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Effects of modulating probiotics on greenhouse gas emissions and yield in rice paddies

Shang-Hung Pao[1], *Hewder Wu*[2], *Hwey-Lian Hsieh*[3], *Chang-Po Chen*[3], *Hsing-Juh Lin*[1,4]*

[1]*Department of Life Sciences and Innovation and Development Center of Sustainable Agriculture, National Chung Hsing University, Taichung, Taiwan*
[2]*Enrich Microbiome Ltd., Tainan, Taiwan*
[3]*Biodiversity Research Center, Academia Sinica, Taipei, Taiwan*
[4]*Institute of Marine Environment and Ecology, National Taiwan Ocean University, Keelung, Taiwan*
**Corresponding author: hjlin@dragon.nchu.edu.tw*

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Abstract: Rice serves as a crucial staple food for nearly half of the world's population. However, rice paddies contribute remarkably to greenhouse gas (GHG) emissions. Prior studies often showed a trade-off between reducing GHG emissions and impairing rice yield. In this study, we explore the possibility of employing modulating probiotics to develop a win-win strategy for enhancing rice yields while reducing GHG emissions. Three paired plots of rice paddies were used in the field experiment during the spring growing season (from February to July 2022). Each pair of plots was divided into control and probiotic addition paddies to investigate the effects of modulating probiotic treatment on GHG emissions using the whole-plant chambers. Our results revealed notable reductions in GHG emissions and increases in rice yield with the probiotic treatment relative to the control. The probiotic treatment resulted in a 47.58% reduction in carbon dioxide (CO_2) emissions, a 21.53% reduction in methane (CH_4) emissions, and an impressive 88.50% reduction in nitrous oxide (N_2O) emissions over the growing season. We also observed a 27.75% increase in rice yield with the probiotic treatment. These findings suggest that employing modulating probiotics has the potential to pave the way for mutually beneficial outcomes, enhancing rice productivity while mitigating the GHG emissions associated with rice cultivation.

Keywords: flooded irrigation; global warming potential; greenhouse gas intensity; microbiome; *Oryza sativa* L.

Agriculture supplies essential sustenance for human survival (Ramankutty et al. 2018). However, the increasing frequency of natural disasters triggered by climate change, such as extreme temperatures, droughts, and floods, has resulted in a pronounced reduction in global agricultural productivity (Hall et al. 2014, Anderson et al. 2020, Nhemachena et al. 2020, Bouabdelli et al. 2022, Zhang et al. 2024). This phenomenon poses a significant threat to global food security. To mitigate food shortages and produce enough food to feed the continuously increasing global population, developing agricultural technologies aimed at increasing productivity has become a priority (Duro et al. 2020). Farmers often apply more fertiliser or increase cultivated areas to enhance agricultural productivity. These practices may adversely impact the environment including water, air, and soil pollution or greenhouse gas (GHG) emissions (Savci 2012, Rahman et al. 2021, Islam et al. 2022, Yadav et al. 2022).

Rice (*Oryza sativa* L.) is a staple food for many Asian countries. Rice paddies cover approximately 46% of the total irrigated area in Asia, and flooded irrigation *via* conventional farming practices for rice cultivation utilises approximately 40% of the world's irrigation water and 30% of the planet's developed freshwater

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resources (Dorairaj and Govender 2023). Due to the flooded conditions typically present in rice paddies during the growth period, anaerobic conditions in the soil may favour the production of methane (CH_4) and nitrous oxide (N_2O) through microbial-mediated mechanisms (Oorts et al. 2007, Vaksmaa et al. 2016, Liu et al. 2019b, Grohs et al. 2024). CH_4 is predominantly generated through microbial methanogenesis, whereas N_2O can be produced *via* diverse microbial processes involved in nitrogen cycling, such as nitrification, denitrification, nitrifier denitrification, and dissimilatory nitrate reduction to ammonium. Increases in rice yield have been attributed largely to advancements in nitrogen fertiliser application. However, the overuse of nitrogen may lead to a decline in nitrogen use efficiency and precipitate a variety of environmental challenges, such as water pollution (Han et al. 2021), soil acidification (Guo et al. 2010), ammonia volatilisation (Guo et al. 2021), and GHG emissions (Sun et al. 2018). In addition to carbon dioxide (CO_2), CH_4 and N_2O are major GHG sources from rice paddies. CH_4 and N_2O from rice paddies are estimated to constitute 15–30% and 11% of global agricultural CH_4 and N_2O emissions, respectively (IPCC 2007, Smith et al. 2007, Saunois et al. 2020, Gupta et al. 2021). Rice exhibits the highest GHG intensity among the major crops (Carlson et al. 2017). The atmospheric concentrations of CH_4, N_2O, and CO_2 have reached 1 866 ppb, 332 ppb, and 410 ppm, respectively (IPCC 2021). Although CH_4 and N_2O have lower atmospheric concentrations than CO_2, their global warming potentials (GWPs) over a 100-year horizon are 27 and 273 times greater than that of CO_2, respectively (IPCC 2021). Sustaining or enhancing rice yield while mitigating GHG emissions from rice fields is challenging.

Several strategies have been employed to mitigate GHG emissions from rice paddies in recent years. Water management techniques (Liao et al. 2020, Feng et al. 2021) and the use of biochar (Zhao et al. 2023) are commonly implemented strategies. Such studies often showed varying effects on rice yield or a trade-off effect between CH_4 and N_2O emissions (Chidthaisong et al. 2018, Kritee et al. 2018, Liu et al. 2019a, b, Yagi et al. 2020). Compared to continuous flooding, noncontinuous flooding practices (intermittent irrigation, alternate wetting and drying, mid-growing season drainage and drying) have been demonstrated to mitigate CH_4 emissions potentially (Xu et al. 2015, Feng et al. 2021). However, water management practices may also trigger significant N_2O emissions or decrease rice yield. Similarly, the application of biochar has resulted in a reduction in CH_4 emissions accompanied by an increase in CO_2 and N_2O emissions or, conversely, other undesired effects such as yield reduction (Liu et al. 2019b, Sun et al. 2019).

