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Optimizing rice-crayfish systems with direct seeding: Impacts on greenhouse gas emissions and economic performance

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ABSTRACT

The rapid expansion of rice-crayfish (RC) systems has raised concerns about increased methane (CH_4) emissions due to prolonged field flooding, especially in long-term practices. While direct seeding (DS) is widely used to reduce CH_4 in rice cultivation, its efficacy and economic viability in RC systems remain unclear. This study aimed to compare DS versus transplanting (TP) in RC systems cultivated for 5 (RC5) and 15 (RC15) years. Results showed that under TP, CH_4 emissions were 22.0 % higher in RC15 than in RC5. Implementing DS reduced CH_4 emissions by 49.9 % in RC5 and 30.1 % in RC15—mainly during the initial drainage stage—reducing the global warming potential (GWP) by 44.5 % and 27.3 %, despite increased nitrous oxide emissions. Mechanistically, DS suppressed methanogenesis by increasing soil redox potential, as indicated by a 14.1–50.9 % reduction in *mcrA* gene abundance, while increasing the abundance of ammonia-oxidizing bacteria genes. The reduced effectiveness in RC15 reflected altered emission drivers, as significant CH_4-WFPS correlations observed in RC5 ($R^2 = 0.96$) were absent in RC15 ($R^2 = 0.09$), limiting water management benefits. Although DS reduced rice yields in RC5 (12.1–10.0 t ha^{-1}), yields remained stable in RC15 (11.8 vs 12.3 t ha^{-1}). Economically, DS improved net ecosystem economic benefits by 3.5 % in RC5 and 12.8 % in RC15 systems, driven by lower crop establishment costs and reduced GWP-associated environmental costs. This study demonstrates that DS is a viable strategy for balancing environmental sustainability with economic profitability in RC systems, though optimal management is modulated by system age.

1. Introduction

Rice is a staple food for almost half of the global population, with an estimated production of 508.7 million tons (FAO.,2020). However, its cultivation is a major contributor to agricultural greenhouse gas (GHG) emissions, accounting for 22 % of methane (CH_4) and 11 % of nitrous oxide (N_2O) emissions globally (EPA, 2020; Intergovernmental Panel on Climate Change IPCC.,2023). As climate change intensifies, developing effective mitigation strategies for rice production has become essential to meet global climate targets while ensuring food security.

In paddy fields, CH_4 is produced by methanogenic archaea under anaerobic soil conditions, while N_2O is primarily generated through microbial nitrification and denitrification processes. These GHG emissions are strongly influenced by soil conditions, particularly soil redox potential (Eh), organic matter availability, and water management practices (Yan et al., 2005; Qian et al., 2023). Understanding these mechanisms is crucial for developing targeted emission reduction strategies.

Recently, an innovative eco-farming system integrating rice and crayfish (RC) has gained popularity among farmers due to high profitability. Since its introduction in Qianjiang County in 2001, RC systems have rapidly expanded across China, covering 1.73 million hectares by 2023 (Cao et al., 2017;National Bureau of Statistics of China.,2024; Wei et al., 2024). While these systems offer benefits like enhanced biodiversity and nutrient cycling (Hu et al., 2021; Sun et al., 2022), their environmental impact, particularly concerning CH_4 emissions, is

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complex and depends heavily on the specific operational mode. Initial studies suggested RC systems could reduce CH_4 emissions by 12–41 % compared to traditional rice monoculture (RM) (Sun et al., 2019; Fang et al., 2023; Guo et al., 2023; Xu et al., 2023b, 2023a). Upon closer examination, these findings mainly apply to co-culture systems where crayfish are present during the rice growing seasons, potentially aerating soils through burrowing and movement activities. The rotation systems present different challenges. In these systems, crayfish are present only during the non-rice seasons. Unlike RM with post-harvest field drainage, RC fields maintain continuous flooding from November to June to support crayfish cultivation, creating more reducing soil environments conducive to CH_4 production (Hou et al., 2021a; Sun et al., 2022). Recent research indicated that CH_4 emissions from the RC rotation mode can exceed those from local rice-wheat systems by 19.5–396.2 %, with peak emissions occurring during initial rice-growing stages (Li et al., 2023; Wang et al., 2024). This emission risk is likely exacerbated by system age. Long-term RC systems (e.g., ≥ 15 years) potentially accumulate more soil organic matter and develop more reduced conditions (Du et al., 2024a), both favoring CH_4 production. Studies have shown a correlation between RC practice duration and increased soil reduction, evidenced by lower soil Eh values and higher reducing substances concentrations (Li et al., 2018b; Yuan et al., 2020). However, the specific impacts of system age (e.g., short-term vs. long-term RC systems) on CH_4 emissions remain poorly understood.

To address this challenge, adapting proven mitigation strategies is crucial. A promising approach involves shifting the planting method from conventional transplanting (TP) to direct seeding (DS). Under TP, seedlings are moved to continuously flooded fields, whereas DS involves sowing seeds directly into non-flooded soil. This practice of DS maintains aerobic conditions during the critical seedling establishment phase, offering a powerful tool to mitigate CH_4 emissions. (Kumar and Ladha, 2011; Liu et al., 2014). Studies have demonstrated that DS can reduce CH_4 emissions by 24–79 % for dry-DS and 8–22 % for wet-DS compared to transplanted rice (Kumar and Ladha, 2011). However, this reduction in CH_4 emissions may be accompanied by an increase in N_2O emissions (Liu et al., 2014; Tao et al., 2016; Qian et al., 2023). More aerobic soil conditions promote nitrification, leading to higher nitrate (NO_3^-) availability. This, in turn, can fuel higher rates of incomplete denitrification, resulting in elevated N_2O emissions (Liu et al., 2014; Kritee et al., 2018). Therefore, it is crucial to provide a comprehensive assessment of overall GHG impacts.

Direct seeding (DS), accounting for 23 % of global rice cultivation, has gained traction in China, particularly in the middle and lower reaches of the Yangtze River—a subtropical alluvial plain with abundant water resources and intensive paddy agriculture that serves as the primary hub for RC farming development (Rao et al., 2007). Given the economic importance of RC systems and the potential of DS for GHG mitigation, a critical knowledge gap exists regarding the efficacy of DS within these specific systems. Particularly, how its CH_4 mitigation performance varies with system age of RC operation (short-term vs. long-term) remains uninvestigated. Furthermore, the economic benefits of DS implementation in RC systems require comprehensive evaluation of both production costs and GHG-related environmental costs.

Based on these considerations, our research aims to: (1) quantify the differential effects of DS and TP on CH_4 and N_2O emissions in RC systems; (2) elucidate how system age (5-year vs. 15-year) influences emissions by investigating soil biogeochemical properties and microbial functional genes; and (3) evaluate the economic feasibility of DS implementation in RC systems. To address these objectives, we conducted comprehensive field experiments comparing GHG emissions, soil properties, microbial dynamics, and economic parameters between DS and TP in both short-term and long-term RC operations. This research provides valuable insights into temporal dynamics of GHG emissions and their mitigation in RC systems, contributing to the sustainable intensification of rice production in evolving agricultural systems.

2. Materials and methods

2.1. Site description

The study was conducted in Haokou town, Qianjiang, Hubei province, China (30°22′N, 112°37′E), located in the middle and lower reaches of the Yangtze River. The soil in this area is classified as stagnic paddy soil according to the Chinese Genetic Soil Classification, corresponding to Stagnic Anthrosols in the Chinese Soil Taxonomy (Institute of Soil Science.,2024) and Aric Anthrosols in the World Reference Base for Soil Resources Classification System (IUSS Working Group, 2022). The soil is derived from fluvial-lacustrine sediments. The region experiences a subtropical monsoon climate. During the rice-growing season (June to October) of the experimental year (2021), precipitation was 1414 mm, mean air temperature was 25.6°C and mean relative humidity was 82.6 % (Fig. S1). Two RC systems, converted from traditional rice-wheat rotation systems 5 years ago (RC5) and 15 years ago (RC15), were selected to represent short-term and long-term RC farming for this research.

2.2. Field management

In each of the RC5 and RC15 systems, a 666.7 m^2 area was divided into six plots. Each plot was approximately 110 m^2 (10 m × 11 m). Three plots were randomly assigned to TP treatment, and three to DS treatment, resulting in three replicates per treatment.

The rice varieties used in this study were selected to represent common practices and agronomic considerations within RC rotation systems. Unlike traditional rice monoculture systems, RC rotations compress the rice growing season to approximately 120–130 days to accommodate the economically critical crayfish cultivation period. For DS treatment, the 'Jiuliangyouhuanghuazhan' variety was selected based on its shorter growth duration (118 days, Hunan Provincial Hunan Provincial Agricultural Department.,2016) and suitability for "simplified cultivation techniques" (Xie et al., 2015). By eliminating the 20–30 days nursery period, DS systems require varieties specifically adapted for rapid field establishment. For TP treatment, the 'Qliangyousimiao' variety was used, a widely adopted cultivar in Hubei with a registered growth duration of approximately 135 days (Du et al., 2024a, 2022). Our experimental timeline (115–129 days) reflects the constrained growing window in these RC systems. Therefore, this study compares two distinct cultivation modes as adapted for RC systems: a DS mode with a shorter-duration variety versus a conventional TP mode with a standard variety, where the choice of variety is an integral component of each respective cultivation mode being evaluated.

