Received: 25 January 2017 | Revised: 15 March 2017 | Accepted: 14 April 2017
DOI: 10.1111/gcb.13737

PRIMARY RESEARCH ARTICLE

WILEY Global Change Biology

Higher yields and lower methane emissions with new rice cultivars

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Funding information
National Key Research and Development Program China, Grant/Award Number: 2016YFD0300903, 2016YFD0300501, 2015BAC02B02; Agro-scientific Research in the Public Interest, Grant/Award Number: 201503122; Central Public interest Scientific Institution Basal Research Fund of Institute of Crop Science; Innovation Program of CAAS, Grant/Award Number: Y2016PT12, Y2016XT01; China Scholarship Council

Abstract

Breeding high-yielding rice cultivars through increasing biomass is a key strategy to meet rising global food demands. Yet, increasing rice growth can stimulate methane (CH_4) emissions, exacerbating global climate change, as rice cultivation is a major source of this powerful greenhouse gas. Here, we show in a series of experiments that high-yielding rice cultivars actually reduce CH_4 emissions from typical paddy soils. Averaged across 33 rice cultivars, a biomass increase of 10% resulted in a 10.3% decrease in CH_4 emissions in a soil with a high carbon (C) content. Compared to a low-yielding cultivar, a high-yielding cultivar significantly increased root porosity and the abundance of methane-consuming microorganisms, suggesting that the larger and more porous root systems of high-yielding cultivars facilitated CH_4 oxidation by promoting O_2 transport to soils. Our results were further supported by a meta-analysis, showing that high-yielding rice cultivars strongly decrease CH_4 emissions from paddy soils with high organic C contents. Based on our results, increasing rice biomass by 10% could reduce annual CH_4 emissions from Chinese rice agriculture by 7.1%. Our findings suggest that modern rice breeding strategies for

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high-yielding cultivars can substantially mitigate paddy CH_4 emission in China and other rice growing regions.

KEYWORDS
meta-analysis, methanogenesis, methanotrophy, roots, soil carbon

1 | INTRODUCTION

Rice (*Oryza sativa* L.) is a staple food for more than half of the people in the world, and global demand for rice is projected to increase from 644 million tons in 2007 to a projected 827 million tons in 2050 (Alexandratos & Bruinsma, 2012). However, rice production is a major source of the potent greenhouse gas methane (CH_4); about 11% of anthropogenic CH_4 emissions come from rice paddies (IPCC, 2013), and among the major cereals, rice has the highest global warming potential (GWP) due to high CH_4 emissions (Linquist, van Groenigen, Adviento Borbe, Pittelkow, & van Kessel, 2012). Therefore, sustainable intensification of rice cropping systems requires increasing yields while reducing CH_4 emissions (Chen et al., 2014; van Groenigen, van Kessel, & Hungate, 2013; Linquist et al., 2012).

Global rice production can be increased through improving yield potential of rice cultivars; the introduction of high-yielding rice cultivars accounts for almost 50% of the recent yield growth in developing countries (Evenson & Gollin, 2003; Peng, Khush, Virk, Tang, & Zou, 2008). Until the beginning of this century, breeding strategies to improve rice yield were mainly focused on increasing harvest index (Hay, 1995; Richards, 2000). This approach may lower CH_4 emissions, as an increase in harvest index with constant plant biomass can decrease the production of root exudates that fuel CH_4 production (Su et al., 2015; Van Der Gon et al., 2002). However, the current harvest index of high-yielding rice cultivars is about 0.55, approaching the theoretical upper limit of 0.65 (Hay, 1995; Peng et al., 2008). Therefore, more recent breeding strategies for increasing yields focus on enhancing biomass while maintaining the current harvest index (Cheng et al., 2007; Peng et al., 2008; Richards, 2000; Yuan, 2015).

These latter breeding strategies could stimulate CH_4 emissions, because recent photosynthate of rice plants can be a major substrate for CH_4 production: with higher biomass production, more substrate could fuel higher CH_4 emission rates (Huang, Sass, & Fisher, 1997; Watanabe, Takeda, & Kimura, 1999). The microorganisms that produce CH_4, methanogenic archaea, also use substrates that are derived from native soil organic carbon (C) (Conrad, 2007; Watanabe et al., 1999), suggesting that the effect of rice cultivars on CH_4 emissions depends on soil C content. Thus, to study the effects of high-yielding cultivars on CH_4 emissions and their possible interaction with soil C availability, we conducted three independent but complementary experiments. (i) We used 33 rice cultivars to quantify the relationship between plant production and CH_4 emission in two otherwise similar paddy soils with different labile soil C contents, (ii) we determined the effect of a high-yielding cultivar on CH_4 emissions in a realistic field setting, and (iii) using the same soils and cultivars as in experiment 2, we grew rice in microcosms and measured CH_4 emissions with and without wheat straw incorporation. Finally, to test the generality of our findings, we conducted a meta-analysis of studies that quantified the effect of high-yielding rice cultivars on CH_4 emissions.

2 | MATERIALS AND METHODS

2.1 | Experiment 1

In this pot experiment, we quantified the relationship between plant production and CH_4 emission in two otherwise similar paddy soils with different labile soil C contents. The experiment was conducted under open field conditions at Pailou experimental station, Nanjing Agricultural University, Nanjing City (118.8°E, 32.1°N), China. Thirty-three rice cultivars approved and released since 2001 in China (Table 1) were tested. Both soils in this experiment were collected from the plow layer of the paddy fields at Jiangpu Farm of Nanjing Agricultural University, Nanjing City. The low C soil was stored outdoors for 3 years before being used; soil labile C content was low because most of the plant residues and other labile C in the soil had been oxidized or mineralized. The soil with a high soil labile C content was collected 5 days before the experiment. Soil labile C content was measured by the $KMnO_4$ oxidation method (Blair, Lefroy, & Lisle, 1995). Soil properties are reported in Table 1.