Probiotics, comprising singular strains or cultures of diverse and interacting microbial species, represent a category of microbial-based inoculants. Their integration into agricultural practices has the potential to enhance crop growth and yield through various mechanisms, such as the improvement of photosynthetic activity, the synthesis of bioactive compounds such as plant growth regulators and enzymes, mitigation of soil-borne diseases, acceleration of the decomposition of lignin materials, facilitation of organic waste breakdown, reduction in the accumulation of toxic ions and subsequent release of inorganic nutrients for plant assimilation (Javaid 2006, Ghormade et al. 2011, Seneviratne et al. 2011, Arora and Mishra 2016, Rajper et al. 2016, Shin et al. 2017, Thakur and Yadav 2024). Some studies have reported comparable or even superior plant growth and product quality when using probiotics, such as *Stenotrophomonas maltophilia* and *Lactobacillus bulgaricus*, compared to conventional farming practices (Nevita et al. 2018, Salim and Jumali 2020). However, despite these advancements, the adoption of probiotics in agriculture remains limited.

Previous studies have shown the undesirable effects of water management techniques, nitrification inhibitors, or modified nitrogen fertilisers on GHG emissions and rice yield. While sometimes effective in reducing GHG emissions, these interventions often lead to trade-offs that can negatively impact crop productivity. We hypothesised that the application of innovative modulation probiotics in flooded rice paddies would significantly reduce GHG emissions while either maintaining or enhancing rice yield compared to conventional farming practices without probiotics during the spring growing season. By introducing probiotics, which have been shown to influence microbial activity, we aimed to develop an environmentally sustainable approach that provides dual benefits. To test the effects of modulation probiotics, CO_2, CH_4 and N_2O emissions were measured from rice paddies under flooded irrigation of conventional farming practices with probiotic treatment relative to the control without probiotic treatment. The rice yield of both the control and probiotic-treated rice paddies was also measured.

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This approach presents the possibility of developing a win-win strategy for mitigating climate change and ensuring food security.

MATERIAL AND METHODS

Study area. Due to the water shortage in Taiwan during 2021–2022, many rice fields in the central and southern regions faced irrigation difficulties. However, northern Taiwan's subtropical monsoon climate conditions have mitigated water scarcity, allowing for the sustained use of flooded irrigation in rice paddies. The experimental paddies were selected from Beitou, northern Taiwan (25°06'N, 121°30'E, Figure 1). The rice cv. Taikeng No. 5 was conventionally cultivated over the region's two growing seasons, spring and summer. During the study period of the spring growing season from February to July 2022, the monthly air temperature and precipitation averaged 17.4 °C and 9.2 mm, respectively. According to the World Reference Base (WRB) classification system (IUSS Working Group WRB 2022), the soil in the experimental paddies was classified as Cambisols. The soil texture was classified as muddy sand. The chemical properties of the topsoil (0–10 cm) were determined as follows: soil pH was measured in a 1:1 soil-to-water suspension using a pH meter, and organic carbon and total nitrogen contents were measured using dry combustion with an element analyser (Unicube, Elementar, Langenselbold, Germany) (Hillel 2003). The results were as follows: pH = 5.4, organic carbon content = 45.86 g/kg, and total nitrogen content = 4.17 g/kg.

Preparation of modulating probiotics. A microbiome is a community of microorganisms living together in any given habitat as a result of complex interactions between microorganisms and the environment (Faust et al. 2015). We introduced microbiota from pristine forests to improve the microbiome of paddy soil. The study of microbiomes has drawn much attention in the past few years, which is based on the concept of applying microorganisms found in the stools of a healthy donor to restore the gut microbiota of a patient suffering from diseases associated with disruption of the gut microbiota (Rohlk et al. 2010, Khoruts and Sadowsky 2011, Berg et al. 2020). In this study, the addition of microbiota to rice paddies was expected to competitively eliminate GHG emission-related microorganisms in the soil of rice paddies in favour of novel microorganisms from pristine forests.

We developed this new method by extracting specific microbiomes from pristine forest soil to reduce GHG emissions from rice paddies. Soil samples were collected from the pristine forests of Baishihu in northern Taiwan. These microbiomes were cultivated

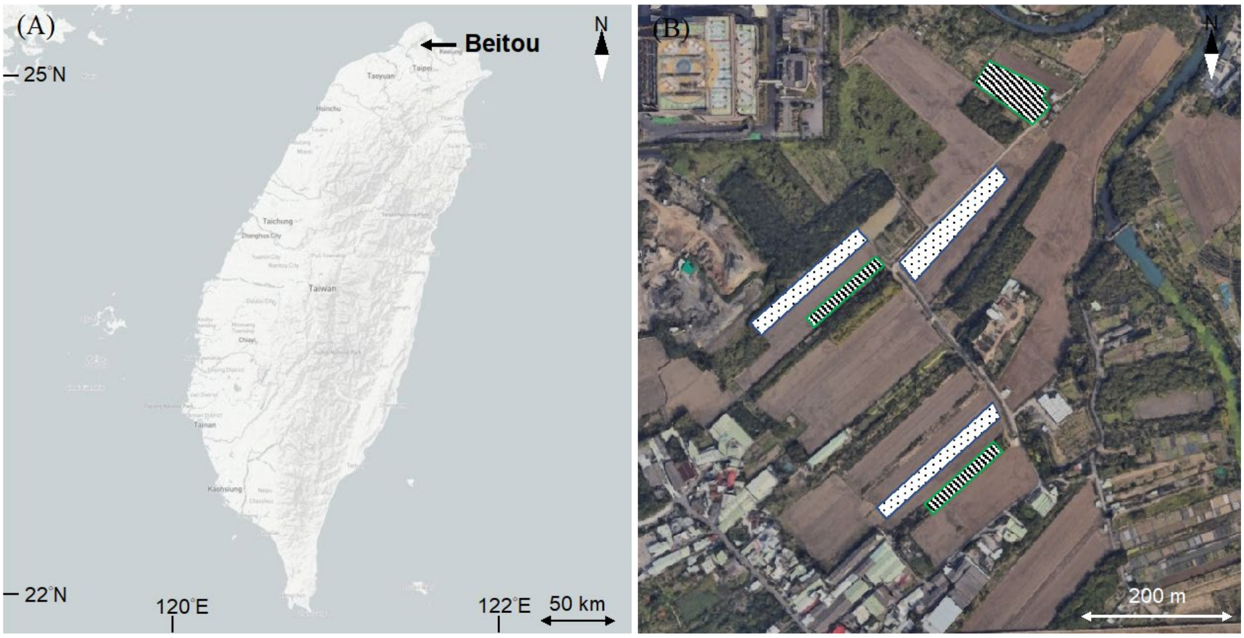

Figure 1. (A) Distribution of experimental sites in this study in Baitou District, Taipei City, northern Taiwan, and (B) allocation of the rice paddies to two treatments: three areas with dots for the control treatment and areas with lines for the probiotic treatment

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with 20–200 g of rice bran, 20–200 g of soybean meal, 5–50 g of molasses, and 100 g of soil sample, which were then placed into 20 L of distilled water. The cultivation process was completed within 7–14 days, depending upon the temperature, establishing a microbial community. Different quantities of the ingredients were used to cultivate the microbiomes. The microbiomes may vary depending on the duration of incubation. For this study, four distinct microbiomes were prepared to inhibit methanogens in Petri dish cultures. The microbiome exhibiting the most robust methanogen inhibition capability was chosen for further use in the field experiments.

