



Article

Effect and Mechanism of Root Characteristics of Different Rice Varieties on Methane Emissions

Zhijuan Qi ^{1,2}, Sheng Guan ^{1,2}, Zhongxue Zhang ^{1,2}, Sicheng Du ^{1,2}, Sirui Li ^{1,2} and Dan Xu ^{2,3,*}

¹ School of Water Conservancy and Civil Engineering, Northeast Agricultural University, Harbin 150030, China; zhijuan.qi@neau.edu.cn (Z.Q.); 18904602113@163.com (S.G.); zhangzhongxue@neau.edu.cn (Z.Z.); dusicheng@neau.edu.cn (S.D.); 13945358017@163.com (S.L.)

² Key Laboratory of Effective Utilization of Agricultural Water Resources, Ministry of Agriculture and Rural Affairs, Northeast Agricultural University, Harbin 150030, China

³ College of Arts and Sciences, Northeast Agricultural University, Harbin 150030, China

* Correspondence: xudan@neau.edu.cn

Abstract: Methane (CH₄), which is an important component of the greenhouse gases from paddy ecosystems, is a major contributor to climate change. CH₄ emissions from paddy ecosystems are closely related to the rice root system; however, how the rice root system affects CH₄ emissions remains unclear. We conducted a field experiment in 2023 at the Heping Irrigation District Rice Irrigation Experiment Station in Qing'an County, Heilongjiang Province. The field experiment used five local rice varieties with similar fertility periods to observe rice root morphology and physiology indexes, CH₄ emission fluxes, and cumulative CH₄ emissions. A structural equation model (SEM) was established to investigate the effects of root characteristics on the CH₄ emissions from rice and understand the potential mechanisms of these effects. The results showed that the seasonal patterns of CH₄ emission fluxes were similar in different rice varieties, and that, during the tillering to heading–flowering stages, the cumulative CH₄ emissions accounted for 89.8–92.6% of the total cumulative CH₄ emissions of rice. Significant negative correlations were observed between CH₄ emission fluxes and root volume, root dry weight, root oxidation activity (ROA), and root radial oxygen loss (ROL) ($r = -0.839, -0.885, -0.401$ and $-0.934, p < 0.05$), while there were significant positive correlations between root diameter; malic acid, citric acid, and succinic acid contents; and CH₄ emission fluxes ($r = 0.407, 0.753, 0.797$, and $0.685, p < 0.05$). The SEM showed that CH₄ emission fluxes were directly influenced by ROL and organic acid contents, while the other root indicators had indirect effects by modulating ROL and organic acid contents. ROL and root volume had the largest total effect, indicating that ROL and root volume were the most significant root physiological and morphological indicators affecting CH₄ emission fluxes. This study provides theoretical support and reference data for achieving sustainable agricultural development in the black soil region of Northeast China.



Citation: Qi, Z.; Guan, S.; Zhang, Z.; Du, S.; Li, S.; Xu, D. Effect and Mechanism of Root Characteristics of Different Rice Varieties on Methane Emissions. *Agronomy* **2024**, *14*, 595. <https://doi.org/10.3390/agronomy14030595>

Academic Editors: Wenxu Dong and José L. S. Pereira

Received: 20 February 2024

Revised: 9 March 2024

Accepted: 14 March 2024

Published: 15 March 2024



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Keywords: rice; methane; root physiology; root morphology; structural equation model

1. Introduction

In recent years, global warming has become an increasingly concerning issue, and the greenhouse effect has garnered significant attention from scholars. Studies have suggested that mitigation pathways should be adjusted to stabilize the climate at a 1.5 °C to 2.0 °C global temperature increase [1]. Methane (CH₄) is a significant greenhouse gas, with a warming potential 25 times greater than that of carbon dioxide (CO₂) [2]. Of the three primary food crops (rice, maize, and wheat), rice has the greatest impact on global warming, with a global warming potential (GWP) approximately 3.75 times higher than that of the other two crops due to its higher CH₄ emissions [3]. Rice is a crucial global food crop. Studies have indicated that rice yields must increase by at least 25% by 2030 to meet the growing population's demand for food [4]. Hence, studying the emission pattern of CH₄

and its influence mechanism in paddy fields is important to practice green development and achieve carbon neutrality in agriculture.

Previous studies have shown that the plant characteristics of rice affect its CH₄ emissions, but the effect of its root system has not been thoroughly investigated. Therefore, this study focuses on the effect of rice root characteristics on the CH₄ emissions from rice fields. The rice root system plays a critical role in plant fixation, water uptake, nutrient absorption, and the synthesis and secretion of organic matter [5]. Additionally, rice roots directly affect the CH₄ emissions from rice fields, exhibiting important effects on CH₄ production, oxidation, and transport [6,7]. Senescent rice root systems provide a substrate for methanogens and promote CH₄ production [8]. However, they also transport oxygen to the soil, creating a suitable environment for methanotrophs, which aid in oxidizing CH₄ [9]. Gutierrez et al. found there to be significant variability in the root oxidative capacity of different rice varieties. Rice roots oxidize inter-root CH₄ by increasing a redox potential in the root oxidation zone, thereby reducing CH₄ emissions [10]. The rice root system is an important transport system for CH₄; research has shown that approximately 90% of the CH₄ produced in rice paddies is released into the atmosphere via the rice root system [11]. It can be thus concluded that the morphology and physiological characteristics of rice roots have a significant impact on CH₄ emissions.

Scholars have drawn differing conclusions regarding the impact of the rice root system on CH₄ emissions in rice fields. Ren et al. showed that rice varieties with well-developed root systems can aid in CH₄ oxidation, leading to a reduction in CH₄ emissions [12]. However, it has also been shown that rice varieties with high root biomass have higher CH₄ emission fluxes [13]. The impact of root oxidation activity (ROA) on CH₄ emissions has been classified as being both promoting and inhibiting. Increased ROA can lead to a greater CH₄ uptake by the rice root system, promoting CH₄ transport and increasing emissions [14]. However, an increase in ROA can also enhance the root system's capacity to oxidize CH₄, thereby reducing CH₄ emissions [15]. Furthermore, significant differences in the quantity and composition of root exudates were noted between the different rice varieties [16]. The influence of organic acids on CH₄ emissions also varies. Studies have shown that CH₄ emissions from rice fields benefit from low-molecular-weight organic acids in root exudates, which are substrates for methanogens [17]. However, Kerdchoechuen et al. discovered that the organic acids in root exudates, such as malic, succinic, and citric acids, decelerated the CH₄ emissions from rice fields [18]. Further investigation is required to determine the effect of rice root characteristics on CH₄ emissions due to the uncertainties presented in the aforementioned studies.

