



Investigation on the feasibility of straw incorporation to improve soil fertility without obviously increasing global warming potential

Mengxue Zhang^{1, 2}, Rujia Liao^{1, 2}, Wenzhao Zhang¹, Cheng Fang¹, Simon Guerrero-Cruz³, András Tánicsics⁴, Baoli Zhu¹, Wenxue Wei¹, Rong Sheng¹

¹Taoyuan Station of Agro-Ecology Research, Institute of Subtropical Agriculture, Chinese Academy of Sciences, Changsha 410125, China

²College of Resource and Environment, University of Chinese Academy of Sciences, Beijing 100049, China

³Department of Water Resources and Environmental Engineering, Asian Institute of Technology, Pathum Thani 12120, Thailand

⁴Hungarian University of Agriculture and Life Sciences, Páter K. u. 1., H-2100, Gödöllő, Hungary

Correspondence to: Rong Sheng (shengrong@isa.ac.cn)

Abstract. The utility of rice straw as an organic fertilizer has been widely recognized as a promising approach to enhancing soil fertility. However, straw return is currently in a dilemma, as it may also provoke greenhouse gas (GHG) emissions, leading to serious environmental consequences. It is urgent to reveal the feasibility of straw incorporation regarding soil fertility improvement without notable increases in GHG emissions. Here, a soil microcosm experiment was employed to investigate the relationships between soil fertility and GHG fluxes and the underlying mechanisms influenced by straw amendments. Paddy soils were collected from a long-term rice straw incorporation field experiment. The dynamics of GHG fluxes and concentrations in soils, and the variations in the abundances of soil microbial communities were systematically determined. The results indicated that continuous rice straw incorporation at half of the harvest (ST1) obviously improved soil fertility but did not induce significant elevation of global warming potential (GWP). The minimal increase in GWP was mainly attributed to the significant reduction in N₂O emission and the slight rise in CH₄ emission compared to straw removal. The main mechanisms for these consequences were that ST1 possessed the highest *nosZII* abundance and the lowest *nirS/nosZII* ratio; meanwhile, its CH₄ production ability fluctuated around the soil CH₄ holding capacity, and most of the produced CH₄ was consumed by methanotrophs. In conclusion, rice straw can be incorporated into paddy soils at a suitable application rate, which can effectively enhance soil fertility without inducing an additional warming effect.

1 Introduction

Rice cultivation not only provides staple food for nearly half of the global population, but also produces massive rice straw that is estimated to be 800 to 1000 million tons·year⁻¹ globally (Yuan et al., 2021; Harun et al., 2022). Rice straw has long been a valuable organic resource that can be incorporated into rice paddies to improve soil productivity (Huo et al., 2024; Zhou et al., 2024). The incorporation can enhance soil carbon (C) sequestration (Chen et al., 2025; Li et al., 2025a). It was estimated that about 15%–25% of the incorporated straw C was converted into soil organic carbon (SOC) (Liu et al., 2023b).



32 Straw return can also provide abundant available nutrients for rice plant growth, including nitrogen (N), phosphorus (P), and
33 potassium (K) (Yin et al., 2018; Van Hung et al., 2020; Wang et al., 2020). Thus, rice straw incorporation has been proposed
34 to be an important agronomic practice for sustainable rice agriculture.

35 However, rice straw return was also revealed to exacerbate greenhouse gas (GHG) emissions from paddy fields (Shi et al.,
36 2023; He et al., 2024). Rice cultivation contributes around 12% of global agricultural GHG emissions (Fao, 2020) with straw
37 incorporation being one of the key drivers. Numerous studies indicated that compared to straw removal, rice straw
38 incorporation substantially promoted methane (CH₄) emissions (Han et al., 2023; Song et al., 2024; Qin et al., 2025). The
39 increases in CH₄ emissions varied widely across observations, which approximately ranged from 23% to 1192% (Shen et al.,
40 2014; Jiang et al., 2019; Lee et al., 2020; Nan et al., 2022; Song et al., 2024). The incorporation may also elevate carbon
41 dioxide (CO₂) fluxes from rice paddies, for example, by 9% to 67% (Shen et al., 2014; Lee et al., 2020; Han et al., 2023;
42 Song et al., 2024). However, the effect of rice straw incorporation on nitrous oxide (N₂O) emissions from rice fields was
43 inconsistent and controversial across studies (Shen et al., 2014; Wang et al., 2015; Han et al., 2023; Qin et al., 2023). The
44 variations in N₂O emissions were about -73% to 137% in comparison with their controls (Shen et al., 2014; Wang et al.,
45 2015; Han et al., 2023; Qin et al., 2023). Despite these issues, managing the straw input rate was suggested to mitigating the
46 straw-induced GHG emissions (Shen et al., 2014; Chen et al., 2018; Li et al., 2024). For instance, incorporating with half of
47 the harvested rice straw effectively reduced CH₄ emission by 48% in relative to the scenario receiving full of the straw (Shen
48 et al., 2014). However, most studies focused either on the influence of straw return on soil productivity (Huo et al., 2024;
49 Zhou et al., 2024) or on GHG emissions (Shi et al., 2023; He et al., 2024), rarely taking both into consideration to reveal the
50 rational straw application. Hence, it is essential to investigate the feasibility of straw incorporation not causing noticeable
51 increases in GHG emissions while improving soil fertility.

52 Here, a soil culture experiment was employed to continue the field experiment with 5-year rice straw incorporation at
53 different rates. The incubation was set with flooding and drying periods. The dynamics of GHG emissions and
54 concentrations in soils were determined, and the variations in the abundance of soil microbial communities involved in GHG
55 production and consumption were measured. This study aimed to explore whether there is a suitable straw application rate
56 that can boost soil fertility without causing elevated GHG emissions, and the related mechanisms.