Field employment of modulating probiotics. Three paired plots of rice paddies were used in a field experiment during the spring growing season (from February to July 2022) to investigate the effects of modulating probiotic treatment on CO_2, CH_4 and N_2O emissions. Each pair of plots was divided into control and probiotic addition paddies separated by ridges at least 20 m apart to prevent unanticipated mutual interference. All the operations in the control and probiotic treatment were the same except for the probiotic addition, following conventional farming measures. After the rice seedlings were transplanted, 2 L of probiotic microbiome solution per hectare was applied to the treatment paddies once a week for a total of eight applications. After the rice seedlings were planted, all the rice paddies were flooded with 3–5 cm of water until the young rice ear formation period. Subsequently, no additional water was applied from the young ear formation period until the rice harvest. This conventional farming method ensured optimal water conditions during the critical early growth periods while allowing for water-saving practices later in the rice cultivation cycle.

Metagenomic analysis of the microbiome after probiotic treatment. A next-generation sequencing approach was used to determine the structure of the microbiome. Illumina-based 16S rRNA gene amplicon sequencing and QIIME 2 analysis (software: QIIME 2 V2020.8 Krona V2.7, QIIME V1.8.0, https://qiime2.org/) were used to provide reproducible information on taxonomy profiling and alpha diversity rarefaction (Bolyen et al. 2019). Metagenomic DNA was isolated from 250 mg of the probiotic samples. Reads were classified using the National Center for Biotechnology Information (NCBI) bacterial database (downloaded in April 2023) according to the 16S metagenomic sequencing library preparation protocol. The V3–V4 region of the 16S RNA gene in the probiotic samples was amplified by PCR using the primers F (5'-GCCTACGGGNGGCWGCAG-3') and R (5'-ACTCWVG- GGTATCTAATCC-3'). Primer sequences were designed for the amplification of the 16S rDNA gene, targeting specific bacteria within the V3–V4 region.

Greenhouse gas measurement. The closed chamber method (Figure 2), as described by Lin et al. (2021), was employed to measure CO_2, CH_4 and N_2O fluxes.

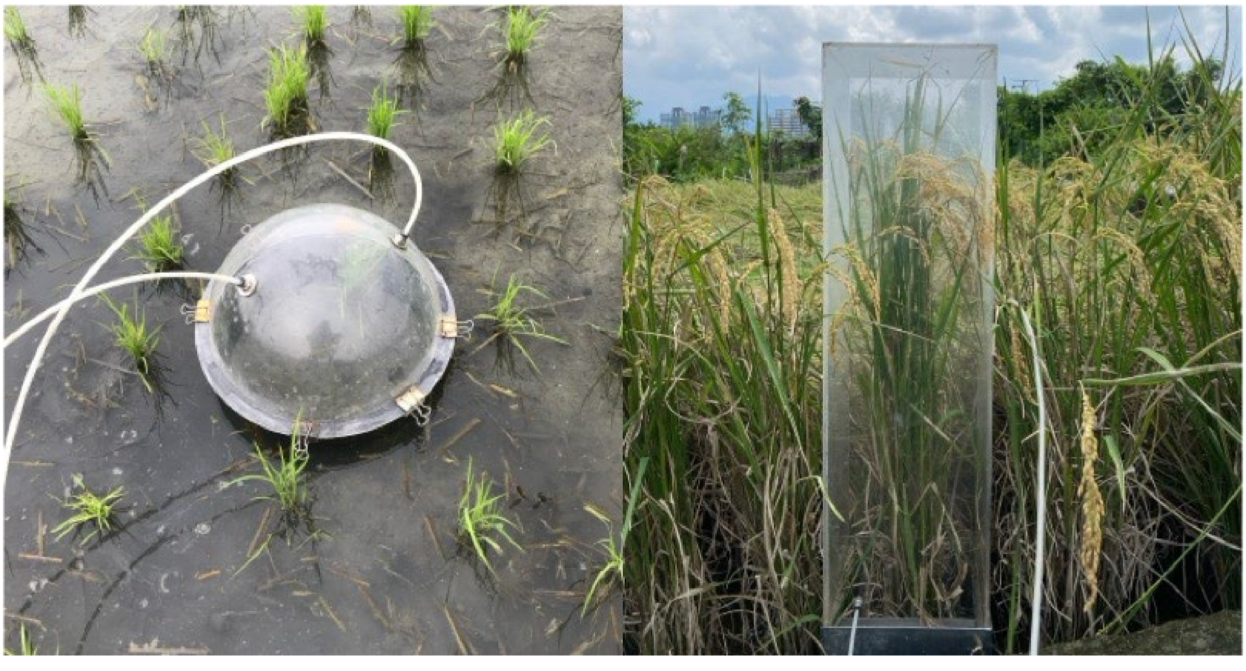

Figure 2. Greenhouse gas measurements in rice paddies in closed chambers

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Portable infrared gas analysers LI-820 (CO_2, LI-COR, Lincoln, USA), LI-7810 (CH_4, LI-COR, Lincoln, USA), and LI-7820 (N_2O, LI-COR, Lincoln, USA) were connected to *in situ* closed chambers with stainless steel bases in the experimental paddies. These whole-plant chambers were inserted to a depth of 10 cm into the soil to ensure no air exchange between the inside and outside environments. The chambers captured both autotrophic emissions derived from the respiration of the rice plants and heterotrophic emissions originating from microbial activity in the soil, allowing for comprehensive measurements of total CO_2 fluxes (Haque et al. 2017). Autotrophic emissions primarily represent CO_2 rice plants release during respiration, while heterotrophic emissions are generated by soil microorganisms breaking down organic matter. To prevent disturbance-related false GHG emissions, measurement locations were chosen approximately 1 m from the ridges, thus avoiding the need to step into the paddies during measurements.