Most studies have examined different indicators of the rice root system as independent factors affecting CH₄ emissions. There is a relative lack of research on the inter-feedback effect among root system indicators. The impact of rice roots on CH₄ emissions is a highly complex process. Therefore, studying the indirect structural relationship of each index is of great significance in understanding the complex process of the CH₄ emissions caused by rice roots. A structural equation model (SEM) has a key advantage in that it can clarify the causal relationships between variables [19]. It is used to conduct a comprehensive analysis, which includes factor and pathway analyses [20]. This method is generally used to investigate the direct and indirect effects of independent variables on dependent variables, as well as to determine the significance of independent variables in relation to dependent variables [21]. A SEM is suitable for examining interdependencies in multivariate data. Hence, it is reasonable to use a SEM to explore the structural relationship between CH₄ emissions and rice morphological and physiological traits.

The northeastern rice area in China is largely situated in the Liaodong Peninsula and north of the Great Wall. It is dominated by single-cropping japonica rice and accounts for 51.9% of the national japonica rice planting area. This region serves as a significant rice production and supply base for China [22–24]. Research into the mechanism of CH₄ emissions from rice paddies in the northeastern region is significant for addressing food security and reducing carbon emissions in China.

In this study, we examined the dynamics of CH₄ emissions, root morphology, root physiological indices, and their influences on the CH₄ emission fluxes in paddy fields of the five major rice cultivars in Northeast China. A SEM was constructed to study the key driving factors and potential mechanism of action of rice root morphology and physiological indices on CH₄ emission fluxes. The objective of this study was to (1) investigate the interactive effects between CH₄ emissions and the rice root indices, as well as the differences between rice cultivars, and (2) elucidate the response mechanism to CH₄ emissions of rice roots. The findings of this study will provide a theoretical reference for the extensive reduction of CH₄ emissions.

2. Materials and Methods

2.1. Site Description

This experiment took place in 2023 at the Heilongjiang Provincial Rice Irrigation Experiment Station, situated in Heping Township, Suihua City. Following the United States Department of Agriculture (USDA) classification, the experimental soil texture was clay loam soil, an albic soil optimal for rice. The local climate is characterized as a cold-temperate continental monsoon type, with an average of 2599 h of sunshine annually, a mean temperature of 2–3 °C, roughly 128 days without frost per year, 350–650 mm of annual rainfall, and 1200–1600 mm of annual evaporation. Figure 1 shows the meteorological changes at the site from rice transplanting to maturity. Before transplanting and fertilization, five-point diagonal sampling was conducted on the 0–20 cm soil layers of the test plot. The samples were mixed and analyzed to obtain the main physical and chemical properties of the soil. The soil's main physical and chemical properties are as follows: the potential of hydrogen (pH) value was 6.4, the organic matter was 40.9 g·kg⁻¹, the alkaline N was 177.8 mg·kg⁻¹, the available *p* was 35.2 mg·kg⁻¹, the available K was 125.13 mg·kg⁻¹, and the total porosity was 61.8%.

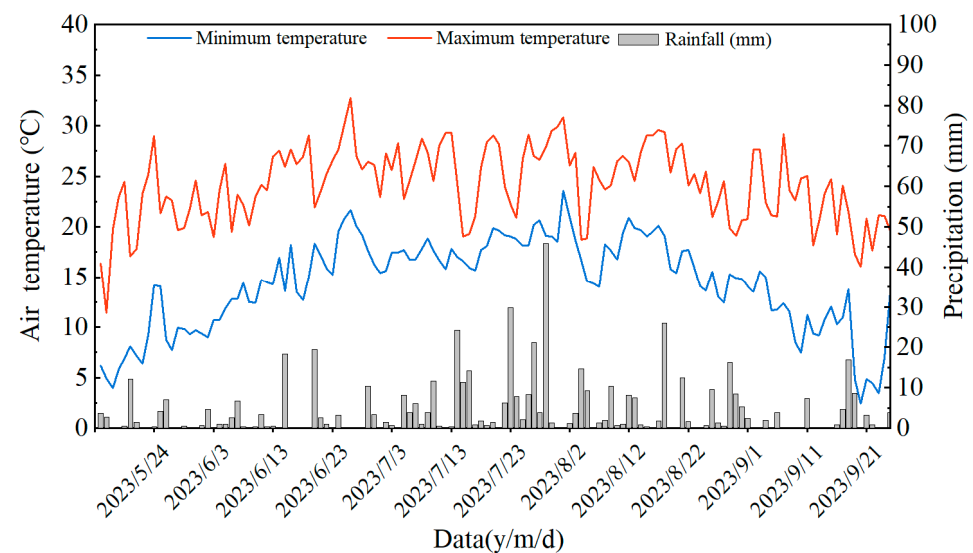


Figure 1. Air temperature and precipitation during the reproductive period of rice.

2.2. Experimental Design

Five main varieties of rice with similar fertility periods, namely Longqing 31, Suijing 18, Longjing 31, Longqing 32, and Longjing 20, which were transplanted on May 22 and harvested on September 24, were used in this experiment. The experiment followed a randomized block design with three replications. The transplanting specifications required a distance of 30 × 13.3 cm and the use of artificial seedlings, with 3 plants per hill. To minimize manual sampling interference, we established separate areas for CH₄ and rice plant collection in this experiment. The CH₄ collection area plot consisted of 15 hills and 10 rows, while the rice plant collection area plot consisted of 15 hills and 20 rows.

The seedlings were of the same size and contained a main stem and two tillers. The tested fertilizers were urea (containing 46% N), superphosphate (containing 12% P₂O₅), and potassium chloride (containing 60% K₂O). Basal fertilizer was applied one day before transplantation. Tillering fertilizer was applied during the tillering stage, and spike fertilizer was applied during the heading–flowering stage. Phosphorus fertilizer (P₂O₅) was applied at a rate of 45 kg·ha^{−1}, and potash (K₂O) at a rate of 80 kg·ha^{−1}. Before transplanting, the seedlings were fertilized with phosphorus once, followed by potash two times at the leaf development (8.5) phenophase, with a ratio of 1:1.