57 **2 Materials and methods**

58 **2.1 Soil collection and rice straw preparation**

59 Soils were collected from a long-term straw return field experiment initiated in 2017, which was located at the Taoyuan
60 Agroecosystem Research Station (28°55' N, 111°26' E), Hunan, China. The region has a subtropical monsoon climate with a
61 mean annual rainfall of 1440 mm and a mean annual temperature of 16.5°C. The soil was derived from quaternary red clay
62 and classified as Ultisol according to USDA soil taxonomy. The experiment contained various rates of rice straw
63 amendments with three replications in a randomized block design. Each plot was 30 m² (7.5 m × 4 m) and the cropping was



single rice. Rice straw was evenly spread on the surface of the corresponding plots and turned over into the soils in each early May, which was about one month ahead of rice seedling transplantation. Besides, urea, superphosphate, and potassium chloride were annually applied to all treatments at $112.60 \text{ kg N} \cdot \text{ha}^{-1}$, $46.33 \text{ kg P} \cdot \text{ha}^{-1}$, and $135.46 \text{ kg K} \cdot \text{ha}^{-1}$, respectively. The soils (0–20 cm) were separately taken from CK, ST1, ST2, and ST3 treatments of the field experiment in May 2022 before straw application. The corresponding straw amounts were 0, 3750, 7500, and $11250 \text{ kg} \cdot \text{ha}^{-1}$, representing 0, 50%, 100%, and 150% of the local rice straw yield, respectively. The soil from one treatment was collected by taking five points following an “S” pattern in each plot and mixed, and then transported to the lab. After removal of visible plant residues and gravel, the soils were pre-incubated under flooding in a greenhouse for 30 days. The soil physicochemical properties were shown in Table 1.

Rice straw was prepared by collecting it from the field in October 2021, followed by air-drying and grinding ($< 1 \text{ mm}$) for the microcosm experiment. The rice straw contained 44.14% of C, 0.817% of N, 2.34% of K, and 0.143% of P.

2.2 Microcosm experiment

The incubation pots were prepared by sealing the bottoms of PVC cylinders (height 15 cm, diameter 15.5 cm). The pots for gas sampling were further equipped as follows (Fig.S1). For soil gas sampling, two holes (diameter 1.7 cm) across the cylinder were drilled at positions of 5 cm from the bottom, filled with a gas-permeable silicone tube (length 15.5 cm, inner diameter 1.2 cm) closed at both ends with silicone septa. One end was connected with a three-way stopcock outside the cylinder via a stainless steel tube (diameter 0.2 cm) through the septum. The drilled holes in the cylinder wall were then sealed. For gas flux sampling, a hollow rectangular groove (deep 2 cm) was fixed on the top fringe of each pot for water sealing during sampling. The gas sampling was carried out using a static chamber (height 29.5 cm, diameter 19.5 cm) fitted with a small electric fan at the inner top.

The pre-incubated soil slurries from different treatments were separately filled into the pots, and each pot contained 1.27 kg (dry weight) of soil to reach about 10 cm in depth. The incubation followed the field regime and the straw amendment rates were calculated based on the field experiment, which were 0, 2.54, 5.08, and $7.62 \text{ g rice straw per pot}$ for CK, ST1, ST2, and ST3 treatments, respectively. Each treatment had eight pots: three for gas sampling, three for soil sampling, and two for replacing sampling-induced soil cylinders to minimize gas exchange from the sampled holes.

After urea ($100 \text{ mg N} \cdot \text{kg}^{-1}$ dry soil) and straw were applied, the soil was mixed thoroughly, and deionized water was added to meet a 3 cm water layer. Then, the microcosms were randomly positioned and incubated in the dark at 30°C for 91 days (28-day flooding and 63-day drying). This incubation period was based on our pre-experiment to cover both CH_4 and N_2O emission peaks. During the flooding, a 3 cm top water layer was maintained with deionized water. The drying process was carried out by removing the top water from the microcosm with a syringe on day 28 and then drying by natural evaporation in the room.



2.3 Gas and soil sampling

Gas samples for both GHG fluxes and soil concentrations were taken at 1–3 day(s) intervals. At each sampling event, after the groove was filled with water and covered by the chamber, 30 mL headspace gas was taken with a syringe at 0 and 60 min separately from each gas sampling pot (Wang et al., 2017; Zhou et al., 2020). The electric fan was running during the sampling period. At the same time, 1 mL soil gas was taken from the buried silicone tube, followed by an equal volume of helium injected back. All the gas samples were stored in 12 mL pre-evacuated exetainer vials (Labco, UK). Soil samples (0–5 cm) were taken every two weeks via a modified syringe sampler with its head cut off. At each sampling event, three cores (diameter 1.5 cm) were sampled from each pot and mixed, weighing about 35 g wet soil. During flooding, the soil samples were collected directly without removing the overlying water to minimize the disturbance (Cai et al., 2022; Cai et al., 2025). Before starting soil sampling, placing the front end of the syringe sampler as close as possible to the soil surface effectively reduced the collection of overlying water. A part of the sample was used for soil moisture measurement, and the rest was flash-frozen in liquid nitrogen and stored at -80°C for molecular analysis. After sampling, the holes were immediately replaced by filling with the cores taken from the soil replacement pots.

2.4 Analysis of gas concentrations and soil properties

Gas samples were analyzed using a gas chromatography (7890A, Agilent, USA) equipped with an electron capture detector for N₂O and a flame ionization detector for CH₄ and CO₂. Gas fluxes were calculated based on the Ideal Gas Law (Eq. 1 and Eq. 2), and cumulative emissions by the Trapezoidal Rule (Eq. 3). Global warming potential (GWP) was calculated using cumulative emissions (Eq. 4).

$$F = \frac{\Delta m}{A \times \Delta t}, \quad (1)$$

Where F is the gas flux ($\mu\text{g} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$); Δm is the mass of gas collected in a single sampling event (μg); A is the soil surface area covered by the static chamber (m^2); Δt is the time interval after chamber closure (h).

$$\Delta m = M \times \Delta n = M \times \frac{pV \times \Delta c}{RT}, \quad (2)$$