Plastic pots (height, 25 cm; diameter, 24 cm) were filled with 7.0 kg of soil that was sieved (6 mm mesh size) to remove stones. Fifteen pots were prepared for each cultivar with each soil. Three pots were used for measuring CH_4 emission, and the other pots for measuring rice productivity traits. Three rice seedlings (28 days old) were transplanted into each pot. Nitrogen was applied as urea, P as calcium superphosphate, and K as potassium chloride in each pot as basal dressing at 165, 88, and 110 kg ha^{-1}, respectively. Side-dressing N fertilizer was added at a rate equivalent at 99 kg ha^{-1} at the tillering stage. During the rice growth period, 2–3 cm water layer overlying the soil surface was maintained.

2.2 | Experiment 2

In this field experiment, we determined the effect of a high-yielding cultivar on CH_4 emissions in a realistic setting. We planted rice seedlings in two adjacent fields at the Jiangpu Farm: one previously fallow field (we will refer to this treatment as “fallow” from now on) with low C content, and one paddy field with high C content. Soil properties are reported in Table 1. We used two cultivars that were

TABLE 1 Main properties of the tested soils and rice cultivars used in our study

	Experiment 1		Experiments 2 and 3	
	Paddy soil	Dried soil	Paddy soil	Fallow soil
Soil organic C (g kg^{-1})	17.8	17.5	23.2	12.0
Soil labile C (g kg^{-1})	3.6	1.4	6.5	1.0
Total N (g kg^{-1})	2.1	2.0	2.3	1.5
Total P (g kg^{-1})	0.6	0.6	0.9	0.7
Total K (g kg^{-1})	13.8	14.0	8.2	11.0
Alkaline hydrolysis N (mg kg^{-1})	96.8	94.1	85.5	86.1
Available P (mg kg^{-1})	28.1	16.6	20.9	22.5
Available K (mg kg^{-1})	244.5	165.0	206.1	138.3
Soil pH	6.8	6.7	6.5	6.9
Rice cultivars	Eryou 084, Fengliangyouxiang 1, Fengyuan 299, Guizhannong, Guodao 1, Hezhanmei, Huaidao 9, Huailiangyou 527, Huiliangyou 6, Jijing 88, Liaoxing 1, Liaoyou 1052, Liaoyou 5218, Longdao 5, Nei2you 6, Ningjing 1, Ningjing 3, Peizafengtai, Qianchonglang 2, Shengnong 016, Shengnong 265, Shengnong 9816, Wuyou 308, Wuyunjing 24, Yangjing 4038,Xindao 18, Xinliangyou 6, Xinliangyou 638,Yliangyou 1, Yliangyou 302, Yangliangyou 7, Yuxiangyouzhan, Zhongzeyou 1		Ningjing 1, Yangdao 6	

both commonly grown at the experimental site and differed strongly in biomass and yield: the high-yielding Yangdao 6 (HY) and the low-yielding Ningjing 1 (LY). The field experiment was conducted in two adjacent fields with six replicates (3 m × 4 m in plot size) for each of the soil × cultivar treatment combination. As a basis for comparison, we also included unplanted plots in our experimental design. The paddy field was in a continuous wheat–rice rotation with adequate plant residues and high labile C content, whereas the fallow field had been fallow for 6 years prior to the experiment. Few weeds grew in the fallow field and were removed before rice planting.

Rice seedlings were transplanted at a hill spacing of 0.25 m × 0.20 m on 30 June 2014. Nitrogen fertilizer (urea) was applied at 225 kg N ha^{-1}, of which 30% was applied before planting, another 30% at tillering, and the remaining 40% at panicle initiation. Phosphorus fertilizer (calcium superphosphate) and K (potassium chloride) were applied as the basal fertilizer at the same rate of 65 kg ha^{-1}. A water layer was kept 4–5 cm above the soil surface during the pre-anthesis period, while alternate wetting and drying irrigation was applied during the postanthesis period.

2.3 | Experiment 3A

In this pot experiment, we used the same soils and cultivars as in field experiment 2. Soils were collected from each field and sieved (6 mm mesh size) to remove stones. Plastic pots (height, 25 cm; diameter, 24 cm) were filled with 7 kg of soil. A nylon mesh bag (diameter, 8 cm; height, 10 cm; mesh size, 37 μm) was placed in the center of each pot to create two soil compartments, that is, the central rooted compartment and the outside nonrooted compartment (Ma, Qiu, & Lu, 2010). Twenty-five pots were prepared for each cultivar in each soil. Five pots were used for CH_4 emission measurements, and the remaining pots were used for measuring plant traits and soil properties. Two healthy rice seedlings were planted in the root bag. Other management practices were similar as described in experiment 1.

2.4 | Experiment 3B

Using the same experimental approach in Experiment 3A, we also measured CH_4 emissions from fallow soil with and without wheat straw incorporation for both the HY and LY cultivars. Wheat straw incorporation is a widely applied management practice in rice agriculture (Singh, Shan, Johnson-Beebout, Singh, & Buresh, 2008) that strongly increases the amount of soil labile C (Liu, Lu, Cui, Li, & Fang, 2014). Before the experiment began, fresh wheat straw was chopped and ground into 5–10 mm segments that were incorporated into the soil in each pot at a rate equivalent to 6 t ha^{-1}. A water layer of 4–5 cm was kept during the pre-anthesis period, while alternate wetting and drying irrigation was applied during the postanthesis period.