From the seedling period to the tillering period, hemispheric transparent chambers with a diameter of 30 cm, height of 16 cm, and a bottom area of 0.071 m^2 were used. From the young ear formation period to the mature period, when the plants grew taller than 30 cm, cuboid transparent chambers measuring 25 cm long × 25 cm wide × 85 cm high with a bottom area of 0.062 m^2 were employed. A black screen was used to cover the chambers to simulate nighttime conditions during daytime CO_2 flux monitoring. Based on a pilot study, both CH_4 and N_2O gas emissions showed no significant differences between day and night. Thus, CH_4 and N_2O fluxes were monitored under light conditions only and then extrapolated to represent the fluxes for the whole day.

Measurements were conducted across four distinct rice growth periods: seedling, tillering, young ear formation, and mature. During these stages, CO_2, CH_4 and N_2O emissions from the probiotic treatments were analysed and compared with those from the control treatments. CO_2, CH_4 and N_2O emissions were randomly measured in three replicates for each experimental paddy during each field survey. Gas fluxes were calculated using the ideal gas law, as expressed in Eq. (1).

$$\text{Flux} = (S \times V \times tc \times M)/(RT \times 1\,000 \times A) \quad (1)$$

where: flux – CO_2 flux (mg/m^2/h), CH_4 flux (mg/m^2/h) or N_2O flux (mg/m^2/h); S – slope of the linear regression line between the gas concentration (ppm) and recorded frequency (CO_2: 30 s, CH_4: 20 s, N_2O: 20 s); V – chamber volume (L); tc – time conversion constant, CO_2 is 120 = 1 h × (60 min/h) × [(60 s/min)/30 s], CH_4 is 180 = 1 h × (60 min/h) × [(60 s/min)/20 s], N_2O is 3 600 = 1 h × (60 min/h) × [(60 s/min)/20 s]; M – molecular weight (g/mol), CO_2 = 44, CH_4 = 16, N_2O = 44; R – ideal gas constant = 0.082 (L atm/K/mol); T – absolute temperature (K); A – bottom area of the chamber (m^2); 1 000 – weight unit transformation constant (µg/mg).

The total CO_2, CH_4 and N_2O emissions for the control and probiotic treatments were estimated over the entire rice growing season, which lasted 144 days, using Eq. (2).

$$\text{Flux}_{\text{total}} = \sum_i^n (\text{Flux}_i \times D_i) \quad (2)$$

where: Flux_i – CO_2 flux (mg/m^2/h), CH_4 flux (mg/m^2/h) or N_2O flux (mg/m^2/h) in the i^{th} sampling interval; D_i – duration in days of the i^{th} sampling interval; n – total number of sampling intervals.

According to the Intergovernmental Panel on Climate Change (IPCC) Sixth Assessment Report (AR6), CO_2, CH_4, and N_2O emissions were converted into CO_2 equivalents (CO_2-e) using the 100-year global warming potential (GWP_{100}) values of 1, 27.2 and 273, respectively. This conversion facilitates the comparison of different greenhouse gas emissions on a common scale.

Rice yield and greenhouse gas emission intensity. Grain harvesting from all paddies occurred on July 11, 2022, during the mature period. After threshing, rice yield measurements were conducted, and the results were converted to kg/ha. This conversion was essential for facilitating comprehensive data analysis and comparison across the controls and probiotic treatments. The greenhouse gas emission intensity (GHGI) was calculated as the GWP per unit of rice yield.

Soil redox potential analysis. After the measurements of GHG emissions, duplicated soil samples within each chamber were collected from depths of 0, 5, and 10 cm using stainless-steel cores (with a diameter of 9 cm and length of 25 cm). The redox potential (ORP) of each depth of the soil samples in terms of Eh was immediately determined using a portable redox potential meter (ORP30, CLEAN L'eau, Taoyuan, Taiwan). The mean ORP value of the duplicated soil samples within each chamber was calculated for each measurement of GHG emission.

Statistical analyses. On each sampling occasion, the mean values of the respective GHG emissions and redox potential were calculated from three replicates for each experimental plot to represent the measurement values of each GHG emission for the controls

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and probiotic treatments. Nonparametric one-way ANOVA was performed to compare the treatment effects at the tillering, young ear formation and mature periods. The significance level for GHG emissions was set at 0.05, whereas the significance level for ORP was set at 0.1. The statistical software SPSS 26 (IBM, Chicago, USA) was used for all ANOVAs.

RESULTS

Microbiome composition for methanogen inhibition. Taxonomic assignments and coverage information were further used to group the assembled sequences into microbial taxa at the species level. Taxonomic profiling of the microbiome at different taxonomic levels was conducted using QIIME 2, revealing 5 phyla, 7 classes, 10 orders, 21 families, 38 genera, and 293 species. Area plots corresponding to the taxonomic distribution were generated for visualisation purposes (Figure 3). Lactobacillaceae constituted 89% of the microbiome, comprising species such as *Lactobacillus buchneri*, *Lactobacillus harbinensis*, and *Lactobacillus parafarragini*, among others. This was followed by Clostridiaceae and Bacillaceae.