Where M is the molar mass of gas ($\text{g} \cdot \text{mol}^{-1}$); Δn is the amount of substance of gas collected in a single sampling event (mol); p is the atmospheric pressure (Pa); V is the active volume of the static chamber during sampling (m^3); Δc is the gas concentration difference (ppm); R is the gas constant ($8.314 \text{ J} \cdot \text{mol}^{-1} \cdot \text{K}^{-1}$); T is the temperature during sampling (K).

$$CE = \sum_{i=1}^n \frac{F_{i+1} + F_i}{1000} \times (t_{i+1} - t_i) \times 24 \times \frac{1}{2}, \quad (3)$$

Where CE is the gas cumulative emission ($\text{g} \cdot \text{m}^{-2}$); F is the gas flux ($\mu\text{g} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$); 1000 in the denominator is to transform μg to g; t is the sampling time (d); i and $i+1$ represent the i^{th} and $(i+1)^{\text{th}}$ sampling events, respectively; 24 is the transform factor from day to hour; n is the total number of sampling events.

$$GWP = CE_{\text{CO}_2} + 27.9 \times CE_{\text{CH}_4} + 273 \times CE_{\text{N}_2\text{O}}, \quad (4)$$



Where the unit of GWP is $\text{g CO}_2 \text{ equivalent} \cdot \text{m}^{-2}$. CE_{CO_2} , CE_{CH_4} , and $CE_{\text{N}_2\text{O}}$ represent the cumulative emissions ($\text{g} \cdot \text{m}^{-2}$) of CO_2 , CH_4 , and N_2O , respectively. The factors 27.9 and 273 are the latest-updated 100-year global warming potentials for CH_4 and N_2O , respectively (Forster et al., 2021).

Soil properties were measured by standard protocols (Bao, 2000). Soil pH was determined using soil slurry at a soil–water ratio of 1:2.5 by a pH meter (FE28–Standard, Mettler Toledo, Switzerland). Soil bulk density (BD) was measured by the ring knife method. Soil cation exchange capacity (CEC) was extracted by 1.66 $\text{cm Co}(\text{NH}_3)_6\text{Cl}_3$ at a soil–extractant ratio of 7:100. Olsen P was extracted by 0.5 M NaHCO_3 at a soil–extractant ratio of 1:20. Soil CEC and Olsen P were quantified colorimetrically via a continuous–flow automatic analyzer (AutoAnalyzer 3, SEAL Analytic, Germany). Available N (Av_N) was determined by the alkaline diffusion method. Available K (Av_K) was extracted by 1 M NH_4OAc at a soil–extractant ratio of 1:10 and analyzed via an atomic absorption spectrometer (novAA350, Analytic Jena, Germany). Soil available manganese (Av_Mn), copper (Av_Cu), and zinc (Av_Zn) were simultaneously extracted by 5 mM $\text{DTPA} \text{--} \text{CaCl}_2 \text{--} \text{TEA}$ at a soil–extractant ratio of 1:2 and determined by an inductively coupled plasma emission spectrometer (ICP–OES 5110, Agilent, USA). Soil total C (TC) and total N (TN) were analyzed by combustion using an elemental analyzer (Vario MAX cube, Elementar, Germany). Soil total P (TP) and total K (TK) were measured by the ICP–OES after digestion by $\text{HNO}_3 \text{--} \text{HClO}_4 \text{--} \text{HF}$.

2.5 DNA extraction and real-time quantitative PCR

Soil DNA was extracted manually as previously described (Chen et al., 2010). Each sample was performed in triplicate. The quality and concentration of DNA were measured by a NanoDrop ND–1000 spectrophotometer (Thermo Scientific, USA). The abundances of bacterial 16S rRNA, fungal 18S rRNA, *mcrA*, *pmoA*, *nirS*, and *nosZII* were determined by real-time quantitative PCR (qPCR). The genes of *mcrA* and *pmoA* were used as markers for methanogens and aerobic methanotrophs, respectively (Liu et al., 2025). The genes of *nirS* and *nosZII* were selected to reflect N_2O production (Chen et al., 2024; Kong et al., 2024) and N_2O reduction (Jones et al., 2013; Hallin et al., 2018; Liu et al., 2023a; Yang et al., 2024), respectively. The qPCR primers and thermal programs were shown in Table S1. All qPCR reactions were conducted in triplicate on 384-well plates by a LightCycler 480II (Roche, Switzerland). Each reaction (10 μL) contained 1 μL of template DNA (5 $\text{ng} \cdot \mu\text{L}^{-1}$), 5 μL of SYBR Green Pro Taq HS Premix (Accurate Biotechnology, China), and 0.3–1.2 μL of each primer (10 μM). Negative controls were included in each plate by replacing the template DNA with sterile H_2O . Standard curves were prepared by ten-fold serial dilutions of target gene-carrying plasmids. The amplification efficiency was 87%–88% for *nosZII* and 90%–102% for other genes.

2.6 Statistical analysis

Statistical tests were performed in IBM SPSS Statistics 25 (NY, USA) and OriginPro 2026 (OriginLab Corporation, MA, USA). Homoscedasticity ($\alpha = 0.05$) was checked with Levene’s test. Significant differences between treatments ($\alpha = 0.05$)



were tested by one-way analysis of variance (ANOVA), followed by Tukey's Honestly Significant Difference (HSD) test when data were homoscedastic or Games–Howell (GH) test when data were heteroscedastic.

3 Results

3.1 Soil properties

Soil physicochemical characteristics were clearly affected by continuous straw incorporation at various rates for five years (Table 1). Although the concentrations of soil TP and TK were not strongly influenced by straw application, the concentrations of TC, TN, available nutrients, and CEC were positively related to the straw incorporation rate and soil BD was negatively related to the rate. When compared with CK, even in the treatment with the least amount of straw (ST1), the TC and TN contents were increased by 4.19% and 2.58%, respectively. ST1 treatment also resulted in obvious increases in Av_N, Olsen P, and Av_K by 6.83%, 15.09%, and 38.52% ($p < 0.05$), respectively. Furthermore, the contents of soil available micronutrients of Mn, Cu, and Zn in ST1 treatment were also increased by 18.48%, 4.57%, and 8.09%, respectively.