For TP, rice seedlings were manually transplanted on June 18, 2021, with a spacing of 20 cm × 26 cm and a rate of 3 plants per hill, resulting in a planting density of approximately 57 plants m^{-2}. For DS, dry seeds were sown on June 18, 2021, with a drone at a rate of 150 seeds m^{-2}. These densities reflect common local practices, where the DS system typically has a higher density than the TP system.

The cropping regime and water management practices at the RC field are representative of common practices in local areas (Wang et al., 2024). The TP and DS plots followed different water management practices from transplanting to mid-season drainage. For TP plots, a shallow standing water layer (< 5 cm) was maintained on the soil surface. In contrast, DS plots were managed without standing water for the first twenty days post-sowing to promote seedling establishment. Thereafter, the same shallow standing water layer was introduced and maintained. After mid-season drainage, both treatments followed the same water regime. The same nitrogen (N), phosphorus (P), and potassium (K) fertilizers were applied in all treatments at rates commonly adopted by local farmers: 128 kg N (as urea), 75 kg P_2O_5 (as calcium superphosphate), and 75 kg K_2O (as potassium chloride) ha^{-1}. For all treatments, 59.2 kg N ha^{-1} was used as basal fertilizer, while the rest was applied as top-dressing. P and K fertilizers were only applied as basal. The basal fertilizer was manually distributed into the soil surface and tilled in. The top dressings were uniformly distributed into the surface water by hand.

2.3. Sampling and measurements

2.3.1. GHG emission measurements

Gas samples were collected using the static chamber method to measure CH_4 and N_2O concentrations by gas chromatography, and emission fluxes were subsequently calculated. The static chamber consisted of two components: (1) a circular base with an inner diameter of 48 cm and outer diameter of 60 cm, placed in the rice field; (2) a cylindrical static chamber with a diameter of 51.5 cm and height of 1 m, externally wrapped with insulation coating (Fig. S2). To mix gases, a fan was installed inside the static chamber. The fan was activated during each gas collection, and sampling time, chamber temperature, and atmospheric temperature were recorded. Gas samples were collected at approximately 5–7 day intervals until harvest. The sampling interval was 10 min, with samples taken at 0, 10, 20, and 30 min from 09:00 am to 11:00 am. At each sampling time, gas samples were collected using gas-tight syringes and stored in aluminum foil gas sampling bags during field collection. After gas collection, samples were immediately transported to the laboratory, where 26 ml of gas was extracted from the gas bags using a 30 ml syringe and injected into 12 ml headspace vials (with butyl rubber sept). The samples were then analyzed using a Shimadzu GC-2010 gas chromatograph (Kyoto, Japan) to determine gas concentrations and calculate emission fluxes.

The CH_4 and N_2O fluxes (mg m^{-2} h^{-1}) were calculated according to the following equation:

$$F = \rho \times \frac{v}{s} \times \frac{dc}{dt} \times \frac{273}{273 + T}$$

Where F is the CH_4 emission rate (mg·m^{-2}·h^{-1}) or N_2O emission rate (μg·m^{-2}·h^{-1}), ρ is the density of CH_4 and N_2O under the standard state (0.714 kg·m^{-3} for CH_4, 1.25 kg·m^{-3} for N_2O), v is the effective volume of the static chamber from the chamber top to the soil surface (or water surface when flooded) (m^3); s is the soil surface area covered by the chamber base (m^2), dc/dt is the rate of concentration change per unit time (μL·L^{-1}·h^{-1} for CH_4, nL·L^{-1}·h^{-1} for N_2O), and T is the average gas temperature (℃) in the chamber.

Cumulative CH_4 and N_2O emissions were calculated from the accumulation of CH_4 and N_2O fluxes throughout the rice growing season between two consecutive measurements.

2.3.2. Sample collection

Soil samples were collected at a depth of 0–20 cm near the CH_4 and N_2O sampling sites during the rice tillering and booting stages from each of the three replicate plots per treatment. The samples were immediately transported to the laboratory and divided into three parts: one part of fresh soil was stored at −20°C for the analysis of ammonia N (NH_4^+), and NO_3^-, dissolved organic carbon (DOC), and microbial biomass carbon (MBC) and nitrogen (MBN); a second part was air-dried for pH analysis; and the third part was stored at −80°C for the detection of functional genes involved in CH_4 and N_2O emissions. The targeted genes included the methanogenic gene *mcrA*, the methanotrophic gene *pmoA*, the nitrifier genes *amoA-A* and *amoA-B*, and the denitrifier genes *nirK*, *nirS* and *nosZ*.

2.3.3. Soil physicochemical property measurements

The concentrations of NH_4^+, and NO_3^- in the 0–20 cm soil were determined using standard soil chemistry methods according to Du et al. (2022). NH_4^+ and NO_3^- concentrations were analyzed using a continuous flow analyzer (Auto-Analyzer 3, Norderstedt, Seal, Germany). DOC was determined by 0.2 M K_2SO_4 leaching method (Wang et al., 2024). MBC and MBN were extracted from chloroform fumigation and unfumigated samples with 0.5 M K_2SO_4 and measured using an automated total organic carbon analyzer (Vario TOC select, Element, Germany). Soil pH was measured using a soil and water mixture at a ratio of 1:2.5.

During gas sampling, ponding depth in the plots was measured using a graduated ruler at three random points near the gas sampling sites. Soil parameters in the 0–20 cm layer, including temperature, volumetric moisture content (VMC), electrical conductivity (EC), and salinity, were measured in situ using a TDR 350 (Spectrum Technologies, Inc., USA). Soil Eh was measured separately using a portable electrochemical analyzer (TR-901, REX, Shanghai, China) equipped with a platinum combination electrode and an Ag/AgCl reference electrode. The electrode was inserted directly into the soil at 10 cm depth and measurements were recorded after stabilization.

To provide a direct measure of soil aeration status, water-filled pore space (WFPS) was calculated as follows:

$$\text{WFPS}(\%) = \frac{\text{VMC}}{\text{Total Porosity}} \times 100$$

Where VMC is the sensor-measured volumetric moisture content and total porosity was calculated from soil bulk density (BD) using an assumed particle density of 2.65 g cm^{-3} (Li et al., 2019; Liu et al., 2014):

$$\text{Total Porosity} = 1 - \frac{\text{BD}}{\text{Soil particle density}}$$

Soil BD for the 0–20 cm layer was measured for each system at the beginning of the experiment by collecting intact soil cores.

2.3.4. Quantitative PCR (qPCR)

Functional genes involved in CH_4 and N_2O emissions in the soil were quantified using qPCR, including methanogenic gene (*mcrA*), methanotrophic gene (*pmoA*), ammonia-oxidizing archaeal and bacterial genes (*amoA-A*, *amoA-B*), and denitrifying genes (*nirK*, *nirS*, and *nosZ*). The genomic DNA was extracted from the soil samples using the Omega DNA extraction kit (cat: M5635–02) following the manufacturer's protocol. The DNA purity was assessed using a Nanodrop 2000 spectrophotometer (Thermo Fisher Scientific, Waltham, USA). qPCR was performed on the Roche LightCycler 480 II Real-Time PCR System (Roche, Switzerland). Each PCR reaction mixture contained 1 μL of DNA template, 10 μL SYBR Premix Ex Taq (TaKaRa, Dalian, China), 0.4 μL of each 10 μM primer and 8.2 μL Milli-Q water. All genes used the same thermal cycling conditions: initial denaturation at 95°C for 5 min, followed by 40 cycles of 95°C for 15 s and 60°C for 30 s. Standard curves were generated using tenfold serial dilutions of known concentrations of plasmid DNA containing the target genes. The plasmids were initially diluted 500-fold, then serially diluted to create standards ranging from $n \times 10^{10}$ to $n \times 10^3$ copies μL^{-1}. These curves were used to calculate the gene copy numbers in the soil samples. Each dilution and sample were analyzed in triplicate to ensure reproducibility. Melting curve analysis confirmed amplification specificity. The primers, sequence, amplification efficiencies, correlation coefficients (R^2), and the literature references for each gene are listed in Table S1.

2.4. Economic data collection and net ecosystem economic benefits (NEEB) calculations

Economic analysis was based on actual farm-level operational data collected during the 2021 growing season. Production costs—including seeds/seedlings, crayfish feed, labor, machinery, electricity, and land rent—were documented based on actual expenditures. To ensure experimental control, fertilizer and pesticide inputs were standardized across all treatments. Rice income was calculated from measured grain yields multiplied by local market price (2.40 CNY kg^{-1}). Crayfish revenue was based on the host farmers' complete, season-long sales records, representing actual market returns.