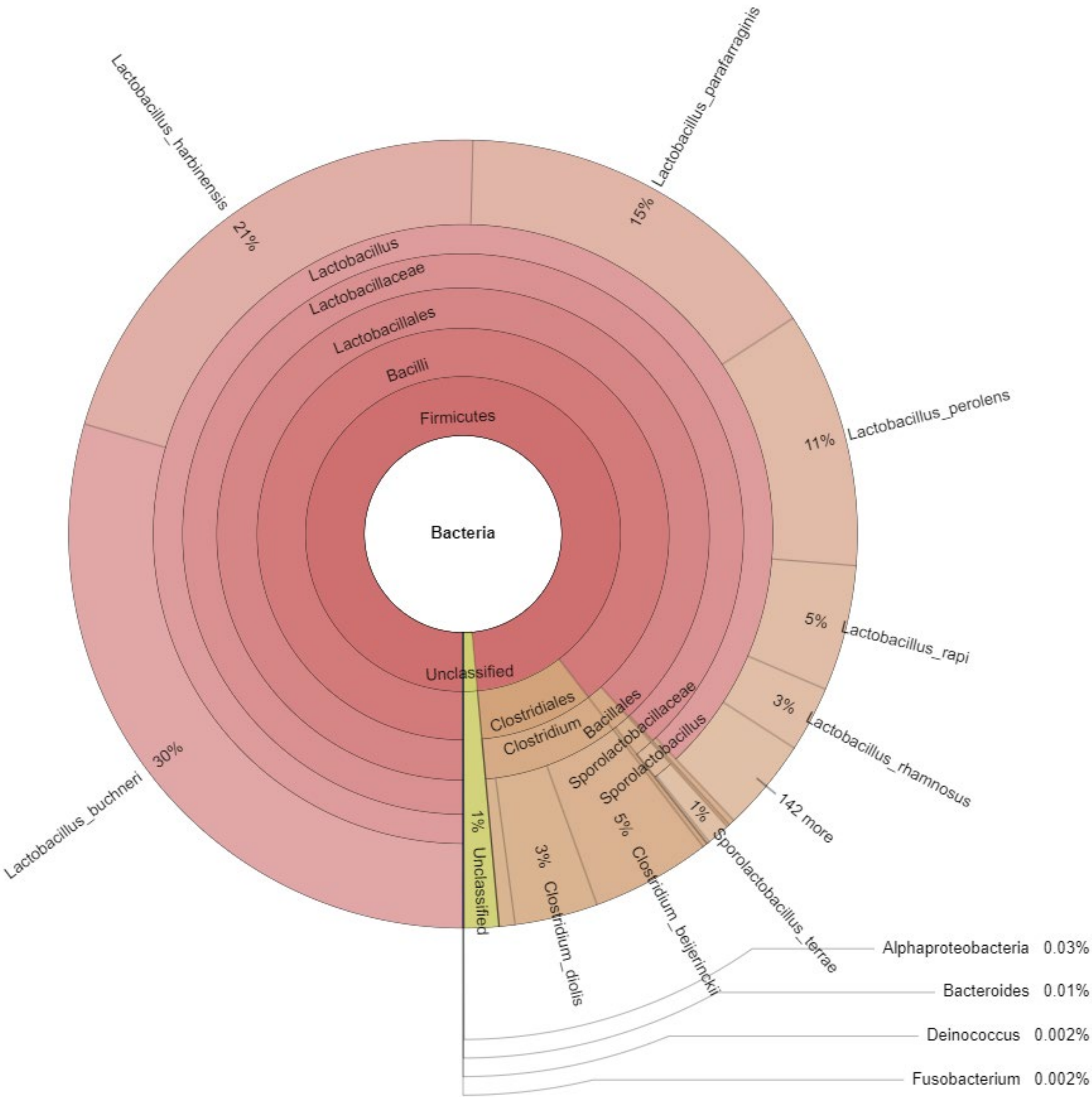

Figure 3. Krona plot of the soil microbiome. The species composition percentages are presented as the normalised proportion of organism-specific *k*-mers observed relative to the total microbial species diversity detected in the samples

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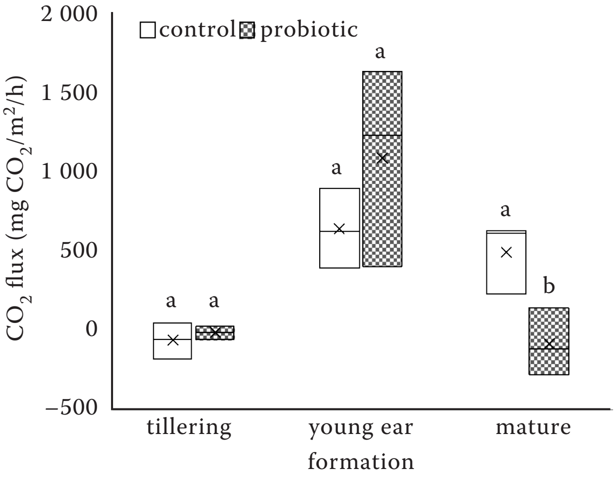

Figure 4. CO_2 emission flux in the control and probiotic treatments during the different rice growth periods (n = 3 plots in each treatment)

Probiotic effects on CO_2 emissions from rice paddies. In the field experiments over the rice growing season, there were significant differences in CO_2 emissions between the control and probiotic treatments during the different rice growth periods (Figure 4, Table 1). The dynamics of CO_2 emission were similar between the controls and probiotic treatments. CO_2 emissions were relatively low during the tillering period and increased during the young ear formation period. The highest emissions were observed during the young ear formation period, followed by a decrease during the mature period. CO_2 emissions did not significantly differ between the control and probiotic treatments during the tillering and young ear formation periods ($P > 0.05$). However, the CO_2 emissions from the controls were significantly greater than those from the probiotic treatments during the mature period ($P < 0.05$).

Probiotic effects on CH_4 and N_2O emissions from rice paddies. CH_4 emissions were relatively high during the tillering period but decreased rapidly following the young ear formation period (Figure 5, Table 1), decreasing to nearly zero during the mature period. During the tillering period, the CH_4 emissions from the controls were significantly greater than those from the probiotic treatments ($P < 0.05$). However, the CH_4 emissions did not significantly differ between the control and probiotic treatments during the young ear formation and mature periods ($P > 0.05$).

During the rice growing season, the pattern of N_2O emissions was similar to that of CH_4 emissions (Figure 6, Table 1). The N_2O emissions during the tillering period were notably elevated but experienced a rapid decline upon entering the young ear formation period. As the rice matured, these fluxes gradually approached zero during the mature period. Notably, the N_2O emissions from the controls were significantly greater than those from the probiotic treatments ($P < 0.05$) during the tillering period. However, no significant difference in N_2O emissions was detected between the control and probiotic treatments during the young ear formation and mature periods ($P > 0.05$).