2.3. Sampling and Measurement Methods

2.3.1. Determination of CH₄ Emissions

CH₄ was collected using the static chamber method [25,26]. A chamber was made of Plexiglas, with a thermometer and a fan installed inside it, and wrapped in aluminum foil for heat insulation. This method ensured an accurate measurement of CH₄ emissions. Before transplanting the rice, a foundation frame made of stainless steel was inserted into the soil at a depth of 20 cm. Six hills of rice were transplanted into each frame according to their specified planting density. During sampling, the chamber was placed onto the frame and the joint between the frame and the lower chamber opening was sealed with water to prevent gas leakage from the chamber. Gas was collected at seven-day intervals after rice transplanting, with sampling between 9:00 and 11:00. Four gas samples from each chamber were injected into the gas collection bag using a 20 mL plastic syringe at 0, 10, 20, and 30 min after the box was closed. The collected gas was analyzed in the laboratory using a gas chromatograph (GC-2010Plus, Shimadzu, Kyoto, Japan).

The CH₄ emission fluxes were calculated using the following formula [25]:

$$F = \rho h \frac{dc}{dt} \cdot \frac{273}{273 + T} \cdot \frac{P}{P_0}$$

where F is the CH₄ emission fluxes (mg·m^{−2}·h^{−1}), ρ is the gas density at a standard state (mg·m^{−3}), h is the effective height of the chamber (m), $\frac{dc}{dt}$ is the slope of the curve of gas concentration versus time (mL·m^{−3}·h^{−1}), T is the average temperature inside the chamber during sampling (°C), P is the air pressure inside the chamber, and P_0 is the standard atmosphere.

The cumulative CH₄ emissions were calculated using the following formula [27]:

$$E_c = \sum_{i=1}^n \frac{F_i + F_{i+1}}{2} (t_{i+1} - t_i) \times \frac{24}{100}$$

where E_c is the cumulative CH₄ emissions (kg·ha^{−1}), F_i and F_{i+1} are the CH₄ emission fluxes at the i th and $i + 1$ st sampling points (mg·m^{−2}·h^{−1}), respectively, and $t_{i+1} - t_i$ are the days between two adjacent samplings (d).

2.3.2. Measurement of the Morphological Indicators of the Rice Root System

Rice roots were sampled at the tillering stage, the joining–booting stage, and the heading–flowering stage. Soil clods of 20 × 20 × 20 cm were dug up from around the plants, placed in a 70-mesh sieve, and cleaned using a hydropneumatic washer. After cleaning, the roots were floated in shallow trays, scanned with a scanner (Expression 12000XL, Seiko Epson, Tokyo, Japan), and analyzed using the WinRHIZO Root Analysis System (LA2400 Scanner, Seiko Epson, Tokyo, Japan) to determine the morphological indicators of the rice root system.

2.3.3. Measurement of the Physiological Indices of Rice Roots

Three hills of rice root systems were sampled from five varieties, using the root extraction method described above, to determine the ROA by measuring the oxidation of alpha-naphthylamine (α-NA) according to the methods of Ramasamy et al. (1997) [28]. The

ROA was expressed as $\mu\text{g } \alpha\text{-NA}$ per gram of dry weight (DW) per hour ($\mu\text{g } \alpha\text{-NA g}^{-1} \text{ DW h}^{-1}$). Rice roots from three additional hills were collected, and the root radial oxygen loss (ROL) was determined using the titanium citrate colorimetric method [29].

2.3.4. Measurement of Organic Acid Content in Rice Root Exudates

The organic acid contents in rice root exudates were determined at the tillering stage, the jointing–booting stage, and the heading–flowering stage. The collected rice roots were washed carefully with deionized water and placed in beakers of deionized water with 1 hill per cup. The sample was subjected to constant temperature and light conditions for 4 h. The root extracts were collected. The extracts were completely freeze-dried using a vacuum dryer (pilot10-15EP, Biocool, Beijing, China) before measurement, and the freeze-dried powder of the extracts was completely dissolved in 2 mL of deionized water and filtered through a $0.45 \mu\text{m}$ filter membrane, and the organic acid concentration was determined using an ion chromatograph (1260 Infinity II Prime, Agilent, Palo Alto, CA, USA) and expressed as the quantity of organic acid produced by a unit of dry weight of the root system over a unit of time.

2.3.5. Data Statistics and Analyses

Origin2019 was used for plotting, and SPSS version 21.0 was used for the statistical analysis of the data. Differences in the indicators in the figures were analyzed using an analysis of variance (ANOVA), and the data were tested using the post hoc least significant difference (LSD) method at $p < 0.05$ and $p < 0.01$. The relationship between root physiological morphology and CH_4 emissions was assessed using a correlation analysis.

First, a set of causal hypotheses between variables was constructed in a SEM, based on theory and previous findings. These were then modified according to whether the fitted indicators, including the comparative fit index (CFI), high goodness of fit index (GFI), normed fit index (NFI), ratio of chi-square to df (CMIN/DF), and low root mean square error of approximation (RMSEA), met the statistical requirements. A SEM model was constructed using AMOS V.24.0 to detect the direct or indirect effects of each physiological index of the rice root system on CH_4 emissions, and the degree of influence of each physiological index on CH_4 emissions was measured using path coefficients. The SEM construction used the standardization of all path coefficients to eliminate the influence of variable dimensions on the results.

3. Results

3.1. CH_4 Emissions

The CH_4 emission fluxes of the five rice varieties showed similar trends throughout the entire growth period (Figure 2), with two peaks. The initial CH_4 emission fluxes of each variety were low. The CH_4 emission fluxes continued to increase from the returning–green stage, reaching their first peak at the mid-tiller stage. Longjing 20 had the highest emission fluxes of $57.74 \text{ mg} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$, which was 9.95–78.77% higher than that of the other four varieties. Subsequently, the rice CH_4 emission fluxes of all varieties decreased rapidly under the influence of rice field sunning until the end of the field sunning stage at the end of tillering. After re-irrigation, they rose sharply again, reaching a second peak at the jointing–booting stage. Longjing 20 had the highest emission flux, reaching $47.64 \text{ mg} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$, which was 12.95–72.02% higher than the other four varieties. The CH_4 emission fluxes then gradually decreased as the growth period progressed and remained at a low level after the rice entered its mature stage.