The global warming potential (GWP) of CH_4 and N_2O emissions was calculated by multiplying the 100-year radiative forcing potential coefficients to CO_2 (28 and 265 used for CH_4 and N_2O, respectively) (Chen et al., 2024). Yield-scaled GWP was calculated as the GWP per unit total yield of rice. GWP costs were calculated based on carbon trade prices (103.7 CNY t^{-1} CO_2eq.) and GWP values (Zhang et al., 2018). Finally, NEEB was calculated using the following equation: NEEB = (Rice revenue + Crayfish revenue) − (All production costs + GWP cost).

2.5. Statistical analysis

A paired *t*-test was used to test for statistically significant differences ($\alpha = 0.05$) in environmental conditions between the DS and TP treatments within each system (RC5 and RC15 separately). A two-way analysis of variance (ANOVA) was used to examine the main effects of treatment (DS vs. TP) and system (RC5 vs. RC15) on CH_4 and N_2O emissions, soil physicochemical properties, and microbial gene abundance. To account for the potential influence of planting density and rice yield on GHG emissions, a two-way analysis of covariance (ANCOVA) was performed. Planting density and rice yield were included as covariates, with establishment method (TP vs. DS) and system age (RC5 vs. RC15) as the main fixed effects. Statistical analysis was performed using SPSS 22.0 (American SPSS Corporation) with significance determined at $p < 0.05$. Spearman's correlation analysis was conducted using OriginPro 2025 (OriginLab Corporation, USA) to test the correlation between CH_4 and N_2O emission flux and soil chemical and microbial parameters.

3. Result

3.1. Seasonal GHG emissions and overall climate impact

The rice growing season was divided into three stages based on growth and development: vegetative phase (transplanting to tillering), reproductive phase (booting to heading), and ripening phase (after heading).

Direct seeding (DS) significantly modified GHG emission patterns compared to TP across both RC systems. Compared to TP, DS significantly reduced seasonal total CH_4 emissions by 49.9 % in RC5 and 30.1 % in RC15 ($p < 0.05$, Fig. 1a). The DS treatment achieved the greatest CH_4 emission reductions during the vegetative phase, decreasing CH_4 emissions by 65.5 % and 56.6 % in RC5 and RC15, respectively ($p < 0.05$). In the reproductive phase, DS significantly reduced CH_4 emissions by 30.1 % in RC5 ($p < 0.05$, Fig. 1a), while no significant change was observed in RC15. Compared to TP, DS significantly increased seasonal total N_2O emissions by 14.4 % in RC5 and 36.2 % in RC15 ($p < 0.05$, Fig. 1b). The N_2O emission increase was most pronounced during the reproductive phase, with 48.2 % and 56.9 % in RC5 and RC15, respectively ($p < 0.05$, Fig. 1b). On average, vegetative phase, reproductive phase and ripening phase contributed 21.5 %, 52.6 %, and 26.0 % to the seasonal total N_2O emission, respectively (Fig. 1b).

The total GWP of GHG emissions (sum of CH_4 and N_2O in CO_2eq.) significantly decreased by 44.5 % in RC5 and 27.3 % in RC15 with DS compared to TP ($p < 0.05$, Fig. 1c). CH_4 was the dominant contributor to GWP across all treatments, contributing 82.4–95.8 % of total GWP (Fig. 1c).

3.2. Temporal dynamics of CH_4 and N_2O emission

Time-series analysis revealed that DS delayed and reduced the CH_4 flux peaks compared to TP (Fig. 2a, b). Peak reductions of 97.4 % and 87.9 % occurred during the early drainage period specific to DS management (0–25 days in RC5, 0–18 days in RC15) (Fig. 2a, b). This early drainage window accounted for 55.8 % and 89.3 % of total seasonal CH_4 reduction, respectively (Fig. 2a, b). In contrast, DS did not significantly alter the temporal distribution patterns of N_2O emissions but substantially enhanced peak emission magnitudes during the reproductive

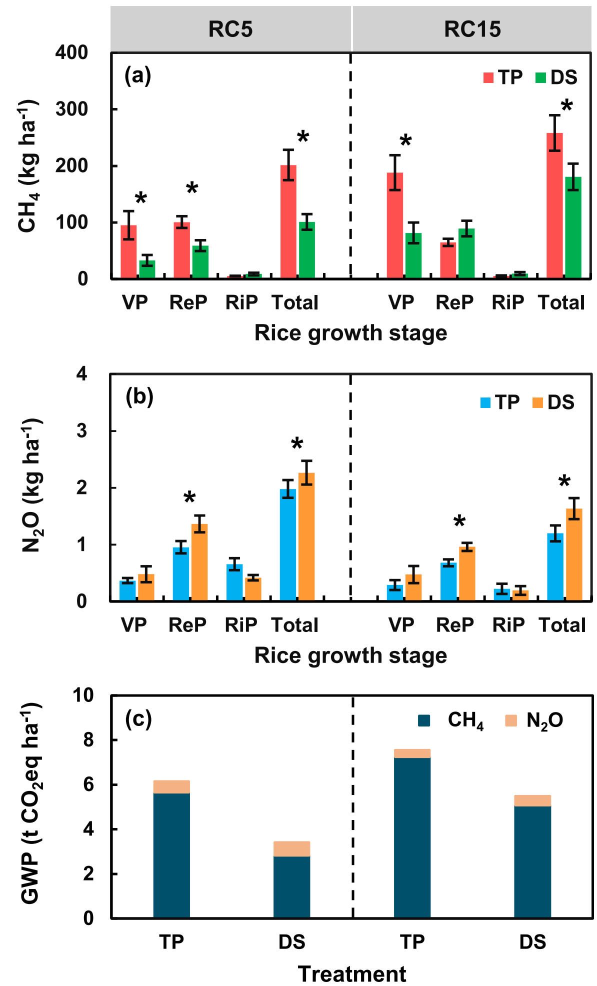

Fig. 1. Seasonal cumulative CH_4 and N_2O emissions and global warming potential (GWP) in RC5 and RC15 systems during the rice growing season (RC5, 120 days; RC15, 118 days). a-b, seasonal cumulative CH_4 (a) and seasonal N_2O (b) emissions presented by growth stage; (c), GWP composition showing CH_4 and N_2O contributions for the entire growing season. TP and DS represent transplanted rice and direct-seeded rice, respectively. VP, ReP, RiP, and Total represent the vegetative phase (from transplanting to tillering), reproductive phase (booting to heading), ripening phase (after heading), and the entire stage, respectively. RC5 and RC15 denote rice-crayfish systems operated for 5 and 15 years, respectively. Values are means with standard deviation. * represents significant difference ($p < 0.05$) between TP and DS within the same system and growth stage.

phase compared to TP, with peak increases of 40.9 % in RC5 and 316.2 % in RC15 compared to TP treatments (Fig. 2c, d).

3.3. CH_4 emission-WFPS relationships in different RC systems

The relationship between CH_4 emissions and WFPS differed markedly between the two RC systems (Fig. 3). In RC5 systems, CH_4 emissions showed a strong exponential correlation with WFPS ($R^2 = 0.96$, $p < 0.001$), with emissions ranging from 0.8 to 43.7 mg m^{-2} h^{-1} across WFPS values of 90.0–99.0 % (Fig. 3a). In RC15 systems, no significant correlation was observed between CH_4 emissions and WFPS ($R^2 = 0.09$, $p = 0.72$), with emissions ranging from 6.2 to 51.1 mg m^{-2} h^{-1} across WFPS values of 82.7–92.8 % (Fig. 3b).