Probiotic effects on soil redox potential. In this study, the soil redox potential of the paddies in the probiotic treatments tended to be greater than that of the controls during the tillering and young ear formation periods in deeper soils (Figure 7). This difference was significant in the depth of 5 cm be-

Table 1. Greenhouse gas (GHG) emissions and rice yield in the control and probiotic treatments during the spring growing season

	Treatment	Rice growth period			Spring growing season	
		tillering (mg/m²/h)	young ear formation (mg/m²/h)	mature (mg/m²/h)	total emission (kg/ha/rice growing season)	yield (kg/ha)
CO_2	control	-61.78^a	641.67^a	495.09^a	$9\,812.55^a$	
	probiotic	-12.92^a	$1\,090.73^a$	-84.46^b	$5\,143.96^a$	
CH_4	control	58.92^a	0.24^a	0.29^a	620.50^a	
	probiotic	15.04^b	2.14^a	0.39^a	486.91^b	
N_2O	control	4.18^a	0.02^a	0.03^a	19.22^a	
	probiotic	0.18^b	0.09^a	0.03^a	2.28^b	
Rice yield	control					$3\,849.28^b$
	probiotic					$4\,917.65^a$

The values with different letters are significantly different between the control and probiotic treatments at $P < 0.05$ level

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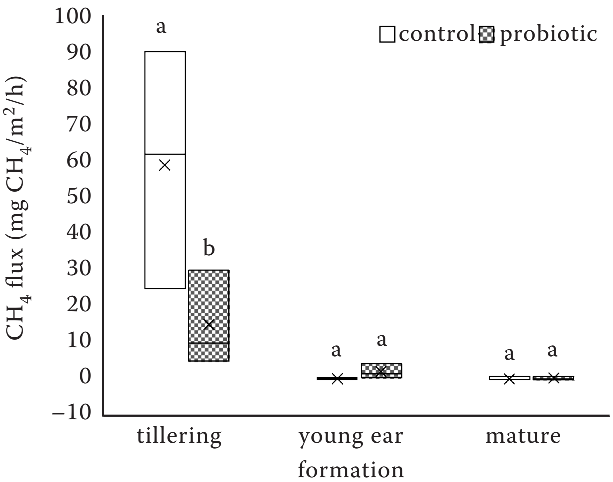

Figure 5. CH_4 emission flux in the control and probiotic treatments during the different rice growth periods (n = 3 plots in each treatment)

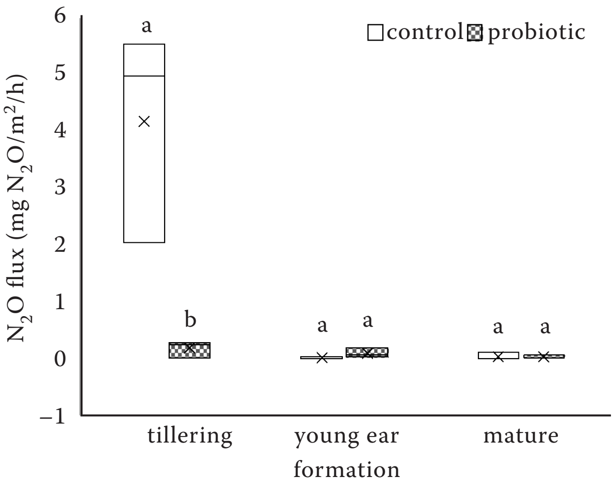

Figure 6. N_2O emission flux in the control and probiotic treatments during the different rice growth periods (n = 3 plots in each treatment)

low the surface (Figure 7B, controls = 81.00 ± 54.37, probiotics = 170.00 ± 80.55, $P < 0.1$). It is reasoned that with increasing rice growth, the increased redox potential provides relatively oxygenic conditions that are not suitable for the activity of CH_4- and N_2O-producing bacteria. The increase in redox potential in the deeper soils of the probiotic-treated paddies through rice growth likely contributed to the reduction in N_2O and CH_4 emissions (Figures 5 and 6).

Total GHG emissions during the rice growing season. Total CO_2 emissions over the rice growing season did not differ significantly between the controls and the probiotic treatments under the same conventional farming conditions (Table 1). Despite this, the total CO_2 emissions of the probiotic treatments were reduced by 47.58% compared to those of the controls. Notably, the total CH_4 and N_2O emissions from the probiotic treatments were significantly lower than those from the controls, demonstrating reductions of 21.53% and 88.50%, respectively, throughout the different rice growth periods (Table 1). These results are better than we

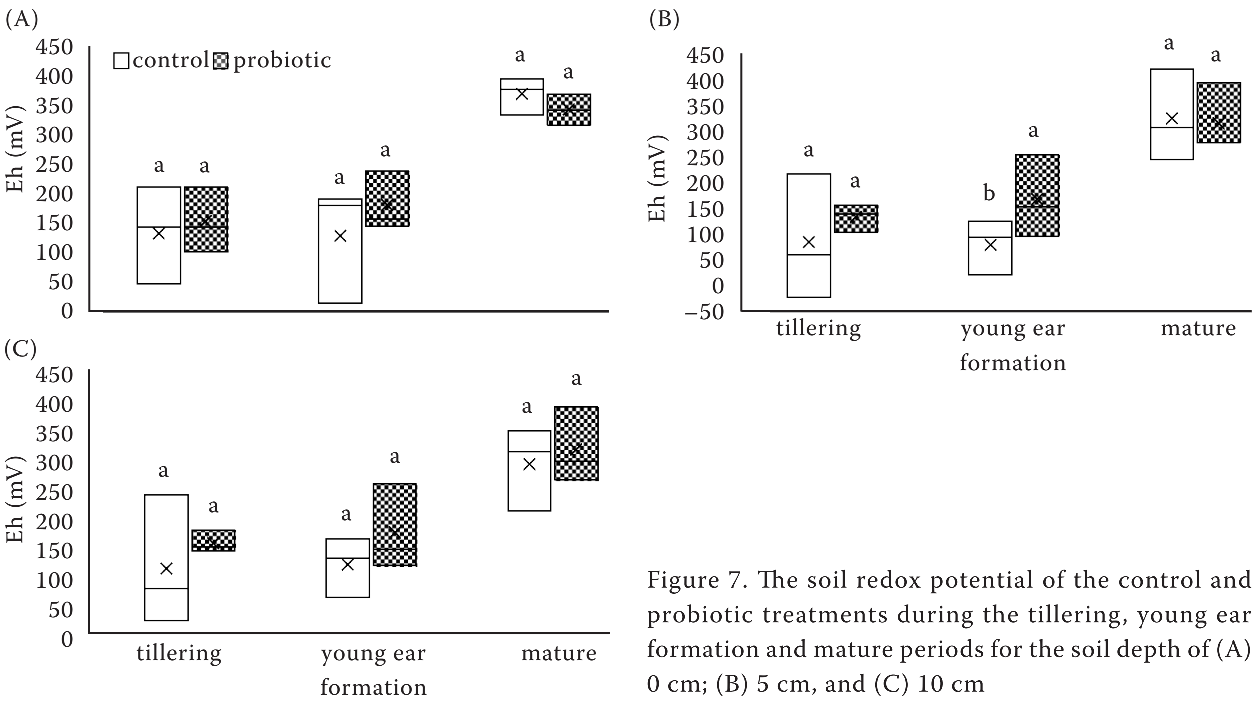

Figure 7. The soil redox potential of the control and probiotic treatments during the tillering, young ear formation and mature periods for the soil depth of (A) 0 cm; (B) 5 cm, and (C) 10 cm

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expected because the probiotic treatments were originally designed to reduce CH_4 emissions. It is clear that probiotic treatments can also reduce CO_2 and N_2O emissions over the rice growing season.