2.5 | Sampling and measurement methods

Methane emissions in all experiments were measured using the static closed chamber method (Zou, Huang, Jiang, Zheng, & Sass, 2005) at 7-day intervals. Methane concentrations were measured by a gas chromatograph (7890A, Agilent Technologies Inc., USA) equipped with a flame ionization detector.

Dissolved organic C (DOC), root biomass and porosity, and soil methanogenic and methanotrophic gene abundances in experiment 3 were measured on the 55th (Part A) and 45th day (Part B) after transplanting, when CH_4 emissions were relatively high and significantly different between the two cultivars. Soil pore water was collected from the root bag compartments using Rhizonsamplers (SMS, Eijkelkamp, Netherlands). About 2-mL soil solution was extracted using a 40-mL vacuum vial to flush and purge the sampler before sampling, and about 20 mL of soil solution was drawn into another vial. All the sampling vials were equilibrated by filling them with pure N_2 gas and 5 mL gas of the headspace was analyzed for CH_4 (Krüger, Frenzel, & Conrad, 2001). The solutions were passed through 0.45 μm membrane filter and analyzed for DOC by a TOC analyzer (multi N/C UV, Analytik Jena AG, Germany).

Fresh soil samples were collected from the rooted compartment. Soil DNA was extracted from 0.25 g soil using a Power Soil DNA Isolation Kit (MoBio, USA). The copy numbers of *mcr*A genes, which represent the abundances of methanogenic archaea in soil, were quantified using the primer pair mcrAf/mcrAr (Luton, Wayne, Sharp, & Riley, 2002). Two forward primers of MB10γ and MB9α and their common reverse primer 533r were used to quantify the 16S rRNA gene copy numbers of the type I and type II methanotrophs, respectively (Henckel, Friedrich, & Conrad, 1999). The quantitative real-time PCR was performed using a Mastercycler ep realplex instrument (Eppendorf, Hamburg, Germany). After sampling the soil, roots were washed with tap water. Rice root porosity (% gas volume/root volume) was measured by the pycnometer method (Jensen, Luxmoore, Van Gundy, & Stolzy, 1969). Aboveground biomass and grain yield were measured at harvest. Rice plants were oven-dried at 105°C for 30 min followed by drying at 70°C to achieve a constant weight.

2.6 | Statistical analysis

Correlations between rice plant traits (e.g., root biomass, aboveground biomass, and grain yield) and total seasonal CH_4 emission were analyzed in experiment 1. We also analyzed the correlation between the relative aboveground biomass and relative CH_4 emissions. The relative aboveground biomass and CH_4 emissions were calculated (*R*):

$$R = xt/xc,$$

where *xt and xc* are the values of the variables (biomass and CH_4 emissions) for a cultivar and the lowest values in each soil, respectively. Analysis of variance (two-way ANOVA) and independent sample *t*-test for a given soil were performed in experiments 2 and 3. All analyses were performed with the statistical package SPSS 18.0. Differences between cultivars were considered significant at $p < .05$.

2.7 | Meta-analysis

We conducted a literature survey of peer-reviewed papers related to rice cultivars and CH_4 emission. Peer-reviewed papers published both in English and in Chinese before June 2016 were collected from the Web of Science and the China National Knowledge Infrastructure. We collated studies that met the following criteria:

1. soil organic C, rice biomass at harvest, and CH_4 emissions were reported simultaneously,
2. CH_4 fluxes had to be measured for an entire rice growth period,
3. if only two cultivars were used in an experiment, the differences in biomass between the two cultivars had to be at least 5%, and
4. rice was grown in paddy soils (i.e., studies on fallow soils were excluded).

In total, we found 18 published papers including 93 observations from 21 sites (Table 2, Data S1 and S2). For each experiment in our dataset, the rice cultivar with the lowest biomass was taken as the control. We tabulate yield data if they were available, but this was not a prerequisite for inclusion of the experiment in our dataset. We included separate observations of rice cultivar effects from a single study site under different experimental treatments (i.e., in multifactorial studies). Observations from different years within the same experiment were also included as separate observations. For each experiment in the dataset, the rice cultivar with the lowest biomass was taken as the control treatment. We quantified the effects of cultivars with high biomass by calculating the natural logarithm of the response ratio (*R*): $\ln(R) = \ln(xt/xc)$, where *xt and xc* are the values of the variables (biomass, yield, HI, or CH_4 emissions) for a cultivar with high biomass and for the control cultivar, respectively (Hedges, Gurevitch, & Curtis, 1999). In addition to ln(*R*), we also used the absolute change in CH_4 emission (ΔCH_4) as effect size to assess the effect of rice cultivars with high biomass on CH_4 emission:

$$\Delta CH_4 = T - C,$$

where T and C are the cumulative CH_4 emissions during the growing season of rice cultivars with high biomass and of the control, respectively. Only data collected from field experiments were used in this ΔCH_4 analysis.

Three outliers of ln (R_{CH4}) with the largest absolute values (−1.02, −1.03, and 0.90) were identified by the descriptive statistics explore of the statistical package SPSS 18.0. These three observations and the corresponding observations for ln ($R_{biomass}$), ln (R_{yield}), ln (R_{HI}), and ΔCH_4 were excluded from further analysis. Because some studies did not report yield, the number of observations for biomass, yield, and CH_4 was not equal. In general, meta-analyses assume data independence. This assumption was violated by including more than one observation from a single study, when multiple cultivars within the same study shared the same control treatment. To examine the influence of nonindependence, we averaged the effect sizes of different cultivars from the same study in order to make sure that only one comparison was used (Data S2).