3.4. Biogeochemical and microbial drivers

Soil physicochemical properties varied significantly between RC5

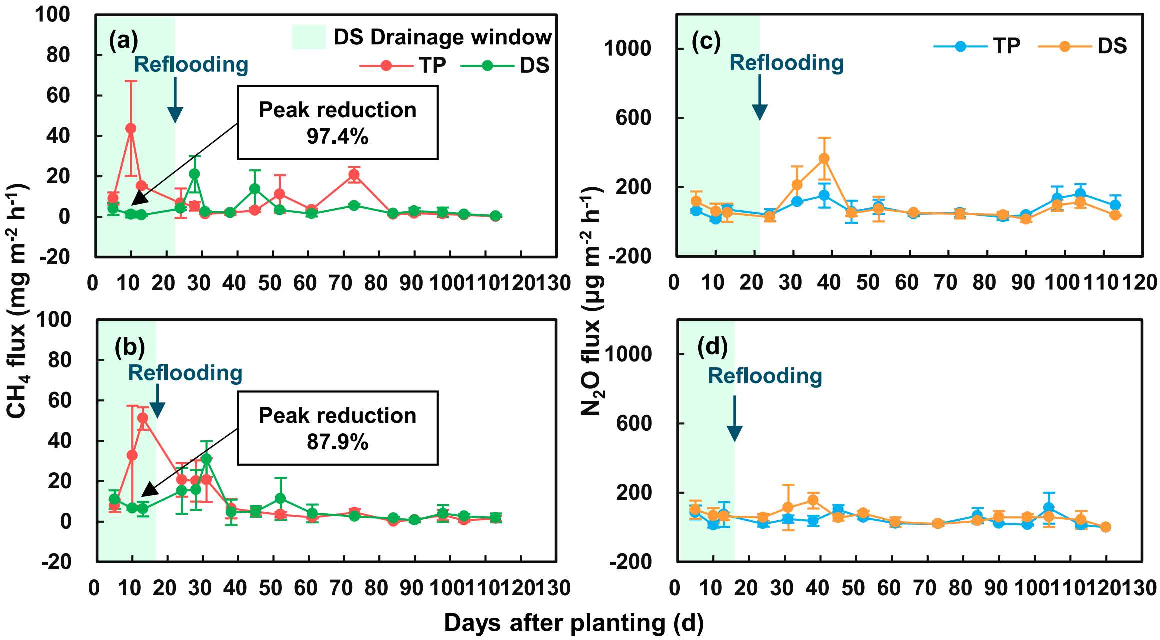

Fig. 2. Temporal patterns of greenhouse gas (GHG) emissions in RC5 and RC15 systems. a-b, CH_4 flux dynamics in RC5 (a) and RC15 (b) with highlighted early drainage periods; c-d. N_2O flux dynamics in RC5 (c) and RC15 (d). Green shading marks the DS early-drainage window (0–25 DAT RC5; 0–18 DAT RC15) where 55.8 % and 89.3 % of total seasonal CH_4 reduction occurred in RC5 and RC15, respectively. Peak reduction percentages show maximum daily reduction rates. TP and DS represent transplanted rice and direct-seeded rice, respectively. RC5 and RC15 denote rice-crayfish systems operated for 5 and 15 years, respectively. The values are means with standard deviation.

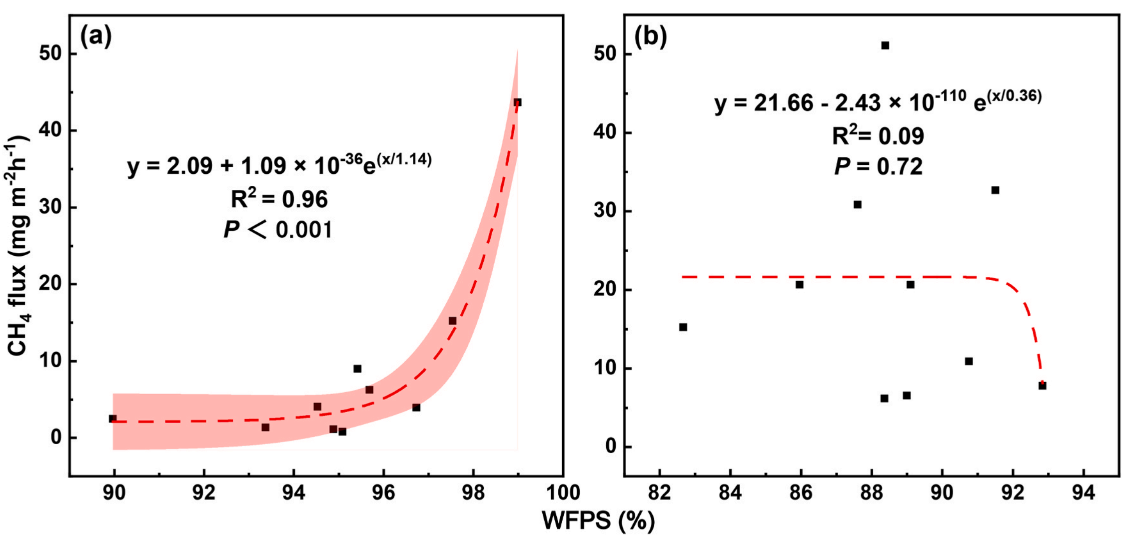

Fig. 3. The correlation between CH_4 emission fluxes and soil WFPS in vegetative phase. a-b, RC5 (a) and RC15 (b). WFPS: water-filled pore space. Solid line represents fitted regression; shaded area indicates 95 % confidence interval. Black squares represent individual data points. RC5 and RC15 denote rice-crayfish systems operated for 5 and 15 years, respectively.

and RC15 systems (Table 1). Compared to RC5, the RC15 systems had significantly lower soil BD (by 15.4 %), higher total porosity (by 20.6 %), and higher concentrations of DOC (by 92.5 %) ($p < 0.001$, Table 1). Soil salinity and EC were also significantly higher by 60.9 % and 62.4 % in RC15, while its WFPS was significantly 7.0 % lower ($p < 0.001$, Table 1).

DS treatment significantly altered the soil environment compared to TP. Within each system, DS imposed an early-season drainage that significantly raised soil Eh ($p < 0.05$, Fig. S3) and lowered WFPS ($p < 0.05$, Table 1). The DS treatment induced system-specific responses in soil carbon and nitrogen pools. Soil DOC levels showed no significant differences between DS and TP treatments in either system (Fig. 4a). In RC5, the DS treatment did not significantly alter MBC, while in RC15 it led to a significant 17.5 % increase during the tillering stage ($p < 0.05$, Fig. 4b). Similarly, NH_4^+-N content increased significantly during the tillering stage only in RC15 ($p < 0.05$, Fig. 4c). NO_3^--N levels were significantly elevated by DS during the tillering stage in both systems ($p < 0.05$, Fig. 4d). MBN content significantly increased under DS during the tillering phase in both systems ($p < 0.05$, Fig. 4e), leading to a consistently lower MBC:MBN ratio ($p < 0.05$, Fig. 4f).

The DS treatment influenced the abundance of key microbial functional genes involved in GHG cycling as well (Figs. 5 and 6). For methanogenesis, compared to TP, DS significantly reduced the copy number of the *mcrA* gene during the tillering stage by 14.1 % in RC5 and

Table 1
Key soil physicochemical properties in RC5 and RC15 systems under DS and TP treatment during the vegetative phase.

Parameter	RC5		RC15		*P* values		
	TP	DS	TP	DS	System	Treatment	S×T
Bulk density (g cm^{-3})	1.3 ± 0.02	1.3 ± 0.02	1.1 ± 0.12	1.1 ± 0.12	*	-	-
Total porosity (%)	49.4 ± 0.8	49.4 ± 0.8	59.6 ± 4.5	59.6 ± 4.5	*	-	-
WFPS (%)	96.2 ± 2.2	94.2 ± 2.5	89.5 ± 2.7	87.7 ± 3.0	***	*	0.97
DOC (mg kg^{-1})	74.2 ± 8.1	69.3 ± 7.4	142.8 ± 12.1	138.5 ± 11.8	***	0.24	0.71
Soil pH	7.3 ± 0.01	7.1 ± 0.01	7.5 ± 0.05	7.4 ± 0.01	***	**	*
Soil salinity (mg kg^{-1})	292.5 ± 16.6	315.0 ± 16.0	470.5 ± 52.3	439.6 ± 48.8	***	0.70	*
EC (μS cm^{-1})	532.8 ± 30.2	573.6 ± 29.1	865.0 ± 79.5	821.1 ± 100.4	***	0.91	*

TP and DS represent transplanted and direct-seeded rice, respectively. RC5 and RC15 denote rice-crayfish systems operated for 5 and 15 years, respectively. Values are means ± standard deviation. *P* values from two-way ANOVA. S×T = System × Treatment interaction. * represents the significant difference ($p < 0.05$). ** represents the significant difference ($p < 0.01$). *** represents the significant difference ($p < 0.001$). WFPS = water-filled pore space; DOC = dissolved organic carbon; EC = electrical conductivity. full model outputs in Table S2.