As shown in Figure 3, the cumulative CH_4 emissions of five rice varieties were in the following order throughout their entire growth cycle: Longjing 20 > Longqing 31 > Suijing 18 > Longqing 32 > Longjing 31. The cumulative emissions of Longjing20 were $457.48 \text{ kg} \cdot \text{ha}^{-1}$, which was higher than the other four varieties by 12.93–43.96%. During the tillering, jointing–booting, and heading–flowering stages, the cumulative CH_4 emissions of each rice variety accounted for 89.8–92.6% of their total cumulative CH_4 emissions, and

there were significant differences in the cumulative CH_4 emissions of the varieties during these three stages ($p < 0.05$). This experiment examined the morpho-physiological traits of rice roots during the tillering, jointing–booting, and heading–flowering stages of rice to determine their relationship to CH_4 emissions.

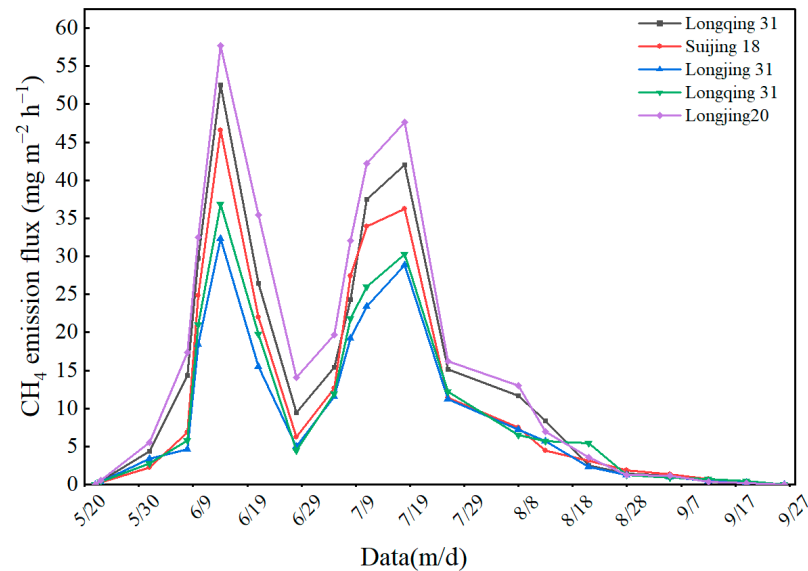


Figure 2. Methane (CH_4) emission fluxes in 2023.

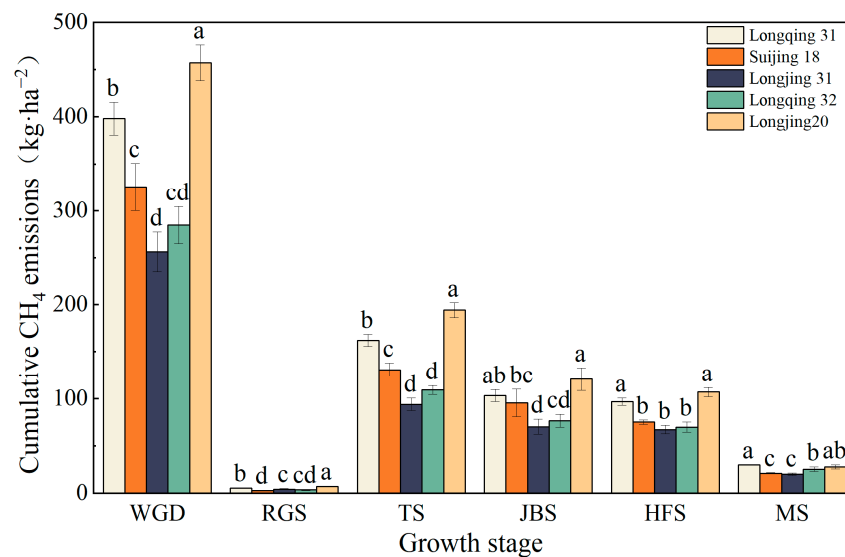


Figure 3. Cumulative CH_4 emissions of different rice varieties at different growth stages. WGD: whole growth duration; RGS: returning–green stage; TS: tillering stage; JBS: jointing–booting stage; HFS: heading–flowering stage; MS: mature stage. Different letters indicate significant differences between rice varieties ($p < 0.05$).

3.2. Morphophysiological Characteristics of the Rice Root System

As displayed in Figure 4, the root dry weight of rice gradually increased from the tillering stage to reach its maximum at the jointing–booting stage. The root dry weights of rice at the tillering and jointing–booting stage were, in descending order, as follows: Longjing 31 > Longqing 31 > Suijing 18 > Longqing 32 > Longjing 20. The dry weights of Longjing 31 at these two stages were 53.17 and $75.69 \text{ g} \cdot \text{m}^{-2}$, respectively. This was higher than those of the other four varieties by 7.4–32.2% and 16.5–32.4%, respectively. At the heading–flowering stage, the root dry weights among rice varieties were, in descending

order, Longjing 31 > Longqing 32 > Suijing 18 > Longqing 31 > Longjing 20. The root dry weight of Longjing 31 was $176.45 \text{ g} \cdot \text{m}^{-2}$, which was higher than that of the other four varieties by 6.5–31.7%. At the tillering stage and jointing–booting stage, the root volume of the rice varieties was in the following order: Longjing 31 > Longqing 32 > Suijing 18 > Longqing 20 > Longqing 31. At the heading–flowering stage, the root volume was highest in Longjing 31 was 14.83 cm^3 and lowest in Longqing 31 was 8.45 cm^3 . The differences between the other varieties were not significant. The root diameter of all varieties reached its minimum value at the heading–flowering stage, except that no noticeable pattern of variation in root diameter was found with the growth period among rice varieties. At the tillering stage, the root diameter of Longjing 20 was significantly smaller than that of the other varieties. At the heading–flowering stage, the root diameter of the rice varieties was largest for Longjing 31, at 0.84 mm, and smallest for Longqing 31, at 0.61 mm, and the differences among the other varieties were not significant.