We used MetaWin 2.1 (Rosenberg, Adams, & Gurevitch, 2000) to generate mean effect sizes and 95% bootstrapped confidence intervals (95% CIs) (4,999 iterations). Because standard deviation values were not reported for most of the observations, we performed our analysis on unweighted effect sizes and on effect sizes that were weighted by replication (Hungate et al., 2009). To compare the differences in effect sizes among soil organic C, soil organic C content was divided into three categories: ≤8 g kg^{-1}, 8–12 g kg^{-1}, and >12.0 g kg^{-1}.

The mean effect sizes for experimental classes were considered to be significantly different from each other if their 95% CIs did not

TABLE 2 Overview of the rice cultivar studies included in our meta-analysis

Site	Country	SOC (g kg^{-1})	No of rice cultivars	*n*	Experimental condition	Mean CH_4 effect (%)	Mean yield effect (%)	Reference
Aichi	Japan	9.8	3	2	Pot	12.1	NA	Watanabe, Yamada, and Kimura (2001)
Assam	India	8.0	2	10	Field	7.8	NA	Gogoi, Baruah, Gogoi, and Gupta (2005)
Assam	India	6.0	2	10	Field	16.1	NA	Gogoi et al. (2005)
Beijing	China	9.9	4	4	Field	19.8	58.5	Wang et al. (2000)
Beijing	China	10.0	3	4	Field	123.9	−11.0	Xu, Wang, Li, and Wang (1999)
Cuttack	India	6.6	2	3	Field	−1.8	32.6	Datta, Nayak, Sinhababu, and Adhya (2009)
Cuttack	India	7.6	10	3	Field	−2.0	66.4	Satpathy et al. (1998)
Danyang	China	19.6	10	3	Field	−22.0	8.5	Zhang et al. (2015)
Hangzhou	China	22.4	6	3	Field	−10.4	4.3	Lu, Chen, et al. (2000)
Java	Indonesia	4.8	2	3	Field	11.6	5.6	Setyanto, Makarim, Fagi, Wassmann, and Buendia (2000)
Jiangdu	China	15.0	2	4	Field	−11.8	−3.3	Tang, Liu, Zhu, and Kobayashi (2015)
Jinxian	China	25.0	9	3	Field	−10.3	11.4	Zhang et al. (2015)
Laguna	Philippines	12.0	5	4	Field	−25.0	NA	Wassmann et al. (2000)
Nanjing	China	17.8	2	3	Pot	−26.0	35.0	Wang et al. (2013)
New Delhi	India	4.5	6	3	Field	42.1	6.3	Mitra, Jain, Kumar, Bandyopadhyay, and Kalra (1999)
New Delhi	Indian	4.1	3	NA	Field	6.0	14.5	Jain et al. (2000)
Sacheon	Korea	9.8	8	3	Field	−5.8	−1.2	Gutierrez, Kim, and Kim (2013)
Shenyang	China	33.7	12	3	Field	−32.7	25.4	Zhang et al. (2015)
Tokyo	Japan	36.3	2	3	Field	−37.3	47.6	Win et al. (2016)
Tsukuba	Japan	7.5	4	3	GC	36.6	35.8	Lou et al. (2008)
Varanasi	India	7.2	3	3	Field	−10.5	5.8	Singh, Singh, and Kashyap (1999)

NA, not reported; GC, growth chamber.

overlap and were significantly different from zero if the 95% CI did not overlap with zero. We used randomization tests included in MetaWin to test for significant differences between study categories. To ease interpretation, the results of this meta-analysis on ln (*R*) were back-transformed and reported as percentage changes (($R-1) \times 100$). Results using the different weighting functions were qualitatively similar (Table S1). In the main report, we provide results of the analyses on effect sizes that were weighted by replication.

2.8 | Extrapolation

To scale up our results, we first determined which experimental conditions were most representative of realistic rice paddy systems. As most rice cropping systems and paddy soil types in the world can be found in China, we took China as a case for assessing the impact of rice cultivar on paddy CH_4 emissions. Based on China's second state soil survey completed in the early 1980s, the arithmetic mean organic C content in the top 15 cm paddy soils was 16.5 g kg^{-1} (See Figure S1), and the mean weighted by area was 14.2 g kg^{-1} (Xie et al., 2007). The percentages of the observations with ≤8 g kg^{-1}, 8–12 g kg^{-1}, and >12.0 g kg^{-1} organic C content to the total observations are 2.7%, 16.1%, and 81.2%, respectively.

Based on the data from the second state soil survey in China (Figure S1) and the meta-analysis, we estimated the effect of increasing biomass on paddy CH_4 emission in China (E):

$$E = \Sigma(\mathrm{EC}_i/\mathrm{EB}_i \times W_i),$$

where EC_i is the mean effect size of high biomass rice cultivars on CH_4 emissions (%) in the *i*th soil in the meta-analysis, EB_i is the mean effect size of high biomass rice cultivars on biomass (%) in the *i*th soil in the meta-analysis, and W_i is the fraction of the area for the *i*th soil to total paddy soil area. We estimated W_i as the ratio of the number of observations in *i*th soil from the soil survey to the number of total observations from the soil survey.