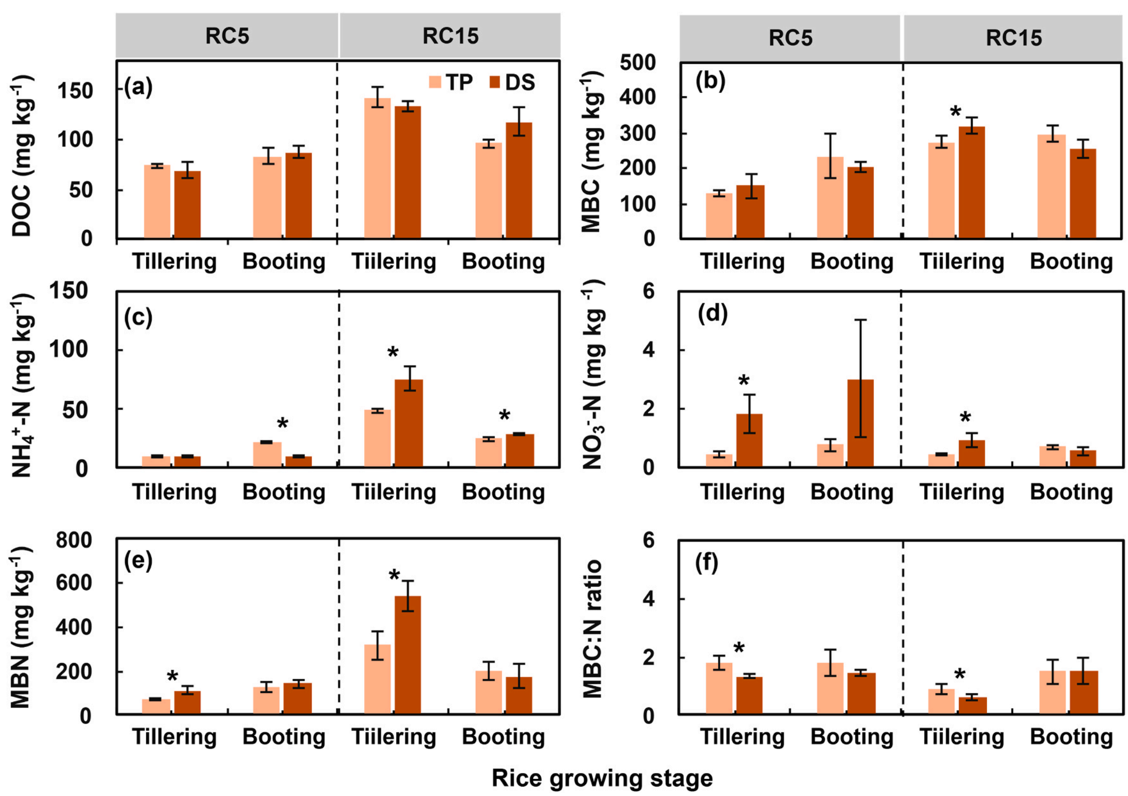

Fig. 4. Soil properties in RC5 and RC15 field soils. a-f, concentrations of DOC (a), MBC (b), NH_4^+-N (c), NO_3^--N (d), MBN (e), and MBC:MBN ratio (f). TP and DS represent transplanted rice and direct-seeded rice, respectively. RC5 and RC15 denote rice-crayfish systems operated for 5 and 15 years, respectively. The values are the means with standard deviation. * represents the significant difference ($p < 0.05$) between TP and DS.

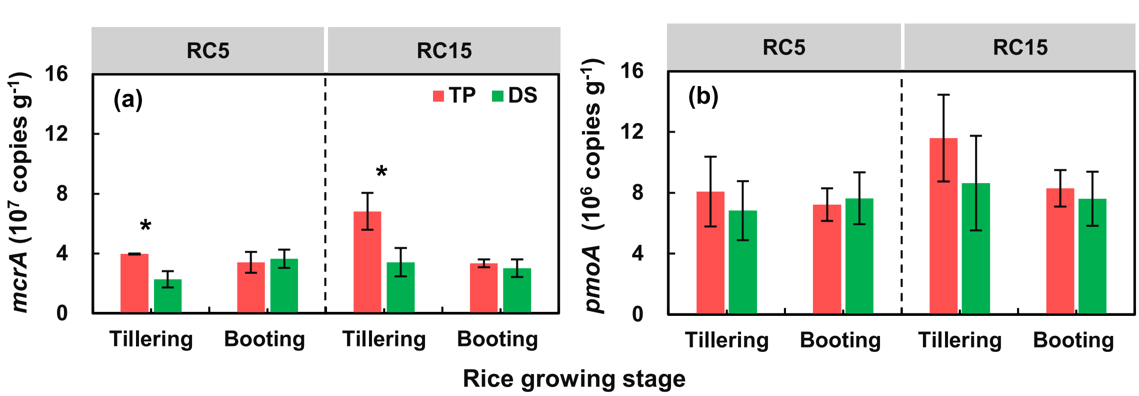

Fig. 5. Copy number of functional genes related to CH_4 emission in field soil of RC5 and RC15. a-b, *mcrA* (a) and *pmoA* (b). TP and DS represent transplanted rice and direct-seeded rice, respectively. The values are the means with standard deviation. * represents the significant difference ($p < 0.05$) between TP and DS.

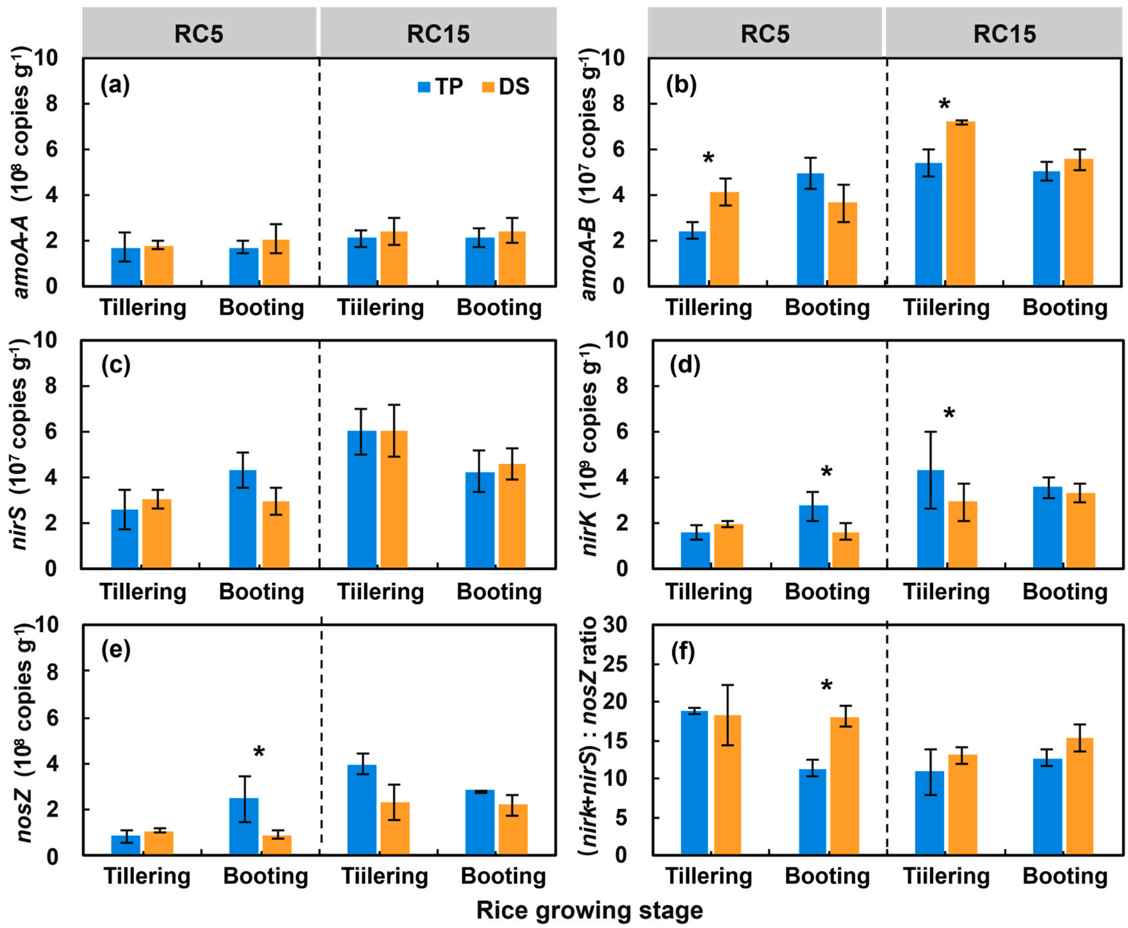

Fig. 6. Copy number of functional genes related to N_2O emission in field soil of RC5 and RC15. a-f, *amoA-A* (a), *amoA-b* (b), *nirS* (c), *nirK* (d), *nosZ* (e) and (*nirK*+*nirS*)/*nosZ* (f). TP and DS represent transplanted rice and direct-seeded rice, respectively. The values are the means with standard deviation. * represents the significant difference ($p < 0.05$) between TP and DS.

50.9 % in RC15 ($p < 0.05$, Fig. 5a, Table S2), while the methanotrophic gene *pmoA* remained unchanged (Fig. 5b). For nitrogen cycling, DS significantly increased the abundance of the ammonia-oxidizing bacterial gene *amoA-B* in both systems (69.8 % in RC5 and 33.2 % in RC15) ($p < 0.05$, Fig. 6b). In RC5, the copy numbers of *nirK* and *nosZ* were significantly lower in DS than TP during the booting stage ($p < 0.05$, Fig. 6d, e), with reductions of 42.0 % and 63.8 %, respectively. In contrast, no significant differences were observed for *nirK* and *nosZ* between DS and TP treatments in RC15 (Fig. 6d, e).