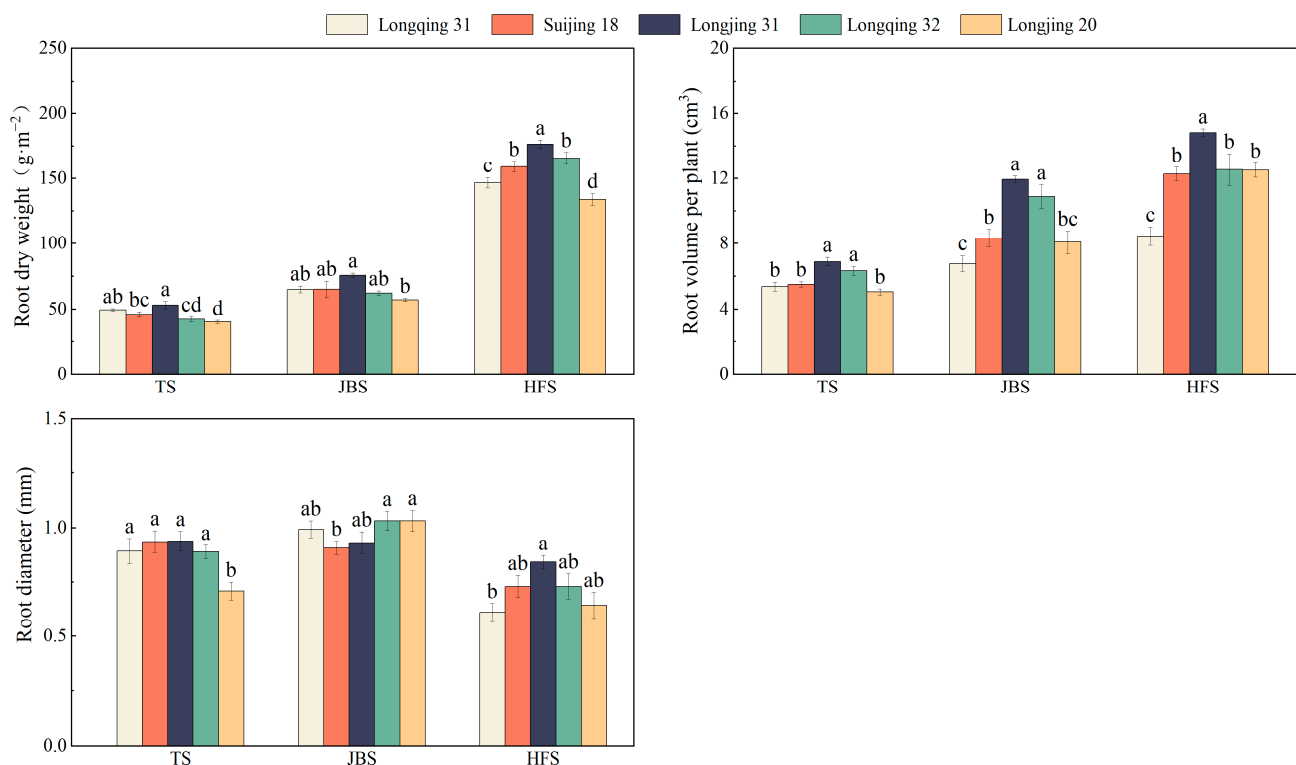


Figure 4. Root morphological indexes of different rice varieties at their main growth stages. Different letters indicate significant differences between rice varieties ($p < 0.05$).

As shown in Figure 5, the ROL of all five rice varieties increased as the rice grew. The ROL showed a similar pattern among the different rice varieties at all stages, with Longjing 31 having the highest ROL ($66.29\text{--}113.10 \text{ mmol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$) and Longjing 20 having the lowest ($45.95\text{--}83.25 \text{ mmol O}_2 \text{ g}^{-1} \text{ DW h}^{-1}$). At the tillering, jointing–booting, and heading–flowering stages, Longjing 31 had a higher ROL than the other varieties by 8.78–44.28%, 4.93–38.19%, and 7.78–35.86%, respectively. The rice varieties showed a pattern of increasing and then decreasing ROA from the tillering stage to the heading–flowering stage, with the highest ROA observed at the jointing–booting stage. The order of ROA from high to low was as follows: Longjing 31 > Longqing 32 > Suijing 18 > Longqing 31 > Longjing 20 (Figure 5).

Table 1 displays the results of the correlation analyses. Among the root morphology indicators, CH_4 emission fluxes exhibited highly significant negative correlations with root volume and root dry weight ($r = -0.839$ and -0.885 , $p < 0.01$) and a positive correlation with root diameter ($r = 0.407$, $p < 0.05$). Among the root physiological indices, CH_4 emission

fluxes showed a significant negative correlation with ROA ($r = -0.404$, $p < 0.05$) and a highly significant negative correlation with ROL ($r = -0.936$, $p < 0.01$).

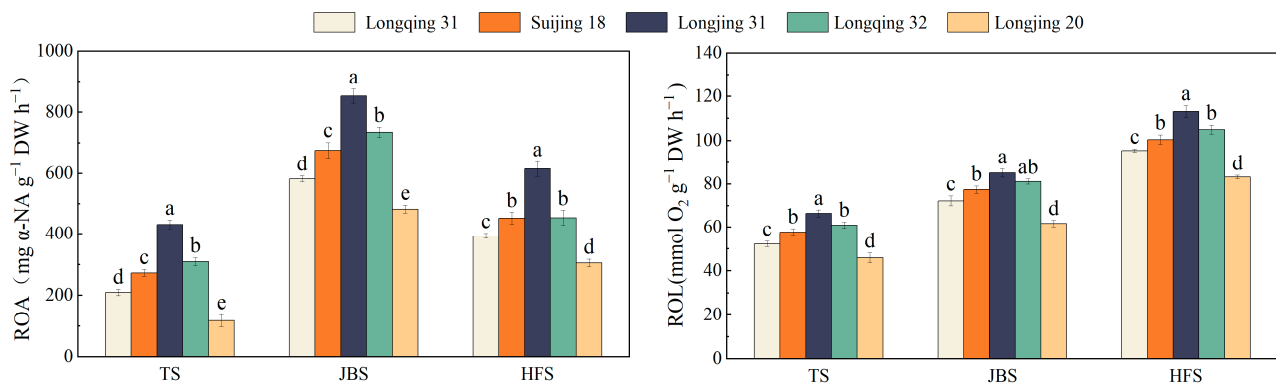


Figure 5. Root physiological indexes of different rice varieties at their main growth stages. Different letters indicate significant differences between rice varieties ($p < 0.05$). DW: dry weight; α-NA: alpha-naphthylamine; ROL: root radial oxygen loss; ROA: root oxidation activity.

Table 1. Correlation analysis of CH₄ emission fluxes with different root indicators in rice.

	CH ₄ Fluxes	Root Volume	Root Diameter	Root Dry Weight	ROA	ROL
CH ₄ fluxes	1					
Root volume	−0.839 **	1				
Root diameter	0.407 **	−0.257	1			
Root dry weight	−0.885 **	0.798 **	−0.594 **	1		
ROA	−0.401 *	0.541 **	0.421 **	0.157	1	
ROL	−0.934 **	0.877 **	−0.346 *	0.910 **	0.511 **	1

Note: * and ** indicate significant correlations at the $p = 0.05$ and $p = 0.01$ levels, respectively.