Table 1: Soil properties after five-year straw incorporation at different rates

| | pH (H ₂ O) (1:2.5) | BD g·cm ⁻³ | CEC cmol ⁺ ·kg ⁻¹ | Av_N mg·kg ⁻¹ | Olsen P mg·kg ⁻¹ | Av_K mg·kg ⁻¹ | Av_Mn mg·kg ⁻¹ | Av_Cu mg·kg ⁻¹ | Av_Zn mg·kg ⁻¹ | TC g·kg ⁻¹ | TN g·kg ⁻¹ | TP g·kg ⁻¹ | TK g·kg ⁻¹ |
|-----|----------------------------------|--------------------------|--|-----------------------------|--------------------------------|-----------------------------|------------------------------|------------------------------|------------------------------|--------------------------|--------------------------|--------------------------|--------------------------|
| CK | 4.90± 0.03 a | 1.45± 0.03 a | 10.85± 0.15 a | 192.79± 5.38 a | 13.19± 1.76 a | 51.09± 2.70 c | 8.28± 0.22 a | 1.75± 0.10 a | 1.36± 0.07 a | 21.74± 0.46 a | 2.057± 0.04 a | 0.618± 0.03 a | 12.16± 0.08 a |
| ST1 | 4.98± 0.05 a | 1.41± 0.01 a | 11.19± 0.23 a | 205.96± 3.59 a | 15.18± 1.68 a | 70.77± 3.62 bc | 9.81± 1.50 a | 1.83± 0.09 a | 1.47± 0.10 a | 22.65± 0.59 a | 2.110± 0.05 a | 0.657± 0.02 a | 12.01± 0.11 a |
| ST2 | 4.93± 0.02 a | 1.34± 0.07 a | 11.25± 0.20 a | 212.07± 8.15 a | 12.57± 1.33 a | 82.35± 5.01 ab | 11.65± 2.30 a | 1.94± 0.07 a | 1.70± 0.07 a | 23.52± 0.70 a | 2.197± 0.07 a | 0.610± 0.03 a | 11.95± 0.19 a |
| ST3 | 5.02± 0.07 a | 1.31± 0.03 a | 11.45± 0.26 a | 209.22± 11.70 a | 16.06± 2.22 a | 105.36± 11.01 a | 16.69± 5.97 a | 1.88± 0.05 a | 1.76± 0.18 a | 23.71± 1.45 a | 2.160± 0.12 a | 0.648± 0.04 a | 12.04± 0.03 a |

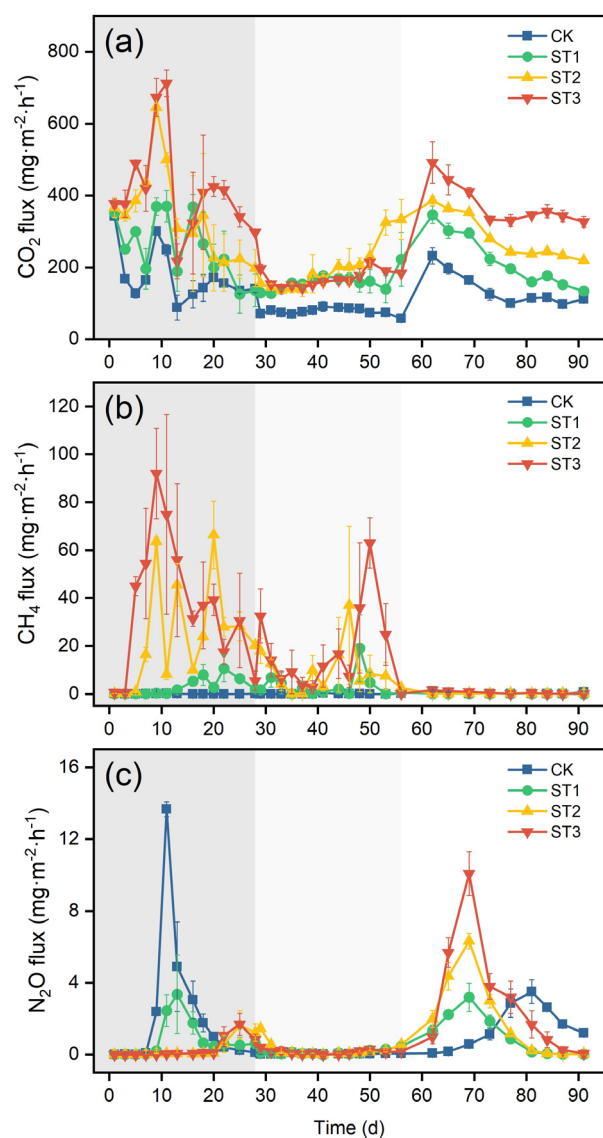
CK, ST1, ST2, and ST3 received 0, 50%, 100%, and 150% of the local harvested rice straw, respectively. Different lower-case letters indicate significant differences between treatments ($\alpha = 0.05$). Data are given in average \pm standard error ($n = 3$). Abbreviations: BD, bulk density; CEC, cation exchange capacity; Av_N, available nitrogen; Olsen P, available phosphorus; Av_K, available potassium; Av_Mn, available manganese; Av_Cu, available copper; Av_Zn, available zinc; TC, total carbon; TN, total nitrogen; TP, total phosphorus; TK, total potassium.

3.2 CO₂, CH₄, and N₂O emissions

Greenhouse gas emissions were obviously influenced by straw incorporation (Fig.1). Generally, the CO₂ flux was positively related to the straw incorporation rate throughout the incubation (Fig.1a). Compared to CK, ST1 caused a significant increase in the cumulative CO₂ emission by 66% ($p < 0.05$, Table 2). With the straw amount increasing, the cumulative CO₂ emissions of ST2 and ST3 treatments rose to 2.2 and 2.5 times those of CK ($p < 0.05$), respectively. A significant difference was also detected between ST2 and ST3 ($p < 0.05$).