3.5. Factors driving GHG emissions: a correlation analysis

During the vegetative phase, CH_4 emissions were significantly positively correlated with ponding depth and negatively correlated with N_2O flux and soil NO_3^--N concentrations ($p < 0.05$, Fig. 7a). During the reproductive phase, CH_4 emissions showed significant positive correlations with soil WFPS, salinity, MBC, DOC, MBN, DON, NH_4^+-N, and the abundance of *amoA-B* and *nirK* genes, but was negatively correlated with N_2O flux and soil temperature ($p < 0.05$, Fig. 7b).

During the vegetative phase, N_2O emissions showed significantly positive correlations soil NO_3^--N concentrations and negative correlations with ponding depth ($p < 0.05$, Fig. 7a). During the reproductive stage, N_2O emissions were highly positively correlated with soil temperature and NO_3^--N, and negatively correlated with WFPS, salinity, MBC, DON, NH_4^+-N and the (*nirK* + *nirS*): *nosZ* ratio ($p < 0.05$, Fig. 7b).

3.6. Rice yield, and NEEB

Compared to TP, DS significantly decreased rice yield in RC5 ($p < 0.05$), while showing no significant change in RC15 (Table 2). The yield-scaled GWP was significantly reduced by 32.9 % and 29.8 % with DS compared to TP in RC5 and RC15, respectively ($p < 0.05$, Table 2). Furthermore, DS significantly increased NEEB by 3.5 % in RC5 and 12.8 % in RC15 ($p < 0.05$, Fig. 8, Table S4). Total production costs decreased from 25.48 to 18.35 thousand CNY ha^{-1} in RC5 and from 25.89 to 18.83 thousand CNY ha^{-1} in RC15 under DS treatment compared to TP. The cost reductions primarily resulted from lower nursery costs (5.88 vs 2.25 thousand CNY ha^{-1}), reduced labor costs (3.60 vs 0.38 thousand CNY ha^{-1}), and decreased GWP costs (0.64 vs 0.36 thousand CNY ha^{-1} in RC5; 0.78 vs 0.57 thousand CNY ha^{-1} in RC15) (Fig. 8, Table S4).

4. Discussion

4.1. CH_4 emissions response to direct-seeding and system age in RC farming systems

RC systems present unique challenges in GHG emissions, particularly CH_4 emissions due to their unique flooding requirements that extend beyond rice growth into winter crayfish rearing (Yuan et al., 2022). This prolonged flooding accelerates the soil gleization process, promoting organic compound accumulation and subsequent CH_4 production (Kögel-Knabner et al., 2010). Moreover, crayfish farming introduces additional carbon inputs, such as feed and crayfish remains (Wang et al.,

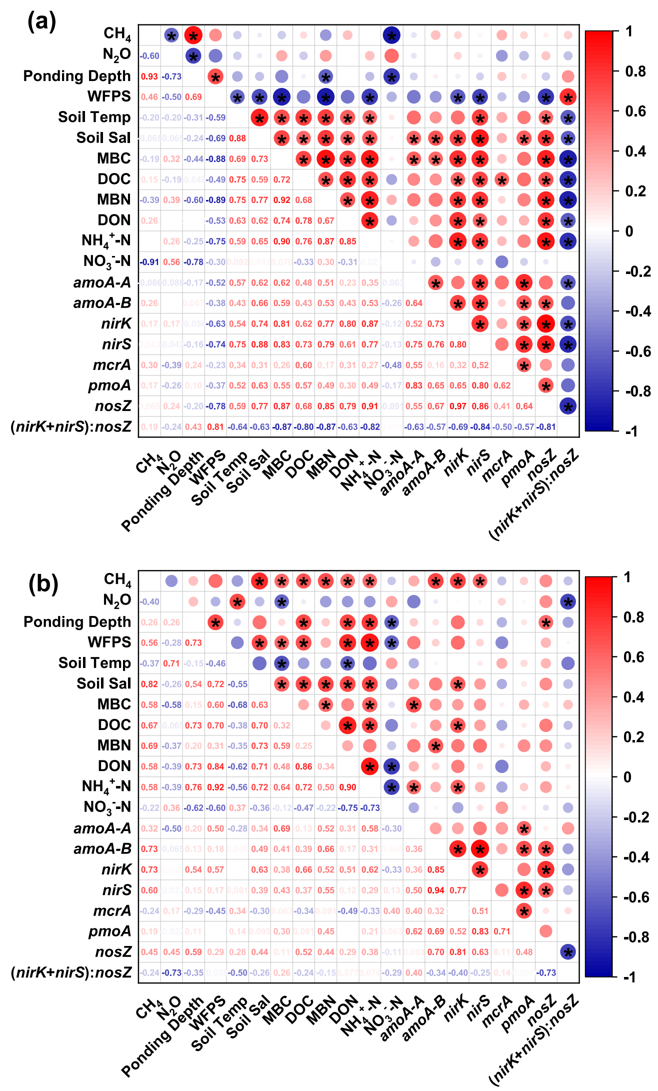

Fig. 7. Spearman correlation coefficients between greenhouse gas (GHG) emissions and key biogeochemical drivers. a-b, vegetative (a) and reproductive (b) stage. TP and DS represent transplanted rice and direct-seeded rice, respectively. * represents the significant difference ($p < 0.05$) between TP and DS. Numbers are Spearman coefficients. Ponding depth: surface water depth; WFPS: water-filled pore space; Temp: temperature; Sal: salinity; MBC/MBN, microbial biomass C/N; DOC/DON, dissolved organic C/N; NH_4^+-N, ammonium-N; NO_3^--N, nitrate-N; *amoA-A/amoA-B*, ammonia-oxidizing archaea/bacteria; *nirK*, *nirS*, *nosZ*, *mcrA*, *pmoA*, functional genes; (*nirK* + *nirS*): *nosZ*, ratio of denitrification to N_2O-reduction genes.

2024). This organic matter input resulted in elevated DOC concentrations, with RC15 showing 92.5 % higher levels than RC5 (Table 1). Under these DOC-enriched conditions, microbial degradation depletes alternative electron acceptors (NO_3^-, sulfate, iron and manganese), creating favorable conditions for methanogenesis (Li et al., 2021). These conditions favor CH_4 generation, as evidenced by our finding that RC15 systems emit 22.0 % more CH_4 than RC5 systems (Fig. 1a). Therefore, interrupting the continuous flooding and implementing moderate aeration are crucial for mitigating CH_4 emissions for RC systems, particularly for long-term practices. Our study demonstrates that compared to TP, DS effectively mitigates CH_4 emissions by reducing flooding time, achieving 49.9 % and 30.1 % reduction in RC5 and RC15 systems, respectively (Fig. 1a). The mitigation effect of DS was less pronounced in RC15, where higher concentrations of DOC and a more intensely anaerobic environment likely sustained a high methanogenic potential that was not fully overcome by the aeration improvements

Table 2
Overall CH_4 and N_2O emissions, Total global warming potential (GWP), rice yield, and yield-scaled GWP for the RC system under DS and TP treatment.

System	Treatments	CH_4 (kg ha^{-1})	N_2O (kg ha^{-1})	Total GWP (t CO_2 eq ha^{-1})	Rice yield (kg ha^{-1})	Yield-scaled GWP (t CO_2 eq kg^{-1})
RC5	TP	201.43 a	1.98 a	6.17 a	12087 a	0.51 a
	DS	100.83 b	2.27 b	3.42 b	10000 b	0.34 b
RC15	TP	258.13 a	1.20 a	7.55 a	11828 a	0.69 a
	DS	180.56 b	1.64 b	5.49 b	12259 a	0.46 b

Note: Different letters indicate statistical significance at $p < 0.05$ within the same system.

from the DS practice.

The primary mechanism behind CH_4 reduction under DS is soil Eh modification. The DS treatment raised soil Eh significantly during the critical early growth phase (93 mV in DS vs. 13 mV in TP, $p < 0.05$, Fig. S3), which suppressed methanogenesis. This is evidenced by reduced *mcrA* gene (a key marker for methanogenic archaea) abundance under DS compared to TP, with a 14.1 % reduction in RC5 and 50.9 % reduction in RC15 during the tillering stage (Fig. 5a). The reduction in *mcrA* gene abundance, without a corresponding increase in *pmoA* gene, indicates that the CH_4 emission reduction primarily results from suppressed methanogenesis rather than enhanced methanotrophy (Fig. 5; Conrad, 2020). Methanogens are strict anaerobes, and even short periods of soil aeration can significantly impact their populations (Yuan et al., 2009). Surface water control emerged as the key driver of this effect. The positive correlation between CH_4 emissions and ponding depth during the vegetative phase demonstrates that surface water presence, rather than soil water content alone, critically regulates oxygen diffusion and subsequent methanogenic activity (Fig. 7a). This observation corroborates Song et al. (2022)'s findings that the presence of surface water significantly impedes oxygen diffusion into the soil, even when underlying soil moisture content remains constant.