Rice yield and greenhouse gas emission intensity. In this study, the rice yield in the probiotic treatments, comprising 89% of the Lactobacillaceae, exhibited a significant 27.75% increase compared to that in the controls ($P < 0.05$). The rice yield of the probiotic treatments was 4 917.65 ± 433.76 kg/ha, significantly greater than that of the controls (3 849.28 ± 436.35 kg/ha) ($P < 0.05$) (Table 1). Furthermore, the total GHG emissions associated with the controls were significantly greater than those associated with the probiotic treatments. The greenhouse gas emission intensity (GHGI) of the controls was significantly greater at 8.30 kg CO_2-e/kg than that of the probiotic treatments (3.86 kg CO_2-e/kg) ($P < 0.05$). The GHGI of the controls was 57.50% greater than that of the probiotic treatments, suggesting that the application of probiotics can improve rice yield and mitigate GHG emissions throughout the spring growing season.

DISCUSSION

Probiotic effects on CO_2 emissions from rice paddies. Lower CO_2 emissions were observed in both the control and probiotic treatments during the tillering period, consistent with the rapid growth phase of rice. This finding suggests that rice, which has the highest photosynthetic rate of its growing season during the tillering period, actively absorbs CO_2 through enhanced photosynthetic activity (Chen et al. 2007, Honda et al. 2021, Ye et al. 2022). As a result, this contributed to a reduction in net CO_2 emissions. Additionally, the CO_2 concentration within the closed chambers displayed a negative trend throughout the day when not covered with black cloths, suggesting a prevalent absorption of CO_2 through plant photosynthesis (Nishimura et al. 2015, Islam et al. 2017).

During the young ear formation period there was a transition period from flooding to drainage, when no additional water was applied, and the rice paddies were allowed to dry. This practice, commonly referred to as mid-growing season drainage, represents one of the basic techniques for enhancing rice yields and conserving water resources. This management practice changed paddy soil from anaerobic to aerobic conditions, which strongly influences soil CO_2 emissions (Miyata et al. 2000, Saito et al. 2005). This is consistent with our observation that CO_2 emissions increase rapidly from the tillering period to the young ear formation period, reaching the highest fluxes throughout the rice growing season. This can be explained by two possible mechanisms observed in paddy soil (Maier et al. 2011, Liu et al. 2013, Nishimura et al. 2015, Min and Rulik 2020). First, flooding rice paddies for subsequent rice cultivation disrupts the oxygen supply from the atmosphere, leading to a reduction in microbial activity and partial inhibition of CO_2 production. Additionally, water replaces the gaseous phase in the soil pores. Given that the CO_2 diffusion rate in water is four orders of magnitude lower than that in air, a portion of the produced CO_2 may become trapped in the soil. When rice paddies shift from flooding to drainage, the accumulated CO_2 in paddy soil is quickly released back into the atmosphere. Second, soil CO_2 emissions are frequently associated with aboveground biomass, as plant tissue generally is a primary source of organic matter to the soil carbon pool (Kara et al. 2014). Furthermore, higher CO_2 emissions have been directly linked to increased rice productivity through the increased use of fertilisers (Maraseni et al. 2009, Min and Rulik 2020).

During the mature period, when the rice paddies were maintained under dry conditions, a decreasing trend in CO_2 emissions was observed. This decrease can be attributed to the decreasing soil water content and soil CO_2 concentration in the dry paddy soil leading to a reduction in the amount of CO_2 stored in the soil. Additionally, the maturation processes of rice plants such as leaf rolling, senescence, and yellowing result in a loss of CO_2 absorption ability (Pham et al. 2022). Therefore, the predominance of CO_2 emissions from rice paddies during this period can be attributed to microbial activity (Min and Rulik 2020). Notably, the CO_2 emissions of the controls were significantly greater than those of the probiotic treatments. This result suggests that the microbial communities in paddy soil were influenced by probiotics, which might favour aerobic microbial activity associated with decreasing CO_2 production.

Probiotic effects on CH_4 and N_2O emissions from rice paddies. Generally, CH_4 and N_2O production and emissions from rice paddies are strongly affected by soil microbes, rice growth periods, and water and fertiliser management (Li et al. 2013, Zhang et al. 2015, Jiang et al. 2019, Feng et al. 2021, Islam et al. 2022, Grohs et al. 2024). The highest CH_4 and N_2O emissions in this study were observed during the

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tillering period. This is attributable to the association of CH_4 and N_2O emissions with high soil water content resulting from flooded irrigation practices. The decomposition of base fertiliser and tillering fertiliser promotes the growth of rice and its roots, while the increase in root exudates provides abundant substrate for CH_4 production (Chen et al. 2019). The decomposition and fermentation of straw, dead branches, and rice leaves may also contribute to the production of CH_4 by methanogens (Gutierrez et al. 2013, Tang et al. 2023, Zhao et al. 2023). High N_2O emissions during the tillering period are highly dependent on high soil water content and nitrogen fertiliser application. This could be attributable to nitrification and denitrification, both of which can lead to N_2O emissions. The CH_4 and N_2O emissions from the controls were significantly greater than those from the probiotic treatments, suggesting that the added probiotics can inhibit the activity of methanogens, nitrifying bacteria, and denitrifying bacteria or cause a change in microbial communities in the soil.