The CH₄ fluxes occurred mainly during flooding (day 0–day 28), and partly during the transition time from flooding to drying (day 29–day 56) (Fig.1b). It was observed that CK emitted minimal CH₄, while ST1 emitted a slightly higher CH₄ than CK. Further increasing the straw rate induced significant elevation of CH₄ fluxes. The more straw input, the more CH₄ was emitted. The cumulative CH₄ emission of ST1 was only 4.41 g·m⁻², while the cumulative CH₄ emissions of ST2 and ST3 were approximately 4 and 8 times higher than those of ST1 ($p < 0.05$), respectively, reaching about 23 and 38 g·m⁻² (Table 2).



186

187 **Figure 1: Dynamics of GHG fluxes during the incubation. (a) CO₂; (b) CH₄; (c) N₂O. Data are given in average ±**
 188 **standard error (n = 3). Grey, lighter grey, and white areas indicate flooding, the early drained period, and the late**
 189 **drained period, respectively.**



Table 2: Cumulative emissions and global warming potential

| | CO₂ (g·m⁻²) | Cumulative emissions CH₄ (g·m⁻²) | N₂O (g·m⁻²) | Global warming potential (g CO₂ equivalent·m⁻²) |
|-----|--|---|--|--|
| CK | 280.19 ± 4.37 d | 0.36 ± 0.02 d | 2.61 ± 0.08 ab | 1003.49 ± 24.74 c |
| ST1 | 465.65 ± 16.07 c | 4.41 ± 0.52 c | 1.63 ± 0.11 c | 1034.95 ± 48.01 c |
| ST2 | 605.91 ± 26.84 b | 23.22 ± 0.93 b | 2.04 ± 0.17 bc | 1810.05 ± 56.46 b |
| ST3 | 695.71 ± 17.59 a | 38.01 ± 0.35 a | 2.80 ± 0.20 a | 2521.49 ± 80.01 a |

Different lower-case letters indicate significant differences between treatments ($\alpha = 0.05$). Data are given in average ± standard error (n = 3).

The dynamics of N₂O emission during the experiment exhibited two peaking periods: one occurred just after nitrogen fertilization and the other happened during drying process, but the variation patterns of the flux peaks between the treatments within the two peaking times were obviously different (Fig.1c). During the first peaking period, CK emitted most N₂O, followed by ST1, while the N₂O emitted from ST2 and ST3 were negligible. However, this order reversed in the latter drying period, where the highest N₂O flux was from ST3, followed by ST2, whereas the N₂O fluxes of ST1 and CK were similarly low, despite that the peak of CK appeared about 10 days late. The cumulative N₂O emission indicated that ST1 emitted significantly lower N₂O than CK ($p < 0.05$) with only 1.63 g·m⁻² (Table 2). Meanwhile, ST2 also generated about 22% lower N₂O than CK, while the treatment receiving the highest amount of straw (ST3) possessed a similar cumulative N₂O emission to CK.

Overall, ST1 displayed a slightly higher GWP than CK without a significant difference, but both ST2 and ST3 showed significantly higher GWPs than CK ($p < 0.05$).

3.3 Dynamics of CO₂, CH₄, and N₂O concentrations in soils

The soil concentrations of the three GHGs were deeply affected by the amendments of rice straw but exhibited distinct patterns (Fig.2). Straw incorporation significantly increased soil CO₂ concentration compared to CK, with the peaking time of straw-amended treatments occurring around 10 days of the incubation (Fig.2a). The outstanding characteristic of the dynamics of CO₂ concentrations was that the increases were proportional to the straw incorporation rates. For example, at the peaking time, the increments of ST1, ST2, and ST3 were approximately 50%, 100%, and 150% against CK, respectively. The soil CH₄ concentrations indicated that straw incorporation resulted in sharp increases since day 3 (Fig.2b). On average, the CH₄ concentrations of ST1, ST2, and ST3 were about 45, 57, and 58 times those of CK during day 1 and day 56. It was also observed that the CH₄ concentrations of ST1 fluctuated around 200 mmol·mol⁻¹. The treatments of ST2 and ST3 further promoted soil CH₄ concentrations but there was no significant difference between them.

The soil N₂O concentrations were only detectable between days 62 and 87 under drying phase (Fig.2c). The unique feature was that the N₂O contents of CK and ST1 were quite similar despite the peaking time in CK was delayed. It was observed



that the N₂O concentration of ST2 was almost two times that of ST1. Although the peak of ST3 was not as high as that of ST2, ST3 maintained high N₂O concentrations for longer in the soil.