3 | RESULTS

3.1 | CH_4 fluxes

As expected, we found in experiment 1 that CH_4 emissions were higher in the soil with high labile C content (Figure 1). In the soil low in labile C, plant productivity was positively correlated with seasonal cumulative CH_4 emissions (Figure 1a). However, we found the opposite relationship for the soil high in labile C (Figure 1b): as the productivity and yield of the cultivar increased, cumulative CH_4

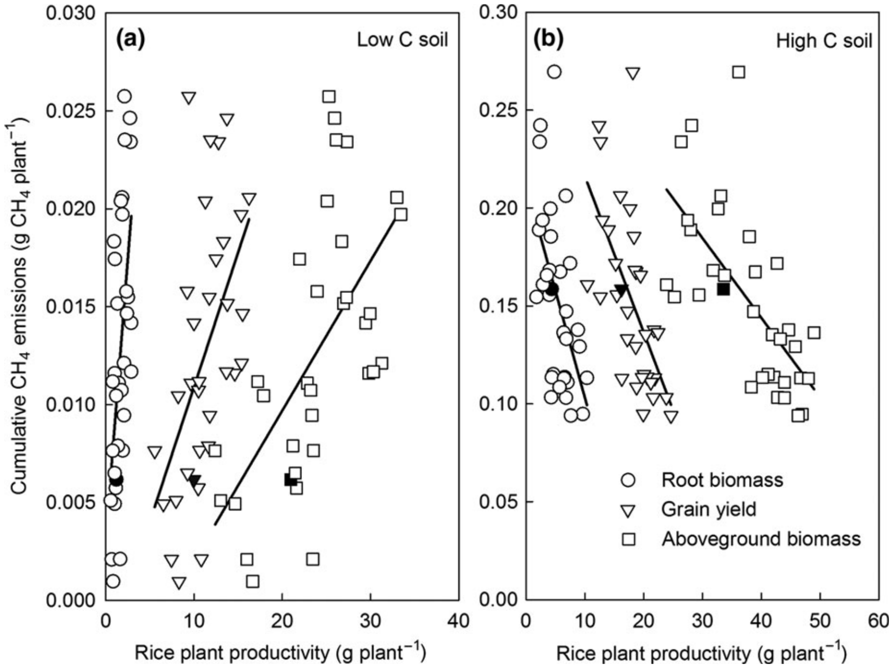

FIGURE 1 Relationships between plant productivity traits (i.e., root biomass, aboveground biomass, and yield) and seasonal cumulative CH_4 emissions across 33 rice cultivars. (a) Soil CH_4 emissions vs. plant productivity in a soil with low labile C content. Cumulative CH_4 emissions were positively correlated with root biomass (r^2 = .34), grain yield (r^2 = .29), and aboveground biomass (r^2 = .38); (b) soil CH_4 emissions vs. plant productivity in a soil with high labile C content. Cumulative CH_4 emissions were negatively correlated with root biomass (r^2 = .30), grain yield (r^2 = .39), and aboveground biomass (r^2 = .46). All correlations were significant at p < .01. The results for cultivar Ninjing 1 (LY in experiments 2 and 3) are indicated by black symbols

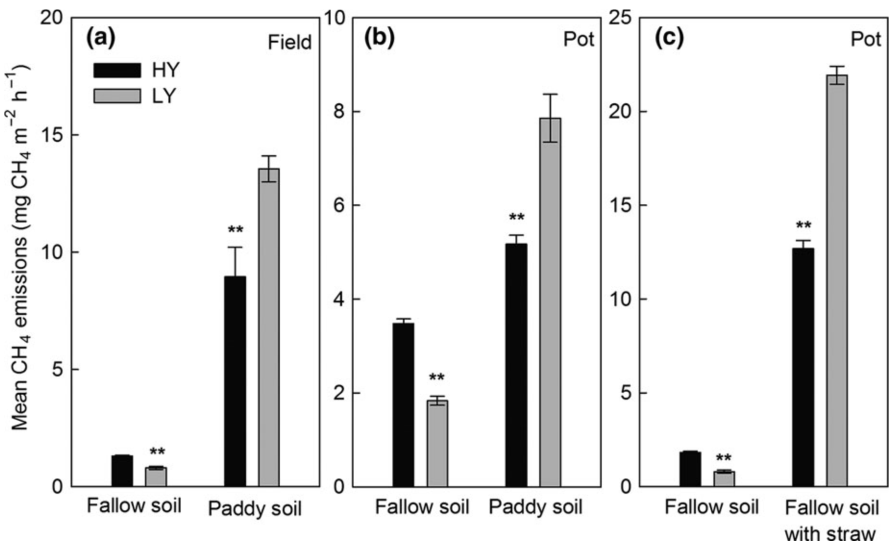

FIGURE 2 CH_4 emissions from a high-yielding (HY) and a low-yielding (LY) rice cultivar, as affected by soil C contents. (a) CH_4 emissions from a fallow soil (low soil C content) and a paddy soil (high soil C content) under field conditions. (b) CH_4 emissions from a fallow soil and a paddy soil under pot conditions. (c) CH_4 emissions from fallow soil with and without straw incorporation under pot conditions. Error bars represent standard error (n = 6 for the field experiment, n = 5 for the pot experiment). ** indicates significant difference between cultivars at p < .01

emissions declined. For every 10% increase in rice aboveground biomass, CH_4 emissions declined by 10.3% (Figure S2).

In experiment 2, we found that in the fallow field, CH_4 emissions were 0.5 mg m^{-2} hr^{-1} higher for the high-yielding cultivar compared to the low-yielding cultivar (Figures 2a and S3). However, in the paddy field, the opposite pattern occurred, and the high-yielding cultivar reduced CH_4 emissions by 4.6 mg m^{-2} hr^{-1} compared to the low-yielding cultivar (Figures 2a and S3).