3.3. Organic Acid Content in Rice Root Exudates

In this experiment, five organic acids—malic acid, acetic acid, citric acid, tartaric acid, and succinic acid—were determined in rice root exudates. Table 2 shows that each rice variety's organic acid components contained higher levels of malic acid ($36.6\text{--}71.9 \mu\text{mol g}^{-1} \text{DW}$) and tartaric acid ($19.6\text{--}50.6 \mu\text{mol g}^{-1} \text{DW}$), followed by citric acid ($11.6\text{--}21.5 \mu\text{mol g}^{-1} \text{DW}$) and succinic acid ($13.2\text{--}32.0 \mu\text{mol g}^{-1} \text{DW}$), and lower levels of acetic acid ($11.4\text{--}18.2 \mu\text{mol g}^{-1} \text{DW}$). Longqing 31 had a significantly higher malic acid content than the other varieties, while Longjing 20 had a significantly higher acetic and citric acid content than the other varieties. The levels of tartaric acid and succinic acid were highest during the tillering stage, followed by the jointing–booting stage and the heading–flowering stage. The succinic acid content for each stage was ranked in the following order: Longqing 20 > Longqing 32 > Longqing 31 > Suijing 18 > Longqing 31. The total organic acid (TOA) of each rice variety was obtained by summing the contents of the five organic acids of each variety, and the results showed that the magnitude of the total organic acid of each variety was in the following order: Longqing 31 > Longqing 20 > Suijing 18 > Longqing 31 > Longqing 32. Table 3 shows a significant positive correlation between CH₄ emission fluxes and TOA ($r = 0.784$, $p < 0.05$), as well as a highly significant positive correlation of CH₄ emission fluxes with malic, citric, and succinic acid contents ($r = 0.685\text{--}0.797$, $p < 0.05$). However, there was no significant correlation ($p > 0.05$) of these fluxes with tartaric or acetic acid. These results suggest that TOA and malic, citric, and succinic acid might contribute to CH₄ emissions.

Table 2. Composition and content of organic acids in rice root exudates ($\mu\text{mol g}^{-1}$ DW).

Growth Period	Rice Variety	Malic Acid	Acetic Acid	Citric Acid	Tartaric Acid	Succinic Acid	TOA
TS	Longqing 31	71.9 a	13.6 b	16.4 bc	50.6 a	21.4 c	173.9 a
	Suijing 18	62.6 b	14.3 b	17.8 b	31.4 c	20.1 c	146.2 b
	Longjing 31	57.4 c	11.7 c	15.4 c	45.7 b	17.9 d	148.1 b
	Longqing 32	49.5 d	12.1 c	16.6 bc	44.3 b	24.2 b	146.7 b
	Longjing 20	64.6 b	16.8 a	21.5 a	33.5 c	32.0 a	168.4 a
JBS	Longqing 31	57.6 a	14.7 b	15.8 bc	26.5 b	19.0 c	133.7 ab
	Suijing 18	51.1 b	15.0 b	15.6 bc	31.5 a	17.7 d	130.9 b
	Longjing 31	49.4 b	12.4 c	14.7 c	30.9 a	15.7 e	123.2 c
	Longqing 32	40.2 c	11.4 c	16.4 b	24.8 b	21.4 b	114.2 d
	Longjing 20	52.5 b	17.2 a	19.8 a	19.6 c	27.1 a	136.1 a
HFS	Longqing 31	53.9 a	15.3 bc	12.4 cd	29.7 b	15.7 c	127.1 b
	Suijing 18	46.9 b	14.9 bc	13.4 bc	36.1 a	14.8 cd	126.2 b
	Longjing 31	45.9 b	13.9 c	11.6 d	34.3 a	13.2 d	118.8 c
	Longqing 32	36.6 c	15.4 b	14.3 b	28.8 b	17.8 b	112.9 d
	Longjing 20	48.4 b	18.2 a	16.5 a	22.4 b	23.5 a	135.4 a

Note: different letters in the same column indicate that the differences between different varieties were significant at $p < 0.05$. TOA: total organic acid.

Table 3. The correlation between CH_4 emission fluxes and organic acids.

Type of Organic Acids	Correlation Coefficient
TOA	0.784 **
Malic acid	0.753 **
Acetic acid	0.001
Citric acid	0.797 **
Tartaric acid	0.191
Succinic acid	0.685 **

Note: ** indicate significant correlations at the $p = 0.01$ level.

3.4. SEM of the Rice Root System with CH_4 Emission Fluxes

A SEM was used to examine the structural relationship between the rice root system and CH_4 emission fluxes. The model fitted well, as indicated by the CMIN/DF, GFI, CFI, NFI, and RMSEA (Figure 6). In relation to the total effects, TOA and root diameter had a positive effect on CH_4 emissions, whereas ROA, ROL, root dry weight, and root volume had a negative effect (Figure 7). The ROL had a direct negative effect on CH_4 emission fluxes, with a direct effect of -0.778 , and an indirect effect on CH_4 emission fluxes by affecting the TOA, with an indirect effect of -0.173 , resulting in a total effect of ROL on CH_4 emission fluxes of -0.951 . TOA had only a direct positive effect on CH_4 emission fluxes, with a direct effect of 0.257 . Moreover, only ROL and TOA, among the root indicators, had a direct impact on CH_4 emission fluxes. The other root indicators had negligible direct effects on CH_4 emission fluxes and an indirect impact on CH_4 emission fluxes by influencing the ROL and TOA (Figure 6). Therefore, ROL and TOA act as direct determinants of CH_4 emissions, and the remaining indicators indirectly affect CH_4 emissions by regulating the ROL and TOA.