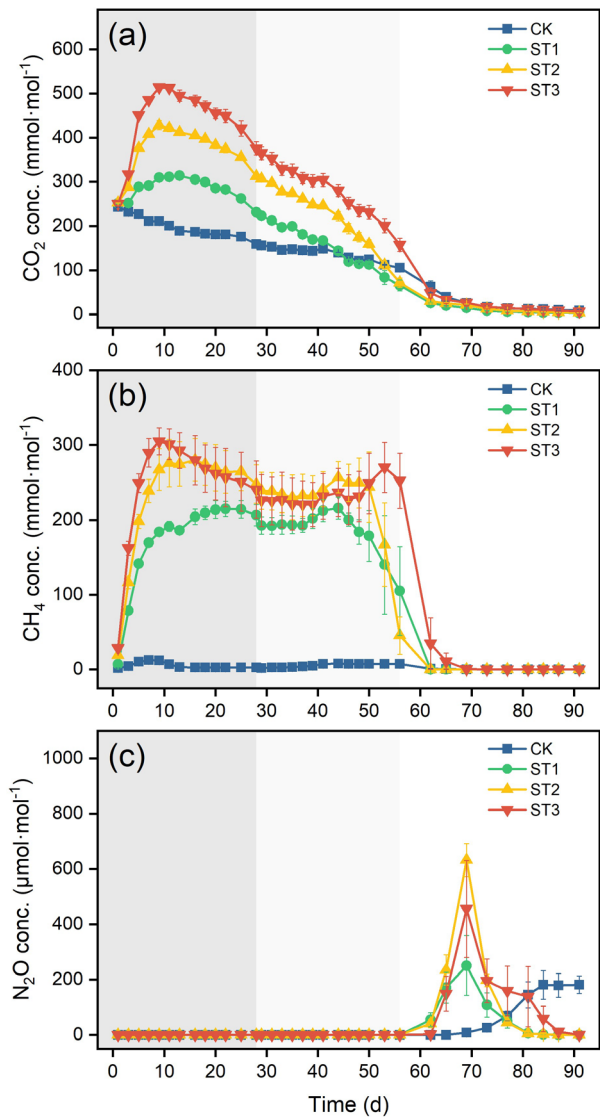


Figure 2: Dynamics of GHG concentrations in soils during the incubation. (a) CO₂; (b) CH₄; (c) N₂O. The abbreviation *conc.* means concentration. Data are given in average ± standard error (n = 3). Grey, lighter grey, and white areas indicate flooding, the early drained period, and the late drained period, respectively.

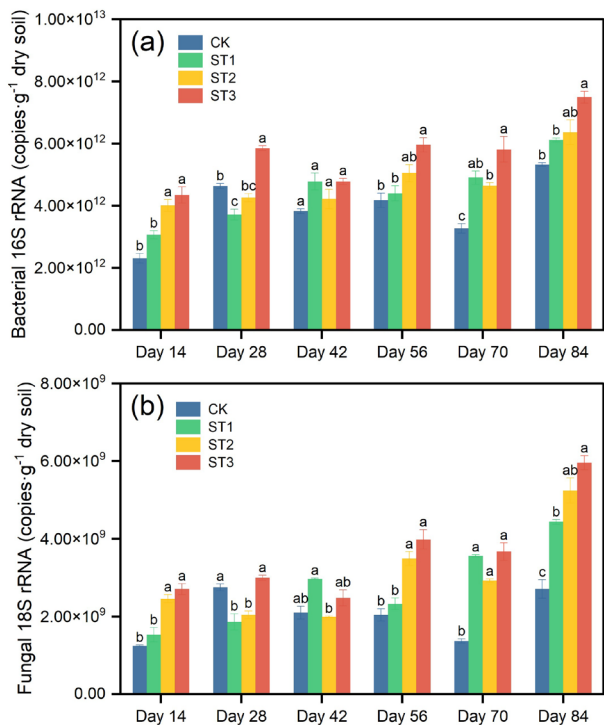
3.4 Variations of microbial abundance

3.4.1 The abundance of bacteria and fungi

In general, the abundance of both bacterial 16S rRNA and fungal 18S rRNA followed the order of ST3 > ST2 > ST1 > CK (Fig.3). The average copy numbers of 16S rRNA were 3.92E+12, 4.50E+12, 4.76E+12, and 5.71E+12 per gram dry soil for



226 CK, ST1, ST2, and ST3, respectively. The average abundances of 18S rRNA were 2.04E+9, 2.78E+9, 3.03E+9, and 3.63E+9
227 per gram dry soil, respectively.



228
229 **Figure 3: Dynamics of bacterial 16S rRNA abundance (a) and fungal 18S rRNA abundance (b) during the incubation. Different**
230 **lower-case letters denote significant differences between treatments ($\alpha = 0.05$). Data are given in average \pm standard error ($n = 3$).**

231 3.4.2 The abundance of methanogens (*mcrA*) and methanotrophs (*pmoA*)

232 The copy number of *mcrA* was obviously affected by straw incorporation and positively related to the straw input rate
233 (Fig.4a). The average *mcrA* abundance during the CH₄ fluxing period between day 14 and day 56 was significantly and
234 positively related to the straw input rate. In comparison with CK, the least increase occurred in ST1 with 32%, while the
235 highest happened in ST3 with 129%.

236 For *pmoA*, although straw incorporation also clearly promoted its copy number, the treatment with the lowest amount of
237 straw (ST1) induced a substantial increase in methanotrophs compared to CK by approximately 81%. Further increasing the
238 straw amount failed to cause significant elevations in comparison with ST1 (Fig.4b).

239 When concerning *mcrA/pmoA*, the ratio of ST1 was quite similar to that of CK, while the ratios of ST2 and ST3 were
240 significantly higher than that of CK (Fig.4c).