Experiment 3A confirmed that the cultivars similarly affected CH_4 emissions in the microcosms as they did under field conditions, with HY increasing CH_4 emissions in the fallow soil, but reducing them in the paddy soil (Figures 2b and S4). The results of experiment 3B indicate that in the fallow soil without wheat straw incorporation, CH_4 emissions for the high-yielding cultivar were 1.0 mg m^{-2} hr^{-1} higher compared to the low-yielding cultivar (Figures 2c and S5). With straw incorporation, however, the pattern reversed: CH_4 emissions for the high-yielding cultivar were 9.2 mg m^{-2} hr^{-1} lower than for the low-yielding cultivar (Figures 2c and S5). These results strongly suggest that the difference in the effect of high-yielding cultivars on CH_4 emissions between fallow and paddy soils in experiments 2 and 3A are due to differences in labile soil C. Taken together, these three experiments provide conclusive evidence that high-yielding cultivars slightly increase CH_4 emissions in low C soils, but greatly reduce CH_4 emissions in high C soils.

3.2 | Soil properties and plant traits

In experiment 3A, we found that the high-yielding cultivar only stimulated methanogens in the fallow soil (Figure 3a), not in the paddy soil. Similarly, in experiment 3B, the high-yielding cultivar only

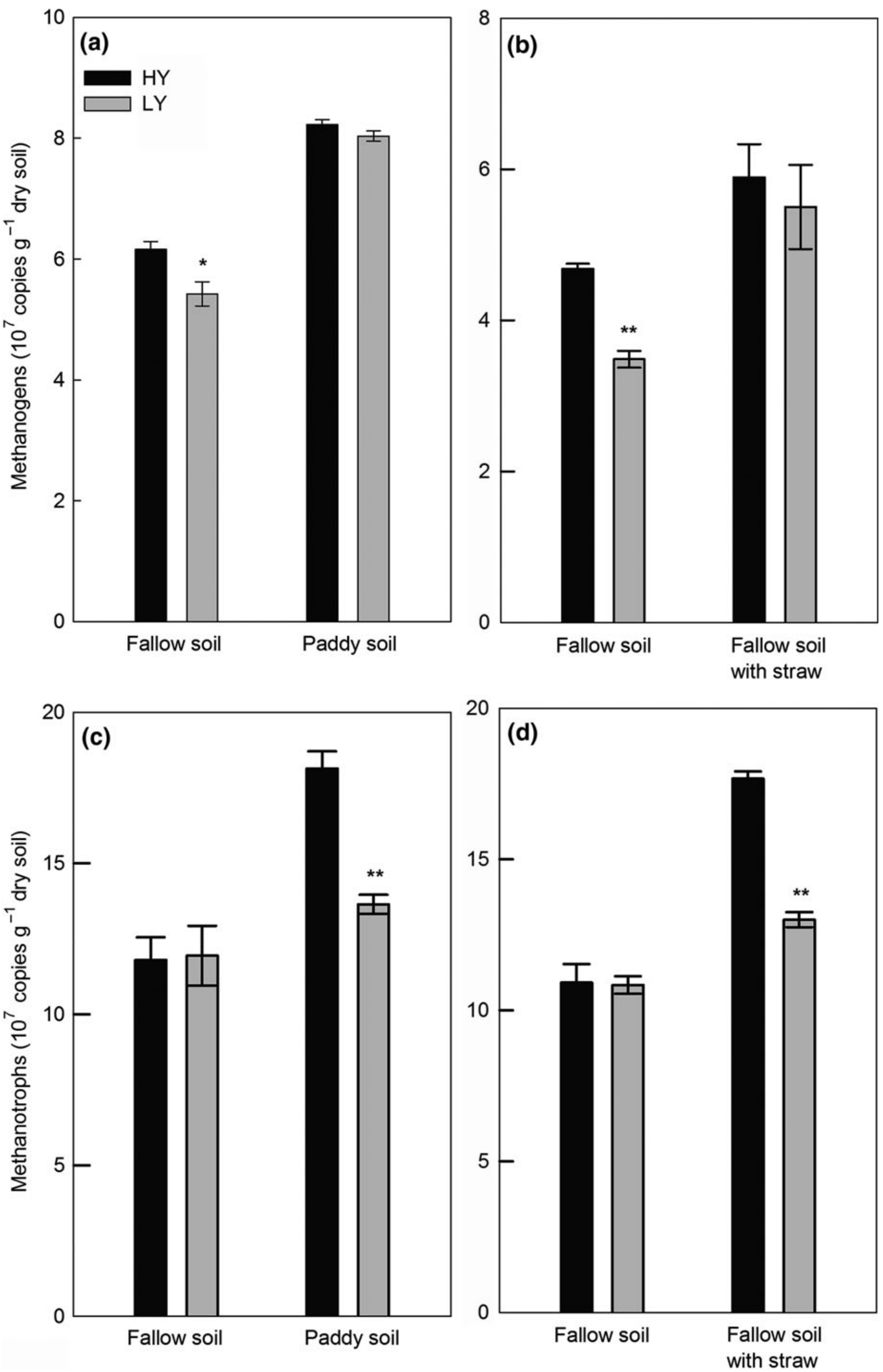

FIGURE 3 Quantification of methanogens and methanotrophs under a high-yielding (HY) and a low-yielding (LY) rice cultivar, as affected by soil C contents. (a) Quantification of methanogens in a fallow soil (low soil C content) and a paddy soil (high soil C content). (b) Quantification of methanogens in a fallow soil with and without straw incorporation. (c) Quantification of methanotrophs in a fallow soil and a paddy soil. (d) Quantification of methanotrophs in a fallow soil with and without straw incorporation. Error bars represent standard errors (n = 5). * and ** indicate significant differences between cultivars at $p < .05$ and 0.01, respectively

stimulated methanogens in the fallow soil without straw incorporation (Figure 3b). By contrast, soil methanotrophs were significantly more abundant in the presence of the high-yielding cultivar than for the low-yielding rice cultivar in the paddy soil and in the fallow soil with straw incorporation (Figure 3c,d). In other words, in the high C soils, the high-yielding rice cultivar enhanced the abundance of microorganisms that consume CH_4.