It is crucial to establish that this effect is genuinely attributable to the management practice itself. The potential influence of planting density and rice variety as confounding factors must be carefully considered when interpreting the results. Systems adopted DS often employ higher planting densities to compensate for poor crop establishment and suppress weed growth (Farooq et al., 2011; Li et al., 2019). Such higher densities can, in turn, increase CH_4 emission through increased root exudates and higher aerenchyma density (Chen et al., 2013; Li et al., 2019; Ge et al., 2024). These factors can enhance CH_4 production and transport from soil to air (Bhattacharyya et al., 2019; Iqbal et al., 2021). Li et al. (2019) found that higher planting density in DS rice systems led to increased CH_4 emissions, driven by greater gross ecosystem productivity and aboveground biomass. This has led to concerns that higher planting densities in DS may offset its CH_4 reduction benefits. Our ANCOVA results also confirm that planting density significantly affects CH_4 emissions ($p < 0.05$) (Table S3). However, even after accounting for planting density variation, DS still shows a significant advantage in reducing CH_4 emissions ($p < 0.05$, Table S3). This finding emphasizes that the CH_4 mitigation potential of DS is primarily driven by altered soil conditions rather than planting density effects. The coupling of variety selection with establishment method presents an additional confounding challenge. However, multiple lines of evidence demonstrate that observed emission reductions were primarily driven by DS water management rather than inherent variety characteristics: Firstly, the CH_4 emission dynamics showed a tight coupling with water status. Most of the reduction occurred during the early drainage period specific to DS, and crucially, emissions from the DS plots increased sharply to track

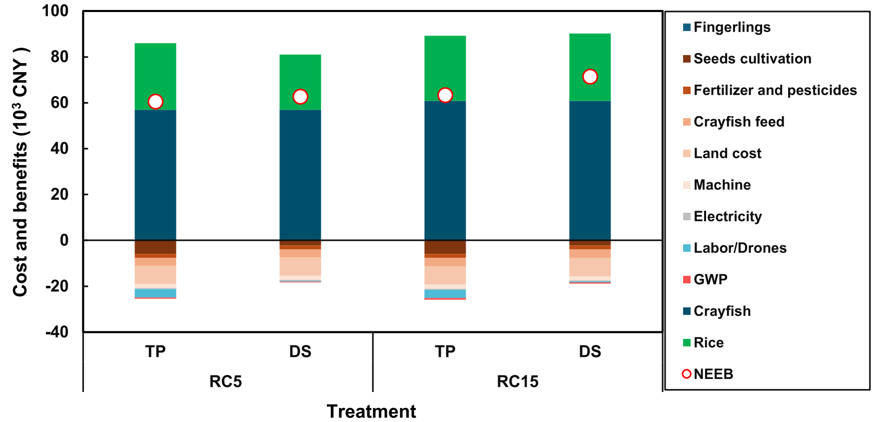

Fig. 8. The net ecosystem economic budget (NEEB) for TP and DS under RC farming. TP and DS represent transplanted rice and direct-seeded rice, respectively. GWP: Global warming potential.

those from TP plots immediately after the fields were reflooded (Fig. 2a, b). This abrupt "on-off" response points to a dominant physical control mechanism—the oxygen diffusion barrier imposed by the surface water layer—as opposed to biological regulation from the plant. The latter, which involves the gradual establishment of variety-specific traits like root architecture for radial oxygen loss and rhizosphere functioning, would develop progressively as the plant matures and thus exert a more constant or gradual influence (Chandrasekaran et al., 2022; Ejiri et al., 2021; Qian et al., 2023). Secondly, ANCOVA results using yield as a covariate confirmed that establishment method effects remain significant after accounting for potential variety differences, though it is important to note that variety traits were not fully isolated in this analysis ($\eta^2 = 0.84$, $p < 0.001$, Table S3).

Importantly, DS effectiveness in mitigating CH_4 emissions was system-dependent, as indicated by the significant interaction between treatment and system age (Table S2). System age fundamentally altered the relationship between WFPS and CH_4 emissions. In RC5 systems, a strong exponential correlation ($R^2 = 0.96$, $p < 0.001$) was observed, operating at high WFPS ranges (90.0–99.0 %), while RC15 systems showed no significant relationship ($R^2 = 0.09$, $p = 0.72$) despite operating at lower WFPS ranges (82.7–92.8 %) (Fig. 3). Both systems exceeded established WFPS thresholds (75–82 %) for methanogenic activity (Xu et al., 2003; Li et al., 2018a). However, the differential responses suggest system-specific regulatory mechanisms operating within these high-WFPS ranges. In RC5, the CH_4-WFPS relationship exhibited an apparent inflection point around 95 % WFPS, with emissions increasing exponentially above this threshold. This suggests that RC5 operates in a moisture-sensitive regime where small WFPS changes near the upper threshold dramatically affect oxygen availability and methanogenic activity. In contrast, RC15 systems predominantly operated below this critical threshold (maximum 92.8 % WFPS) and consequently exhibited a weaker response to WFPS variations (Fig. 3). Moreover, the higher DOC concentrations and altered soil structure in RC15 systems may create conditions where factors beyond moisture—such as substrate availability, soil physical heterogeneity, or microbial community composition—become increasingly important for regulating methanogenic activity (Table 1).

These findings highlight the critical need for system age-specific management approaches in RC systems. While DS remains effective across all system ages, the diminished efficacy in long-term systems suggests that precision water management alone may be insufficient for optimal CH_4 mitigation in aged RC systems. For younger RC systems, water-saving practices like DS are highly effective due to the tight coupling between soil water content and methanogenic activity. Management should focus on optimizing drainage timing and intensity to maximize the oxidative stress period for methanogenic populations (Qian et al., 2023). For mature RC systems, complementary strategies targeting substrate management become essential. These may include: (1) pre-planting straw removal to reduce labile carbon inputs (Jiang et al., 2019; Wang et al., 2024), (2) strategic application of alternative electron acceptors such as sulfate-based fertilizers to compete with methanogenic pathways (Shrestha et al., 2010), and (3) enhanced soil aeration timing to overcome the substrate-saturated conditions that maintain high methanogenic potential.

4.2. N_2O emissions response to direct-seeding and system age in RC farming systems

Emissions of N_2O in agricultural soils are primarily driven by nitrification and denitrification processes, which are regulated by soil temperature, moisture, pH, substrate concentration and microbial communities (Butterbach-Bahl et al., 2013; Hu et al., 2015; Qiu et al., 2024). Compared to traditional RM, RC systems generally reduce or do not significantly change N_2O emissions (Fang et al., 2023; Guo et al., 2023; Xu et al., 2023b). Our study showed that RC15 emitted 27.8–29.4 % less N_2O than RC5 (Fig. 1b), enhanced mitigation potential with system maturation. This reduction is likely associated with more complete denitrification in RC15, as indicated by the lower (*nirK* + *nirS*)/ *nosZ* ratio (Fig. 6f, Table S2), favoring N_2 over N_2O formation (Butterbach-Bahl et al., 2013). Despite these inherent N_2O mitigation benefits of mature RC systems, the introduction of DS management creates a complex trade-off scenario. While DS reduces CH_4 emissions, it tends to increase N_2O emissions (Tao et al., 2016; Qian et al., 2023). This trade-off may undermine the N_2O mitigation potential of long-term RC systems, highlighting the need to carefully balance these trade-offs when adopting DS practices.

Increased N_2O emissions under DS are primarily attributed to changes in soil hydrology. Specifically, DS led to frequent aerobic-anaerobic alternations during early growth stages, in contrast to the continuous flooding in TP. These oscillating conditions are likely to enhance both nitrification and denitrification processes, increasing N_2O production due to incomplete denitrification during transient cycles (Kritee et al., 2018; Verhoeven et al., 2018). This mechanism is supported by elevated soil NO_3^--N content and *amoA-B* gene abundance during the tillering stage ($p < 0.05$, Figs. 4d, 6d), indicating enhanced nitrification (Du et al., 2024a). The increased MBN content, coupled with a decreased MBC:MBN ratio, further suggests a shift towards a more efficient N cycling microbial communities ($p < 0.05$, Fig. 4e and f), potentially accelerating N turnover and subsequent N_2O production (Mooshammer et al., 2014). Moreover, the delayed application of tillering fertilizer in DS, closer to the mid-season drainage period (Table S5), likely increased the availability of N during key microbial activity periods, further promoting N_2O emissions (Venterea et al., 2016; Gaihre et al., 2020).

