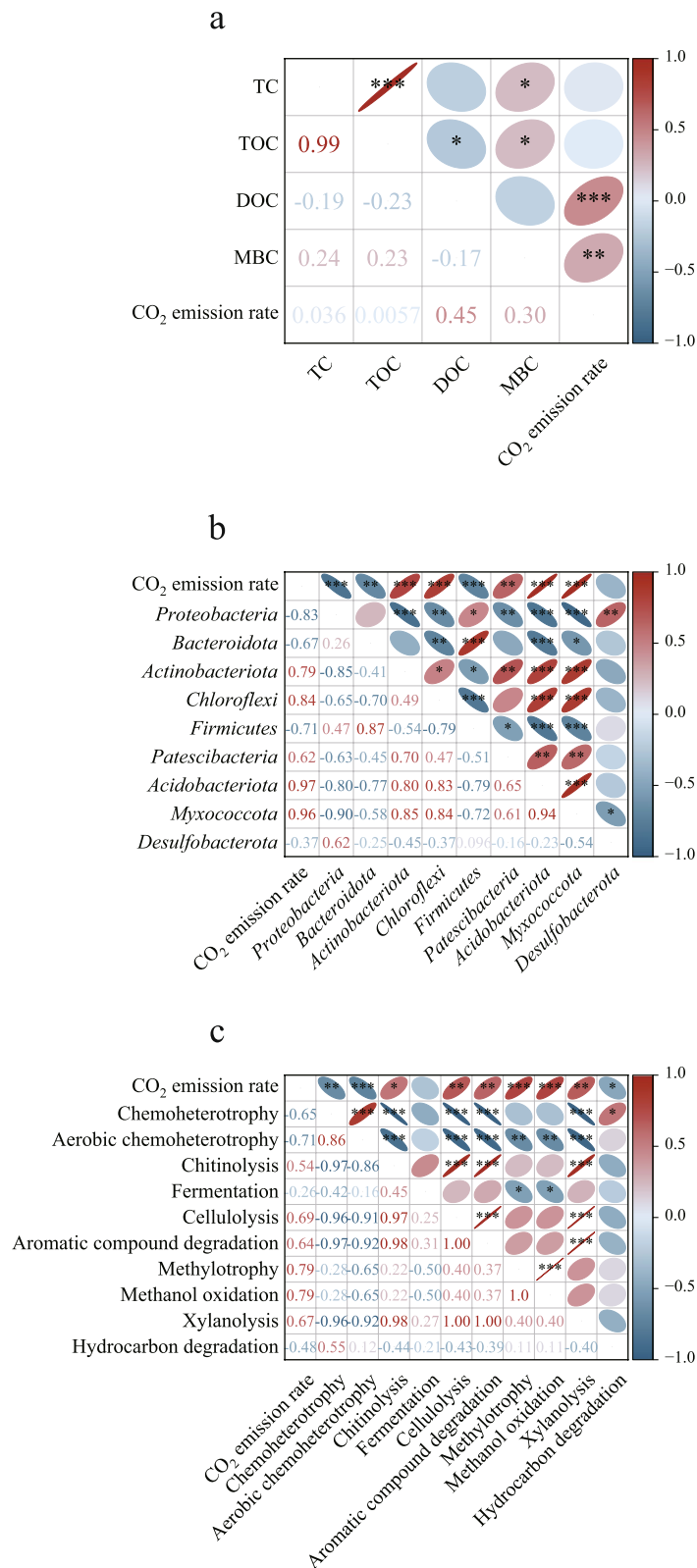


Fig. 5 Pearson's correlation between CO₂ emission rate and carbon fraction content (a), abundance of major bacterial phyla (b), as well as abundance of functional bacteria (c) (* $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$). The values in the graph are Pearson's correlation coefficients

showed that biochar aged for more than a year increased soil CO₂ emissions by 44.3% compared to fresh biochar. This may be due to aged biochar releasing more DOM that is easily utilized by microorganisms (Quan et al. 2020; Yang et al. 2022a), and the speculation was supported by the remarkable ($p < 0.001$) positive correlation between soil CO₂ emission rate and DOC content in our study. Additionally, the aging effect gave biochar a larger surface area to fix more carbon, which provided an attractive habitat for microorganisms and boosted SOM mineralization (Feng et al. 2022).

4.2 Changes in bacterial communities and functions under biochar amendments

Our results showed biochar shifted bacterial diversity and composition, which is closely related to the transformation of SOC (Sun et al. 2020; Yang et al. 2022a; Yu et al. 2022). The abundance of *Proteobacteria* was increased with biochar addition and was negatively correlated with soil CO₂ emission rate. *Proteobacteria*, the dominant phylum in all samples, are copiotrophic bacteria essential for soil carbon fixation (Zheng et al. 2022a; Zhang et al. 2023). Biochar reduced the abundance of *Chloroflexi* and *Acidobacteria* which are oligotrophic bacteria found in low-nutrient environments (Yang et al. 2021; Zhang et al. 2022a). The oligotrophic bacteria that depend on recalcitrant carbon tend to decompose carbon at a low rate, so the presence of massive oligotrophic bacteria in the environment can promote carbon accumulation (Zheng et al. 2022b). However, there is a significant positive correlation between CO₂ emission rate and the abundance of *Chloroflexi* and *Acidobacteria* ($p < 0.001$), suggesting that the reduction of *Chloroflexi* and *Acidobacteria* instead inhibited SOC mineralization in our study.