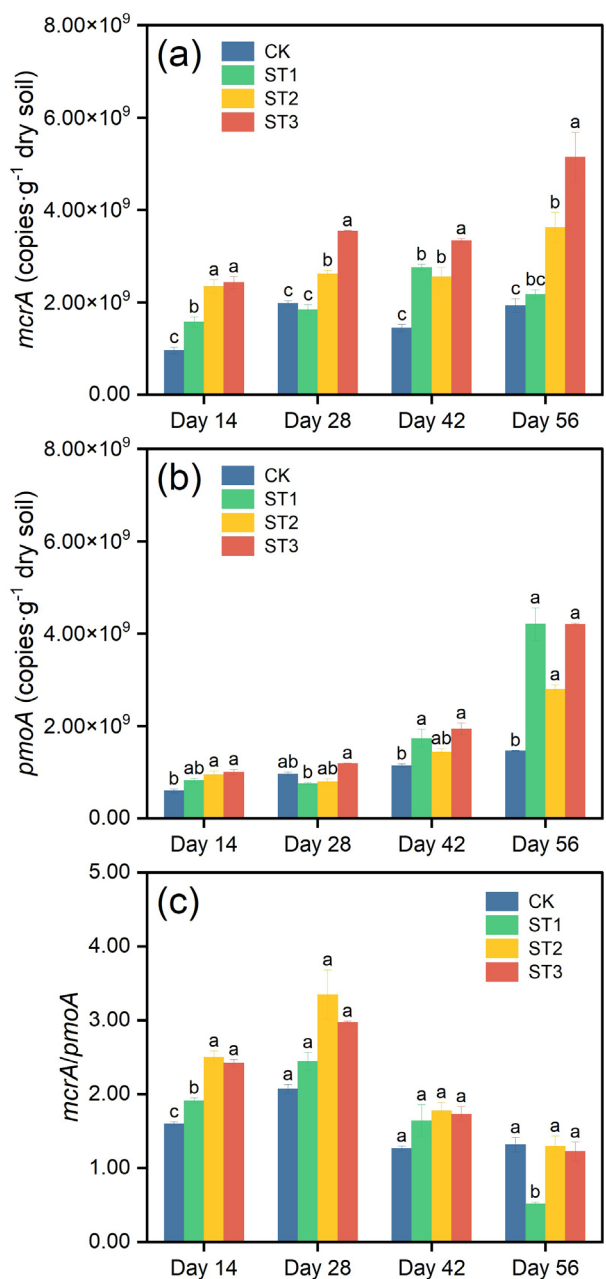


Figure 4: Dynamics of *mcrA* abundance (a), *pmoA* abundance (b), and *mcrA/pmoA* ratio (c) during the CH₄ fluxing period. Different lower-case letters denote significant differences between treatments ($\alpha = 0.05$). Data are given in average \pm standard error ($n = 3$).

3.4.3 The abundance of N₂O-producing (*nirS*) and N₂O-reducing (*nosZII*) communities

The population size of *nirS* was relatively stable, and the variations among the treatments were negligible under flooding (Fig.5a). However, under drying, the copy number of *nirS* increased and was clearly affected by the straw incorporations. All



the straw-amended treatments outstandingly increased *nirS* abundance compared to CK. Among the treatments, ST3
possessed the highest copy number of *nirS*, while ST2 and ST1 had similar lower abundances.

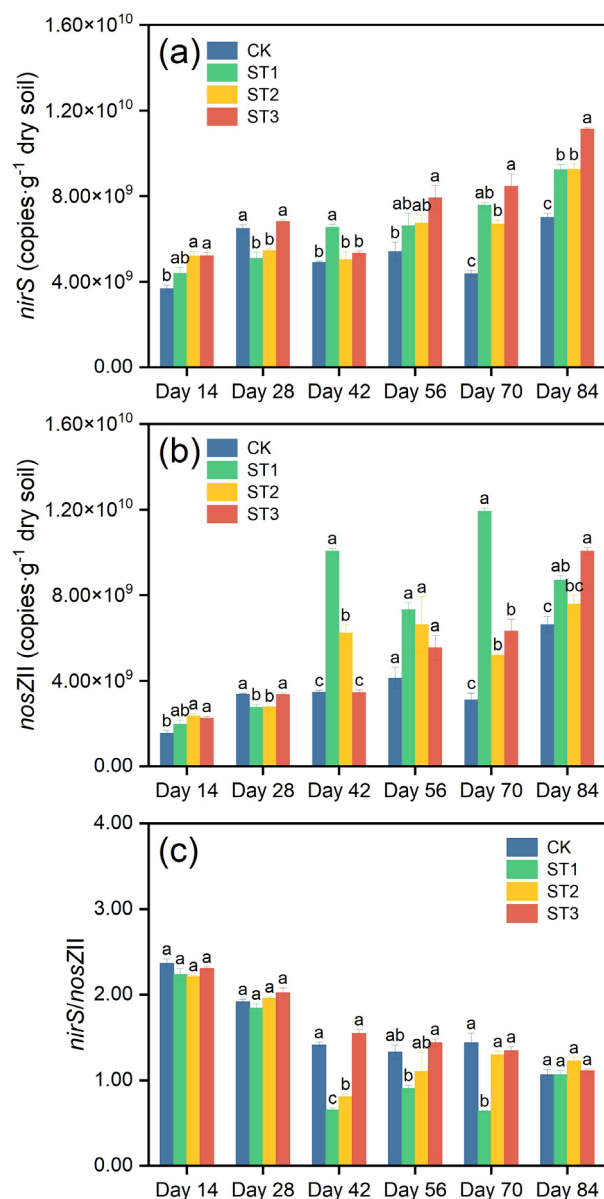


Figure 5: Dynamics of *nirS* abundance (a), *nosZII* abundance (b), and *nirS/nosZII* ratio (c) during the incubation. Different lower-case letters denote significant differences between treatments ($\alpha = 0.05$). Data are given in average \pm standard error ($n = 3$).

In general, the dynamics of *nosZII* abundance during the incubation were similar to the variations of *nirS* abundance (Fig.5b). Interestingly, the abundance of *nosZII* in ST1 was the highest, which was significantly higher than the second highest treatment (ST3) during drying, especially during the peaking time of N_2O flux on day 70.



When concerning the abundance ratio of *nirS/nosZII*, ST1 displayed the lowest average ratio of 0.81, while the average ratios of other treatments were higher, ranging from 1.11 to 1.36 (Fig.5c).

4 Discussion

Rice straw is an important organic resource and has been used to improve soil productivity (Huo et al., 2024; Zhou et al., 2024), which was also observed in this study. Since rice straw return may also exacerbate GHG emissions from paddy fields (Shi et al., 2023; He et al., 2024), which could offset the benefits of rice straw returning to paddy systems, it is urgent to investigate the feasibility of straw incorporation in relation to soil fertility improvement and GHG emission control. We hypothesized that there should be a suitable straw incorporation amount, which could not only modify soil fertility, but also generate minimal GHG emissions without causing a significant increase in GWP.