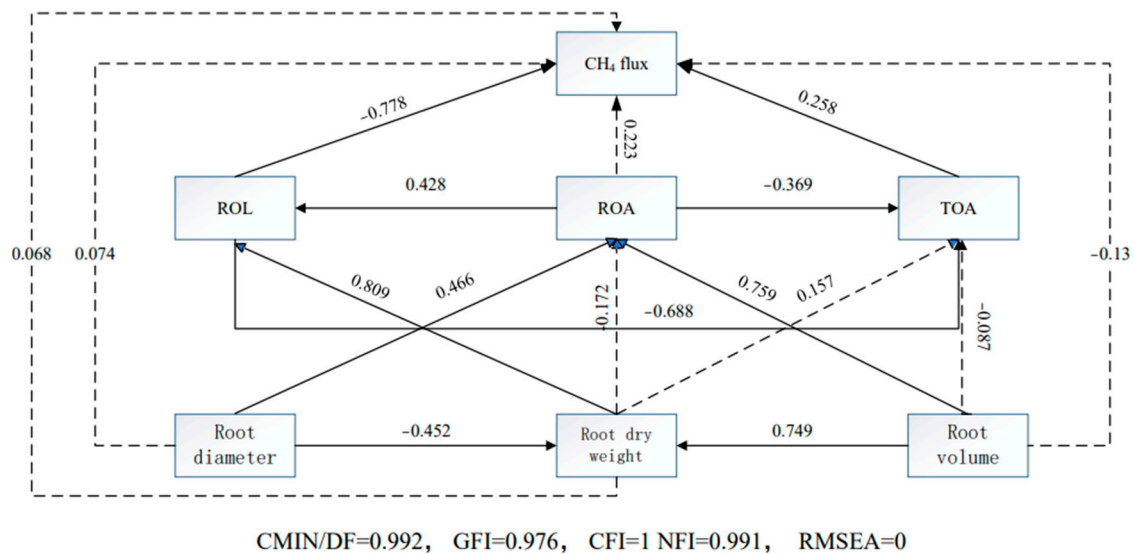


Figure 6. A structural equation model (SEM) was developed to investigate the relationship between CH₄ emission fluxes and rice roots. The paths that are significant ($p < 0.05$) are indicated by solid arrows, while nonsignificant paths ($p > 0.05$) are indicated by dashed arrows. The standardized path coefficient is shown next to each arrow. CFI: comparative fit index; GFI: goodness of fit index; NFI: normed fit index, CMIN/DF: chi-squared degree of freedom ratio; RMSEA: low root mean square error of approximation.

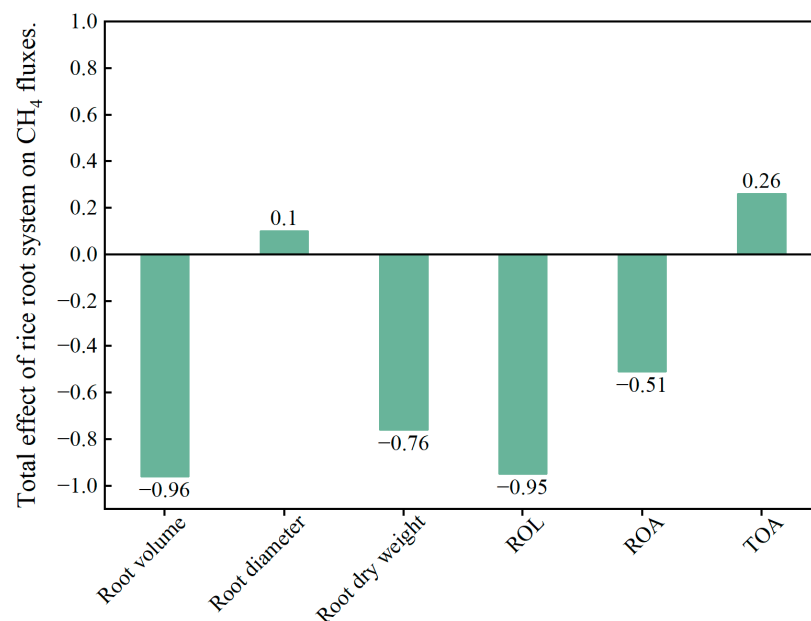


Figure 7. Total effect of the rice root system on CH₄ fluxes. Positive values indicate a positive effect while negative values indicate a negative effect.

4. Discussion

4.1. CH₄ Emission Patterns of Different Rice Varieties

In the present study, CH₄ emission fluxes from different rice varieties showed similar seasonal patterns of change, with two peaks. The first peak appeared at the rice tillering stage. This was because of the application of tiller fertilizer and the increase in temperature, which resulted in the production of organic matter that provided substrates for CH₄ production. Moreover, rice plant growth and root respiration became vigorous [30], leading to an increase in CO₂ production. This CO₂ was then used by methanogens to produce CH₄ [31]. Moreover, rice root aeration tissues were more active during the tillering stage, which

enhanced the ability of rice root aeration tissues to transport CH_4 [32]. The application of spike fertilizer increases their carbon source, leading to a rise in CH_4 emission fluxes in rice at the jointing–booting stage. Nevertheless, after entering the heading–flowering stage, rice gradually shifts from nutritional growth to reproductive growth [33], at which point part of the carbon fixed by rice is allocated to the reproductive organs of rice, resulting in less carbon resources allocated to methanogens, leading to a gradual decrease in the CH_4 emissions from rice fields and thus forming a second peak in the jointing–booting stage. Throughout the whole growth period, Longjing 31 had the lowest cumulative total CH_4 emissions, which were 10.05–43.97% lower than that of the other cultivars (Figure 3). From the tillering stage to the heading–flowering stage, Longjing 31 had a significantly higher root volume, root dry weight, ROL, and ROA than the other varieties (Figure 4). This finding is consistent with the results of previous research, indicating that rice varieties with well-developed root systems and a high oxygen secretion capacity promote CH_4 oxidation and decrease CH_4 production [15,18]. Therefore, it can be concluded that rice roots are a key factor contributing to the differences in CH_4 emissions among rice varieties.

4.2. Influence of Root Physiological Morphology on CH_4 Emissions

Several studies have revealed that ROL plays a crucial role in the root system, contributing to the variations in CH_4 emissions from rice fields. It has also been observed that ROL varies significantly among rice varieties [34,35]. This study obtained a similar finding. This study found that ROL had the strongest direct negative impact on CH_4 emission fluxes ($\beta = -0.778$) and indirectly affected CH_4 emission fluxes by influencing the TOA in rice ($\beta = -0.173$). This indicates that ROL plays a dual role in the oxidation and production of CH_4 in paddy soils, as shown in Figure 6. ROL refers to the ability of the rice root system to release oxygen into the inter-root zone. This process increases the redox potential (Eh) of rice soil, improves soil reduction conditions, and alters the pH of the root system, which is conducive to rice growth and development [36]. ROL is a positive physiological process that allows rice to adapt to flooded environments [37]. The higher the ROL, the higher the oxygen content of the soil between the roots and the greater the formation of aerobic micro-regions in the rice roots to promote CH_4 oxidation [26]. The oxygen released by rice roots can oxidize harmful components that form due to the long-term anoxia of root soil, such as Fe^{2+} , Mn^{2+} , S^{2-} , HS^- , and organic acids. The strength of the ROL determines the amount of organic acids that will be oxidized and consumed, indirectly reducing CH_4 generation [38]. It has been suggested that enhancing ROL leads to an increase in the iron film on root surfaces [39]. The main components of the root's iron film are Fe^{3+} oxides, such as hydrated iron oxides. The reduction process of these oxides can effectively inhibit CH_4 emissions [40,41]. Jiang et al. showed that rice promotes root CH_4 oxidation by increasing ROL, thus reducing CH_4 emissions [42].