Despite the lack of significant interaction between planting method and system age for N_2O emissions, we observed system-specific responses to DS treatment. In RC5, DS significantly reduced the (*nirK* + *nirS*)/ *nosZ* ratio ($p < 0.05$, Fig. 6f), suggesting enhanced incomplete denitrification (Knowles, 1982). This system-specific response was accompanied by differential pH dynamics, where DS significantly reduced soil pH in RC5 but not in RC15 (Fig. S4). Lower pH inhibits N_2O reductase activity, promoting incomplete denitrification and N_2O emissions (Knowles, 1982; Žurovec et al., 2021). The observed pH reduction in RC5 may be due to lower N uptake efficiency by seedlings during early DS stages, resulting in N surplus (Li et al., 2010; Sandhu et al., 2015). This surplus NH_4^+ undergoes nitrification, releasing hydrogen ions (H^+) and lower pH (Zhou et al., 2014). Additionally, DS rice releases more root exudates, such as organic acids, which further decrease pH (Liu et al., 2022). In contrast, the stable pH in RC15 suggests improved soil buffering capacity, possibly due to prolonged flooding and regular lime application for disinfection (Hou et al., 2021b; Du et al., 2024b). These practices likely increase pH by inhibiting nitrification and neutralizing acidic ions. Soil Eh also exhibited system-specific patterns. In RC5, higher soil Eh under DS compared to TP persisted into the early reproductive phase (Fig. S3), while RC15 showed differences only during the vegetative phase. The persistent high Eh, combined with decreased pH in RC5, likely promotes incomplete denitrification (Pan et al., 2022). The stable Eh and pH in RC15 suggest a more resilient denitrifying community in long-term systems. Additionally, two-way ANOVA revealed significantly higher salinity and EC levels in RC15 compared to RC5, which were associated with lower N_2O emissions (Table S2). This suggests that long-term RC systems can suppress N_2O emissions through the accumulation of salts. Previous studies have shown that the input of crayfish feed, excreta, and high soil water content in RC systems contribute to this accumulation (Hou et al., 2021b; Du et al., 2024b). Under high salinity conditions, increased osmotic pressure stresses nitrifying bacteria, reducing N_2O emissions (Adviento-Borbe et al., 2006). These mechanistic interpretations are strongly validated by our correlation analysis (Fig. 7). Across both growth phases, N_2O emissions showed a significant positive correlation with their primary substrate, NO_3^--N, confirming that substrate availability is a key controller.

Our findings emphasize the need for efficient N and water management strategies to reduce N_2O emissions in RC systems under DS. Optimizing N use efficiency through synchronized N supply with crop demand is crucial, requiring precise management of fertilizer source, rate, timing, and application methods (Venterea et al., 2016). Specifically, reducing basal and tillering fertilizer while increasing panicle fertilizer proportions could minimize N availability during peak N_2O emission periods, particularly during drainage transitions (Zhang et al., 2022). Advanced N management approaches, including nitrification inhibitors and controlled-release fertilizers with deep placement, have demonstrated significant potential in reducing N_2O emissions from DS systems by up to 95 % by slowing the conversion of ammonium to nitrate, thereby limiting substrates for denitrification (Gaihre et al., 2020; Xu et al., 2023a). Given the system-specific responses observed, implementing real-time monitoring of soil parameters (moisture, Eh, pH, and N levels) enables dynamic adjustment of management practices, while strategic lime application could effectively regulate pH and mitigate N_2O emissions (Žurovec et al., 2021).

4.3. *Economic benefits and application prospects of DS in RC farming systems*

As global labor shortages and water resource tensions become increasingly prominent, DS technology is rapidly gaining popularity worldwide (Rao et al., 2007; Sha et al., 2019). Our findings demonstrated that DS implementation in RC systems offered both environmental and economic benefits, with NEEB improvements of 3.5 % in RC5 and 12.8 % in RC15 systems (Fig. 8), translating to economic gains of 2.12 and 8.10 thousand CNY ha^{-1}, respectively (Table S4). These improvements are consistent with extensive international research documenting that direct seeding reduces production costs by 3–30 % (US\$9–125 ha^{-1}) through eliminating nursery raising, seedling transplanting, and intensive land preparation while adopting precision seeding or drone broadcasting (Kumar and Ladha, 2011; Bhushan et al., 2007). However, our findings extend these observations to integrated RC systems and reveal important system age dependencies.

The main cause of the economic benefit of DS was a fundamental restructuring of production costs. In our study, the cost of crop establishment was reduced by 89.4 %, falling from 3.60 thousand CNY ha^{-1} for manual transplanting to just 0.38 thousand CNY ha^{-1} for drone seeding. This significant cost saving is consistent with international findings, which report that direct seeding can decrease labor costs for crop establishment by over 75 % (Kumar and Ladha, 2011). While DS required a higher seed density, this increase cost was more than offset by eliminating nursery infrastructure and mechanization benefits. This mechanization advantage aligns with broader agricultural transformation trends addressing rural labor shortages across Asia (Becker et al., 2024; Fang et al., 2024). Additionally, quantifiable climate benefits through GWP cost reductions (0.21–0.29 thousand CNY ha^{-1}) provide additional economic value that increases with carbon pricing mechanisms (Table S4) (Zhang et al., 2018; Frank et al., 2024).

A major finding in our study was the system age-dependent economic performance of DS, which mirrored the environmental benefits. The NEEB improvement in RC15 was nearly three times greater than in RC5, primarily driven by differential yield responses (Table 2). Despite substantial cost savings (6.85 thousand CNY ha^{-1}), RC5 systems experienced a reduced rice income (5.01 thousand CNY ha^{-1}), while RC15 systems achieved yield parity with TP (Table S4). This finding reveals that yield stability amplifies economic returns and suggests considerable economic resilience of the DS model even under yield penalties. The enhanced benefits in mature systems demonstrate the potential for achieving optimal economic-environmental synergies in integrated farming.

Transitioning DS technology from controlled experimental plots to widespread commercial application requires addressing additional economic and agronomic challenges. Weed competition poses the greatest risk, potentially causing yield losses of 40–100 % if mismanaged (Xu et al., 2019; Rathika et al., 2020). This may necessitate higher herbicide expenditures than what was used in our standardized protocol. Yield instability, particularly in newer systems or adverse conditions, remains a primary economic risk (Farooq et al., 2011; Kumar and Ladha, 2011; Negi et al., 2024). Additionally, our analysis reveals that crayfish feed represents a substantial cost component (13.6–14.3 % of total production costs) (Table S4). Recent research on rice-crayfish systems demonstrates significant feed optimization potential through natural food supplementation and improved management practices. For instance, Hou et al. (2021a) reported that RC systems can achieve 38 % higher feed use efficiency. Furthermore, comprehensive life cycle assessments show that feed accounts for a substantial portion (23 %) of the total cost in RC systems, highlighting this as a key area for economic improvement (Sun et al., 2022).

Successful scaling in China's 1.73-million-hectare RC sector requires supportive policy and targeted interventions: (1) technical training programs for DS-specific water and weed management to ensure yield stability; (2) financial instruments such as specialized insurance products to de-risk farmer adoption (Mao et al., 2025); and (3) integration of GWP reductions into carbon market mechanisms, allowing farmers to monetize environmental benefits (Frank et al., 2024). Realizing this potential requires system-specific optimization, with priority research on yield stabilization in newer systems and long-term soil health assessment across diverse geographical conditions.

5. Conclusions

This study demonstrated that DS is a viable strategy for enhancing both the environmental sustainability and economic profitability of RC systems, but its effectiveness is strongly modulated by system age. Long-term RC practices exhibited higher CH_4 emissions, highlighting the increasing emission risks with system age. Direct seeding (DS) significantly reduced CH_4 emissions through enhanced soil Eh and suppressed methanogenic activity in the peak emission phase, with greater efficacy observed in short-term systems. This mitigation potential was diminished in the RC15 system, where high levels of accumulated DOC appeared to sustain methanogenesis, overriding the moderating effect of lower WFPS conditions. While DS increased N_2O emissions, the net reduction in GWP demonstrates its viability as a climate change mitigation strategy. Economic analysis indicated improved NEEB due to reduced establishment and mechanization costs, though yield variability suggests the need for careful management in newer fields. Long-term RC cultivation showed more stable responses, suggesting soil and microbial adaptation over time. These findings underscore the importance of system-specific management for sustainable rice cultivation and GHG mitigation. Future research should focus on optimizing DS across different agro-ecological zones and understanding its long-term impacts on soil health and microbial dynamics, which are crucial for developing climate-smart agricultural practices.

CRediT authorship contribution statement

FuLin Zhang: Resources, Investigation. **Ying Xia:** Investigation. **Yinghua Yin:** Writing – review & editing, Validation. **zhai limei:** Writing – review & editing, Validation, Supervision, Resources, Funding acquisition, Conceptualization. **Yilin Liu:** Writing – review & editing, Writing – original draft, Formal analysis, Conceptualization. **Shaopeng Wang:** Writing – review & editing, Validation. **Jijakli M.:** Writing – review & editing, Validation, Supervision. **Hongbin Liu:** Validation, Supervision. **Xianpeng Fan:** Investigation.

Declaration of Competing Interest

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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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.still.2025.107004.

Data availability

Data will be made available on request.

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