In experiment 3A, root biomass and DOC values were significantly higher for HY than for LY in both the fallow soil and the paddy soil (Table 3). Similar results were found in the experiment 3B, although straw addition reduced root biomass for both rice cultivars. These results suggest that the high-yielding cultivar enhanced C input to all soils. The root porosity of HY was significantly higher compared to LY in both soils in experiment 3A (Table 3). Similarly, in experiment 3B, root porosity was significantly higher for HY than for LY in both the fallow soil and the fallow soil with straw. Straw addition significantly reduced root porosity ($P < .01$). The yield of Yangdao 6 was between 37.2 and 91.8% higher than for Ninjing 1 in experiment 3. In comparison, the yield of the highest yielding cultivar in experiment 1 was 62.7% and 51.9% higher than that of Ninjing 1 for the low and high soil C soil, respectively (Figure 1). Thus, even though Yangdao 6 was not included in experiment 1, its yield increase relative to Ninjing 1 is comparable to that of other high-yielding cultivars included in our study.

TABLE 3 Plant traits, dissolved organic C and CH_4 in soil pore water, and Types I and II methanotrophs for a high-yielding (HY) and a low-yielding (LY) rice cultivar in experiment 3

	Fallow soil		Paddy soil	
Experiment 3A	**HY**	**LY**	**HY**	**LY**
Root biomass (g plant^{-1})	5.6 ± 0.2**	3.6 ± 0.1	7.1 ± 0.9*	4.2 ± 0.3
Root porosity (%)	39.6 ± 2.7*	33.3 ± 1.1	43.4 ± 0.7*	37.7 ± 1.5
Dissolved organic C (mg L^{-1})	82.0 ± 4.2**	68.5 ± 1.7	132.3 ± 3.7*	111.6 ± 3.4
Type I methanotrophs copies (10^7 copies g^{-1} dry soil)	4.7 ± 0.4	5.1 ± 0.6	7.9 ± 0.3*	6.6 ± 0.2
Type II methanotrophs (10^7 copies g^{-1} dry soil)	6.9 ± 0.4	6.8 ± 0.6	10.2 ± 0.4*	7.0 ± 0.2
Aboveground biomass (g plant^{-1})	40.2 ± 1.6**	26.4 ± 1.6	55.8 ± 2.0**	41.5 ± 1.8
Grain yield (g plant^{-1})	21.1 ± 1.0**	11.0 ± 0.8	27.2 ± 1.8**	18.9 ± 0.7
	Fallow soil without straw		**Fallow soil with straw**	
Experiment 3B	**HY**	**LY**	**HY**	**LY**
Root biomass (g plant^{-1})	4.0 ± 0.4*	2.5 ± 0.3	3.3 ± 0.2**	2.0 ± 0.1
Root porosity (%)	36.7 ± 2.8*	28.5 ± 0.7	23.1 ± 0.1*	17.9 ± 0.5
Dissolved organic C (mg L^{-1})	74.5 ± 1.5*	63.9 ± 0.6	123.1 ± 2.4**	101.0 ± 3.1
CH_4 in soil pore water (p.p.m.v)	193.3 ± 15.4*	87.6 ± 10.5	1553.9 ± 31.6*	3397.2 ± 521.5
Type I methanotrophs copies (10^7 copies g^{-1} dry soil)	4.1 ± 0.1	4.2 ± 0.2	6.2 ± 0.8*	4.7 ± 0.2
Type II methanotrophs (10^7 copies g^{-1} dry soil)	6.8 ± 0.6	6.7 ± 0.4	11.45 ± 0.9*	8.3 ± 0.4
Aboveground biomass (g plant^{-1})	38.6 ± 0.7**	28.1 ± 0.7	35.1 ± 1.5**	25.1 ± 0.3
Grain yield (g plant^{-1})	19.9 ± 0.4**	14.5 ± 0.8	17.9 ± 0.7**	13.0 ± 0.4

Mean ± standard error (n = 5).
* and ** indicate significant differences between cultivars at $p < .05$ and .01, respectively.

3.3 | Meta-analysis and extrapolation

Our meta-analysis confirmed that on average, rice cultivars with high biomass significantly increased CH_4 emissions from lower organic C soils (≤8 g kg^{-1}), but significantly reduced CH_4 emissions from higher organic C soils (>12 g kg^{-1}) (Figure 4). High biomass rice cultivars increased yields in all soil organic C classes to a similar extent (Table S1). The average increase in biomass for studies included in our meta-analysis was 29.8% and 25.6% in the low C soil and high C soil, respectively (Table S1). The meta-analysis of independent data showed the same trends as the analysis on nonindependent data (Table S1), suggesting the robustness of our results.

Based on the soil survey and our meta-analysis, we estimated the effect of high-yielding cultivar breeding strategy on Chinese paddy CH_4 emission by calculating an area weighted effect size. Accounting for the percentage of Chinese rice paddies with ≤8 g kg^{-1}, 8–12 g kg^{-1}, and >12.0 g kg^{-1} organic C contents, we estimated the effect per unit biomass enhancement on CH_4 emissions to be −0.71. In other words, increasing plant biomass by 10% can reduce annual CH_4 emission from Chinese rice agriculture by 7.1%.