Following the tillering period, the CH_4 and N_2O emissions decreased rapidly to nearly zero as a result of mid-growing season drainage and remained nearly zero through the mature period. The aerobic environment might facilitate CH_4 oxidation, thereby reducing the amount of CH_4 emitted to the atmosphere (Liu et al. 2019a, b, Liao et al. 2020). Previous studies reported that mid-growing season drainage effectively reduced CH_4 emissions from rice paddies but led to an increase in N_2O emissions (Ali et al. 2013, Kudo et al. 2014, Grohs et al. 2020). These observations imply a trade-off effect between reducing CH_4 and reducing N_2O emissions from rice paddies. However, our results indicate that N_2O emissions did not increase despite soil drainage. This could be attributable to greater nighttime warming during the spring-summer inhibiting the activity of soil nitrification and denitrification bacteria, consequently reducing N_2O production and emission (Zhang et al. 2020).

Probiotic effects on soil redox potential. When organic matter is decomposed by soil microorganisms, it generally follows a series of consecutive processes as aerobic respiration, nitrate reduction, general acid fermentation, sulfate reduction, and methane fermentation. During these processes, the redox potential decreases as the acceptor of hydrogen (i.e., the oxidant) is used. Methanogens are a group of extremely anaerobic bacteria that can use H_2 to reduce CO_2 to CH_4 (Kim et al. 2016). Similarly, denitrifying microbes require anaerobic or hypoxic conditions to reduce NO_3^- to N_2O (Pan et al. 2022). Therefore, waterlogged soil is conducive to the activity of CH_4- and N_2O-producing bacteria.

Our study revealed unexpected differences in GHG emissions under specific conditions. While we expected that using probiotics, especially *Lactobacillus* species, would mainly improve soil aeration and support aerobic processes, we found that under prolonged waterlogging, these probiotics also reduced the activity of methanogens. This discovery is consistent with recent studies indicating that lactic acid bacteria can decrease ammonia emissions and encourage nitrification in agricultural soils (Raman et al. 2022). Further investigation is needed to understand how the presence of *Lactobacillus* species, the primary group of lactic acid bacteria in the probiotic treatments, can affect both soil aeration and methanogen activity under different moisture levels. This could have implications for managing GHG emissions in rice paddies.

Total GHG emissions during the rice growing season. Rice paddies often emit large amounts of GHGs into the atmosphere due to flooded irrigation practices. Previous studies have indicated that some practices commonly employed to mitigate GHG emissions from rice paddies, such as alternate wetting and drying methods and biochar application, may inadvertently lead to increased GHG emissions due to variations in environmental conditions (Ali et al. 2013, Kudo et al. 2014, Xu et al. 2015, Liu et al. 2019b, Sun et al. 2019, Yagi et al. 2020).

Considering that trade-off effects may occur among CO_2, CH_4 and N_2O emissions, it is essential to integrate the total GHG emissions to assess overall performance. The total GHG emissions of the controls (31.94 Mg CO_2-e/ha) were significantly greater than those of the probiotic treatments (18.99 Mg CO_2-e/ha). Both treatments demonstrated that CH_4 emissions were the main contributor to total GHG emissions, accounting for 52.85% and 69.74%, respectively. This is similar to previous studies (Pittelkow et al. 2013, Tarlera et al. 2016, Oo et al. 2018) which have reported that N_2O emissions contribute much less to total GHG emissions than CH_4, with N_2O in this study accounting for 16.43% of the total GHG emissions in the controls and 3.18% of the total GHG emissions in the probiotic treatments. Although N_2O contributes the least to the total GHG emissions, it has the highest GWP, reaching 273 relative to CO_2

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for a 100-year time horizon. Therefore, N_2O cannot be ignored in evaluating GHG emissions from rice paddies.

Rice yield and greenhouse gas emission intensity. Previous studies have explored practices for increasing rice yield while reducing GHG emissions. However, achieving a balance between these two objectives is often challenging. For example, nutrient management practices, such as the application of organic fertilisers to paddy soils and crop straw return, have been widely studied (Linquist et al. 2012, Sun et al. 2019, Grohs et al. 2020). Such practices can increase soil carbon content, thereby enhancing CH_4 emissions *via* the stimulation of soil methanogens. However, curtailing organic fertiliser usage may impede the soil nutrient supply, potentially exerting adverse effects on soil fertility and crop yield. Jiang et al. (2017) indicated that higher-yielding rice cultivars could reduce CH_4 emissions more effectively than their lower-yielding counterparts. Nevertheless, this strategy is applicable primarily in fertile soils, as higher-yield cultivars may exacerbate CH_4 emissions in low-fertility soils. The most common technique for mitigating CH_4 emissions from rice paddies is water management control, such as mid-growing season drainage or implementing water-saving irrigation practices during the rice growing season (Liu et al. 2019b, Sun et al. 2019). While mid-growing season drainage has demonstrated significant potential for reducing CH_4 emissions, it concurrently triggers the production and emission of N_2O (Chidthaisong et al. 2018, Kritee et al. 2018).

In this study, relative to the controls, the probiotic treatments produced comparable grain yields, which increased by 27.75% and decreased the GHGI by 57.50%. *Lactobacillus* species have been shown to enhance the production and nutrient absorption of various crops such as wheat, soybean, mung bean, and rice (Hu and Qi 2010, Javaid 2011, Javaid and Bajwa 2011, Dawood et al. 2013, Lamont et al. 2017, Raman et al. 2022). The enhanced productivity observed in crops treated with *Lactobacillus* compared to untreated ones is attributable to the accelerated decomposition of organic compounds into nutrients readily available to plants. This indicates the possibility of achieving a win-win strategy by employing probiotic treatments, not only enhancing rice productivity but also mitigating GHG emissions from conventional rice cultivation.

This study enhances our understanding of how probiotics can reduce CH_4 and N_2O emissions from rice paddies, offering a strategy to mitigate agriculture's impact on climate change. By addressing both GHG emissions and rice yield, the research underscores a sustainable agricultural practice that boosts productivity while preserving environmental health. The findings can inform farmers and policymakers on adopting probiotics as a cost-effective, eco-friendly alternative to traditional methods, contributing to both food security and environmental sustainability. However, this study was only conducted during the spring growing season, which may not necessarily represent the effects during the summer growing season. Further study should explore the effects of probiotics in different seasons and their interaction with various rice cultivars under different environmental conditions to better understand the durability and consistency of the observed results, as variations in plant physiology may lead to differential effects on GHG emissions and yield. Additionally, taking into account external factors such as water availability and climate variability could offer a more comprehensive understanding of the effectiveness of probiotics in various environments. By addressing these aspects, future studies could refine application methods for greater environmental and agricultural benefits.

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