ROL has been linked to many indicators in rice roots [43,44]. This study demonstrated a significant and positive correlation between root dry weight, root volume, ROA, and ROL (Table 1). These factors had direct or indirect positive effects on ROL (Figure 6). The metabolic capacity of rice is enhanced by a larger root system, resulting in a higher ROA and its ability to power the ROL, which in turn promotes CH_4 oxidation [45,46]. Moreover, the adventitious roots and lateral branches that develop in flooded soils are the primary sources of oxygen release from the root system. This oxygen release promotes CH_4 oxidation [47]. Furthermore, this study identified a significant negative correlation between ROL and the root diameter of rice (Table 1). This may be because rice with a higher internal oxygen diffusion capacity can grow faster in submerged soil, which has a significant positive effect on lateral root development [48], and because the presence of a large number of lateral fine roots will reduce the average root diameter of rice.

4.3. Effect of Organic Acids on CH_4 Emissions

Organic acids are significant constituents of rice root exudates and serve as crucial substrates for methanogens [49]. Our experimental results showed that malic, citric, and

succinic acid were positively correlated with CH₄ emission fluxes (Table 3), and the SEM showed that organic acids directly and positively affected CH₄ emission fluxes (Figure 6). This may be because organic acids are easily decomposed into methanogen substrates, which promotes CH₄ production [50]. Organic acids are recognized as phytotoxins in anaerobic soils. Elevated levels of organic acids hinder root growth and decrease rice activity [48], leading to an increase in root apoplastic matter. This, in turn, provides more carbon sources for methanogens, resulting in increased CH₄ emissions. Conversely, Liu et al. demonstrated a significant negative correlation between CH₄ emission fluxes and organic acids [51]. This difference may be attributed to the varying soil physicochemical properties and microbial compositions at the two experimental sites. Furthermore, a significant negative effect of ROA on total organic acids was found in this experiment (Figure 6), which was attributed to the ability of methanotrophs to consume the organic acids such as malic, succinic, and acetic acids in root secretions [52,53], and methanotrophs' activity was enhanced when ROA was high [10]. This resulted in an increase in the consumption of organic acids, leading to a decrease in the organic acid content of soil.

4.4. A Strong Rice Root System Reduces CH₄ Emissions

This study's SEM revealed that only ROL and TOA had direct effects on CH₄ emission fluxes ($\beta = -0.778$, $\beta = 0.258$). ROA, root dry weight, and root volume only indirectly regulated CH₄ emission fluxes through their effects on ROL and TOA (Figure 6). This indicates that the greater the root volume, root dry weight, and ROA, the greater the positive effect on ROL and the stronger the negative effect on TOA. In other words, a well-developed rice root system increases the effect of transporting O₂ to the soil to promote CH₄ oxidation and reduces the effect of transporting carbon to the soil to promote CH₄ production, and both effects reduce CH₄ emissions. Since the total effect of ROL and root dry weight on CH₄ emission fluxes was significantly higher than that of the other root indicators (Figure 6), low CH₄ emissions from rice fields can be ensured by selecting rice varieties with high ROL through some easily measurable root indicators, such as root volume.

5. Conclusions

In Northeast China, we conducted a field experiment to investigate the effect and mechanism of action of the root characteristics of different rice varieties on CH₄ emissions. This study found that CH₄ emissions from various rice varieties exhibited similar seasonal trends. The cumulative CH₄ emissions from the tillering stage to the heading–flowering stage accounted for 89.8–92.6% of the total cumulative emissions of these varieties during the entire growth period. A correlation analysis revealed that rice root volume, root dry weight, ROA, and ROL were significantly negatively correlated with CH₄ emissions ($r = -0.839$, -0.885 , -0.404 , and -0.936 , $p < 0.05$), and that root diameter and the root exudate contents of malic, citric, and succinic acid were significantly positively correlated with CH₄ emission fluxes ($r = 0.407$, 0.753 , 0.797 and 0.685 , $p < 0.05$). The SEM indicated that ROL and TOA had direct effects on CH₄ emission fluxes, while the other root indicators had indirect effects. The most important physiological and morphological indicators of the root system that influence CH₄ emission fluxes are ROL and root volume, in terms of their total effect on the SEM ($\beta = -0.95$ and -0.96); this finding has significant implications for selecting rice varieties that emit less CH₄. Our results suggested that rice roots are a key factor in the differences in CH₄ emissions from rice paddies. Screening rice varieties by ROL and root volume is an effective means of achieving low CH₄ emissions from rice paddies and promoting sustainable agricultural development.

CH₄ emissions are determined by both methanogens and methanotrophs. This study did not provide sufficient information on this topic. Therefore, future research should focus on the impact of microorganisms and plants in the rhizosphere on CH₄ emissions.

Author Contributions: Conceptualization, Z.Q. and S.G.; methodology, S.G.; software, S.L. and D.X.; validation, D.X., S.L. and S.G.; formal analysis, S.G. and S.D.; investigation, Z.Z.; resources, D.X.; data curation, D.X. and Z.Z.; writing—original draft preparation, S.G.; writing—review and editing, S.G. and S.D.; visualization, Z.Z.; supervision, Z.Q., D.X. and Z.Z.; project administration, D.X.; funding acquisition, D.X. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the National Key Research and Development Program of China (No.2022YFD2300301) and the Northeast Agricultural University Scholars Plan Academic Backbone Program (No.21XG18).

Data Availability Statement: The data presented in this study are available on request from the corresponding author.

Acknowledgments: We would like to thank the Heilongjiang Water Resources Research Institute for providing us with the test site. We would also like to thank Northeast Agricultural University for providing experimental support.

Conflicts of Interest: The authors declare no conflicts of interest.

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