We found that ST1 treatment clearly improved soil physicochemical properties. More importantly, it failed to significantly increase GWP compared to the treatment without straw input (CK). Among CO₂, CH₄, and N₂O, N₂O has the highest warming potential over a 100-year horizon, followed by CH₄ and CO₂ (Forster et al., 2021). It was detected that there were two peaks of N₂O fluxes, which were consistent with other studies (Zhou et al., 2020; Senbayram et al., 2022; Li et al., 2025b): one was under flooding just after nitrogen fertilization and the other occurred during drying. We found that only CK emitted a large amount of N₂O while the emissions from straw-amended treatments were negligible during the flooding phase. This would be partially due to the competition of soil microorganisms for soil available nitrogen. Generally, organic materials incorporated into paddy soil will stimulate mass propagation of soil microorganisms, and these fast reproducing microbial communities will compete for soil free nitrogen as their nutrient (L'espérance et al., 2024; Zhang et al., 2025). On the contrary, the nitrogen fertilizer in CK could be an available nitrogen source for nitrification and denitrification. As a consequence, this treatment emitted a lot of N₂O. However, during drying, oxygen continuously penetrated the soil profile, and abundant available nitrogen was released mainly through the mineralization of soil organic matter. Organic matter also contributed more electron donors to denitrification when the soil moisture declined (Yi et al., 2022). These means if a soil contains higher SOC, it would produce more mineral nitrogen as the substrate and provide more electron donors for N₂O production and reduction. Although ST1 contained slightly higher SOC than CK, there was no clear difference in N₂O fluxes between them during the drying process. The reasons for this phenomenon would be as follows. N₂O emission largely relies on N₂O production ability and consumption activity, which are driven by the related functional microorganisms (Hu et al., 2015). Among these microorganisms, the denitrifiers of *nirS*-type and *nosZII*-type communities were indicated as the active microbial groups in paddy soils (Jones et al., 2013; Wei et al., 2015; Jin et al., 2020; Chen et al., 2024; Yang et al., 2024). It was detected that ST1 treatment contained a relatively low abundance of *nirS* and the highest *nosZII* copy number among the treatments, as well as the lowest *nirS/nosZII* ratio. These results strongly suggested that ST1 would possess relatively low N₂O production and high N₂O transformation capabilities. As a result, the N₂O emission from ST1 was significantly lower than that from CK.



289 Applying organic materials to paddy fields often intensified CH₄ flux from soils (Han et al., 2023; Song et al., 2024; Qin et
290 al., 2025). Similar results were also observed in this study, and the CH₄ emission was significantly and positively related to
291 the straw input rate. Interestingly, the cumulative CH₄ emission from ST1 treatment was quite low with less than 5 g·m⁻².
292 Further increasing the straw incorporation rate sharply elevated CH₄ emission, such as the cumulative CH₄ emissions of ST2
293 and ST3 were about 5 and 9 times those of ST1, respectively. The question is why ST1 treatment maintained such a low
294 level of CH₄ flux. CH₄ emission depends on CH₄ production and consumption in soil, which are driven by methanogens and
295 methanotrophs (Conrad, 2020; Nwokolo and Enebe, 2025). The population size of *mcrA* in ST1 was clearly higher than that
296 in CK but significantly lower than ST2 and ST3, indicating that the CH₄ production capacity of ST1 would be higher than
297 that of CK but lower than the treatments receiving higher amounts of straw. Another important aspect in determining CH₄
298 flux is the soil CH₄ consumption capability (Conrad, 2020; Nwokolo and Enebe, 2025). CH₄ consumption in a soil would be
299 strongly linked to its CH₄ holding capacity (Ariani et al., 2022) because this gas remaining in the soil would be mostly
300 transformed by methanotrophs. Once CH₄ producing ability is over the soil CH₄ holding capacity, the extra CH₄ would be
301 emitted into the atmosphere. We observed that the soil CH₄ holding capacity was about 190 mmol·mol⁻¹ under the anaerobic
302 environment, which was determined from the soil CH₄ concentrations where CH₄ emissions were almost undetectable. We
303 also observed that soil CH₄ concentrations of ST1 fluctuated about 200 mmol·mol⁻¹ under anaerobic conditions, and
304 coincidentally, the CH₄ emission of this treatment was minimal. While the CH₄ concentrations in ST2 and ST3 were clearly
305 over 190 mmol·mol⁻¹, CH₄ emissions notably occurred. Therefore, the CH₄ production activity in ST1 treatment was slightly
306 over the soil CH₄ holding capacity, which would be the main mechanism for its minimal CH₄ flux among straw-amended
307 treatments.

308 **5 Conclusion**

309 Rice straw could be incorporated into paddy soil at a suitable amount. Compared to no straw input, it could not only improve
310 soil fertility, but also avoid significantly increasing GWP. The major contributors to this consequence were strongly linked
311 to the highest *nosZII* copy number and the lowest *nirS/nosZII* ratio, and the CH₄ producing ability fluctuated around the soil
312 CH₄ holding capacity and most of the produced CH₄ was consumed by soil methanotrophs. Because different soils possess
313 various soil properties, their CH₄ holding capacities and nitrogen transformation processes would be different. Therefore, the
314 feasibilities of straw returning for different soils require further investigations.

315 **Data availability**

316 Data will be made available on reasonable request.



317 **Supplement link**

318 The link to the supplement will be included by Copernicus, if applicable.

319 **Author contributions**

320 **MZ:** Conceptualization, Data Curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing -
321 Original Draft, Writing - Review & Editing. **RL:** Data Curation, Formal analysis. **WZ:** Conceptualization, Resources,
322 Supervision, Writing - Review & Editing. **CF:** Resources. **SGC** and **AT:** Writing - Review & Editing. **BZ:**
323 Conceptualization, Resources, Supervision, Writing - Review & Editing. **WW:** Conceptualization, Methodology, Resources,
324 Supervision, Validation, Writing - Original Draft, Writing - Review & Editing. **RS:** Conceptualization, Funding acquisition,
325 Resources, Supervision, Writing - Original Draft, Writing - Review & Editing.

326 **Competing interests**

327 The authors declare that they have no conflict of interest.

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341 **Review statement**

342 The review statement will be added by Copernicus Publications listing the handling editor as well as all contributing referees
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