Contrary to previous studies of a steady rise in the soil cumulative CO₂ emissions (Yang et al. 2022b, 2022a), our research found a significant decrease in the soil cumulative CO₂ emissions from day 15 to 30 and the negative CO₂ emissions in the biochar treatments. (Fig. 2c and d). The soil CO₂ released by the decomposition of organic matter in the early stage could be absorbed by the alkaline soil through abiotic processes (Gao et al. 2020). In addition, it was observed that biocrust such as mosses grew on the soil surface during the incubation period, which absorbed CO₂ through photosynthesis, and biochar stimulated the growth of mosses and accelerated the efficiency of photosynthesis. Moreover, about 90% of *Proteobacteria* are detected to have phosphoenolpyruvate carboxylase and pyruvate carboxylase genes (Akinyede et al. 2022), and thus abundant *Proteobacteria* favored the tricarboxylic acid cycle (carbon fixation pathway). As nutrients were depleted later, the activity of organisms involved in CO₂ fixation was inhibited, therefore,

the soil cumulative CO₂ emissions began to increase after 30 days.

Biochar has a significant effect on carbon metabolism and synthesis (Zhang et al. 2023). The relative abundance of cellulolysis bacteria, aromatic compound degradation bacteria, and xylanolysis bacteria was lower in the biochar treatments than in the control on day 60. This indicated that biochar inhibited SOC mineralization by regulating functional microorganisms, as demonstrated by a significant ($p < 0.01$) positive correlation between the relative abundance of cellulolysis bacteria, aromatic compound degradation bacteria, xylanolysis bacteria and soil CO₂ emission rate. Furthermore, biochar suppressed the degradation of cellulose and hemicellulose containing large amounts of O-alkyl C (Dou et al. 2023), thus resulting in the production of fewer nutrients (glucose and monosaccharides), which inhibited the activity of microorganisms to degrade SOM.

The functional bacteria associated with denitrification participate in the complete reduction of NO₃⁻ to NO₂⁻, NO, N₂O and N₂. The relative abundance of nitrous oxide denitrification bacteria was the highest in the SBC treatment ($p < 0.05$, Fig. 4d), which could explain the reduced soil cumulative N₂O emissions in the SBC treatment. Our results confirmed previous findings that biochar increased N₂O reductase activity and facilitated the reduction of N₂O to N₂, thereby mitigating N₂O emissions (Dong et al. 2020; Han et al. 2022a). Feng et al. (2022) revealed that aged biochar stimulated the colonization of nitrifying bacteria (AOA) and accelerated the process of nitrification, thus promoting soil N₂O emissions. In our study, the abundance of nitrous oxide denitrification bacteria was the lowest in the OSBC-amended soils (Fig. 4d), which resulted in massive N₂O emissions that could not be converted to N₂. This indicates that nitrous oxide denitrification bacteria are not adapted to an environment altered by aged biochar.

4.3 Inadequacies and prospects

The study only investigated areas less affected by tidal action, but did not consider what the effects of biochar on saltmarshes would be in a flooding state. Besides, due to the limited conditions, we did not accurately distinguish the source of carbon using isotopic labeling methods, and the results defaulted to CO₂ originating mainly from liable organic matter (*Enteromorpha prolifera*). Future research will focus on exploring the feasibility of applying biochar in practical engineering.

5 Conclusion

Biochar is an effective amendment for mitigating carbon loss due to the degradation of saltmarshes. However, limited studies have investigated the effects of biochar on

the carbon pool, GHG emissions and functional microorganisms of saltmarsh soil with allochthonous organic matter addition. Therefore, in this study, we added fresh biochar or aged biochar to saltmarsh soils mixed with *Enteromorpha prolifera*, and investigated the effects of biochar on soil carbon content, greenhouse gases, and microorganisms by a 60-day laboratory simulation. Our results suggested that both fresh and aged biochar mitigated SOC mineralization and global warming potential. This is mainly attributed to allochthonous organic matter protection from mineralization and reduction of bacteria involved in carbon decomposition. Further in situ studies will be conducted to evaluate the effects of biochar application on the carbon sinks, global warming potential, and ecological functions in saltmarshes.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1007/s44246-023-00087-9>.

Additional file 1: Fig. S1. Proportion of MBC (microbial biomass carbon) and DOC (dissolved organic carbon) in TOC (total organic carbon) at the end of cultivation. CK: soil amended with *Enteromorpha prolifera*; SBC: soil amended with SBC and *Enteromorpha prolifera*; CBC: soil amended with CBC and *Enteromorpha prolifera*; ABC: soil amended with ABC and *Enteromorpha prolifera*; OSBC: soil amended with OSBC and *Enteromorpha prolifera*; OCBC: soil amended with OCBC and *Enteromorpha prolifera*; OABC: soil amended with OABC and *Enteromorpha prolifera*. Bars with different lowercase letters indicate statistically significant differences ($p < 0.05$) between treatments. Error bars show means \pm standard error ($n = 3$).

Fig. S2. The images of different treatments. SBC: soil amended with SBC and *Enteromorpha prolifera*; CBC: soil amended with CBC and *Enteromorpha prolifera*; ABC: soil amended with ABC and *Enteromorpha prolifera*; OSBC: soil amended with OSBC and *Enteromorpha prolifera*; OCBC: soil amended with OCBC and *Enteromorpha prolifera*; OABC: soil amended with OABC and *Enteromorpha prolifera*.

Authors' contributions

All authors contributed to the study conception and design. Yiyi Zhang performed methodology, experiments and wrote original draft; Yuzhou Huang performed material preparation, data collection and analysis; Jing Hu, Tao Tang and Caicai Xu performed investigation and material preparation; Kokoe Sunday Effiong performed data collection and analysis; Xi Xiao performed supervision and funding acquisition. All authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets used or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing 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.

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