4 | DISCUSSION

All our experiments and our meta-analysis show that high-yielding cultivars slightly increase CH_4 emissions in low C soils, but greatly reduce CH_4 emissions in high C soils. Why does the effect of high-yielding cultivars on CH_4 emissions depend on soil C availability? The production of CH_4 is primarily determined by substrate availability (Conrad, 2007), which was enhanced by the high-yielding cultivar, as indicated by both higher root biomass and higher dissolved organic C content in soil pore water of the high-yielding rice cultivar in all the soils used in our experiments. This reflects the higher root productivity of the high-yielding cultivar, providing increased substrate availability for CH_4 production through root exudates (Huang et al., 1997). Still, net CH_4 emissions from rice paddies are determined by the balance between the activities of methanogenic archaea, the microorganisms that produce CH_4, and methanotrophic bacteria, the microorganisms that consume CH_4 (Conrad, 2007). Changes in the activities of either microbial group could explain the decline in net emissions observed with the higher-yielding cultivars on high C soils.

Methane oxidation and methanotrophic growth are controlled by CH_4 and O_2 availability (Conrad, 2007; Hanson & Hanson, 1996). We propose that the higher root biomass and root porosity of the high-yielding cultivar (Table 3) facilitated O_2 transport into the rhizosphere, stimulating CH_4 oxidation (Ma et al., 2010). This mechanism is particularly important in high C soils, where O_2 is more likely to be limiting (Ma et al., 2010). By contrast, in the fallow soil without straw incorporation, methanotrophic growth was likely limited by low CH_4 availability, especially for the Type II methanotrophs (Conrad, 2007; Hanson & Hanson, 1996). Indeed, CH_4 oxidation in paddy soils only occurs at CH_4 concentrations ≥500 p.p.m.v. (Cai, Zheng, Bodelier, Conrad, & Jia, 2016), far higher than what was found in

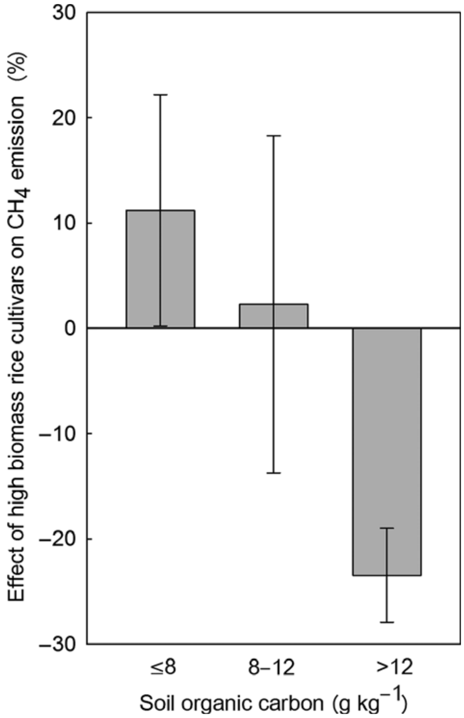

FIGURE 4 Results of a meta-analysis on the effect of high-biomass rice cultivars on CH_4 emissions under different soil organic C contents. Results are based on 33, 25, and 35 observations for the soil organic C $\leq$ 8 g kg^{-1}, 8–12 g kg^{-1}, and >12.0 g kg^{-1} class, respectively. Error bars indicate 95% confidence intervals. The effect of high-yielding cultivars on CH_4 emissions differed significantly between experimental classes (p = .0002)

the fallow soil in experiment 3B. Thus, our results suggest that rice cultivars affect net CH_4 emissions by altering the availabilities of resources that affect microorganisms that both produce and consume CH_4, and that the soil context determines the direction of the effect: High-yielding rice cultivars promote CH_4 production and emissions by increasing C substrate availability for methanogens when soil C content is low, but facilitate CH_4 oxidation by increasing O_2 transport and promoting methanotrophic organisms when soil C availability is high.

The generality of our findings was further confirmed by the results of our meta-analysis. We can only speculate about the mechanisms underlying the mitigation effect of high-yielding cultivars on CH_4 emissions in our meta-analysis. Indeed, high-yielding rice cultivars differ from low-yielding cultivars in many different ways that could potentially affect CH_4 emissions. For instance, compared to low-yielding cultivars, high-yielding cultivars have been shown to increase allocation to panicles (Jiang et al., 2016; Richards, 2000), and to differ in plant growth parameters (Gogoi, Baruah, & Gupta, 2008), root exudation (Lu, Wassmann, Neue, & Huang, 2000), and root oxidation activities (Zhang, Xue, Wang, Yang, & Zhang, 2009). However, our own data show that high-yielding cultivars increased root porosity, root biomass, and methanotrophic activity across multiple independent experiments. These data suggest that the effect of high-yielding cultivars on O_2 transport may be general, occurring under a wide range of environmental conditions and explaining the pattern found across the experiments synthesized in the meta-analysis.

In our extrapolation, we estimated the effects of a further 10% increase in plant biomass. This represents a realistic scenario: Plant breeding efforts have increased the biomass of super rice cultivars in China by about 25% from 2000 to 2015 and are expected to increase a further 10% by 2020 (Peng et al., 2008; Yuan, 2015). In absolute terms, the reduction in the CH_4 emissions caused by rice cultivars with high yield in high organic C soils was an order of magnitude larger than the emission increment in the low organic C soils (Table S1). Moreover, organic C of China's paddy soils has increased by 7.5% from 1979–1982 to 2007–2008 (Yan, Cai, Wang, & Smith, 2011) and will likely continue to increase due to the increasingly common management practice of crop straw incorporation (Liu et al., 2014; Singh et al., 2008). Thus, our estimate of a 7.1% reduction in CH_4 emissions due to high-yielding cultivars is conservative, and the real effect may be larger.

Our findings suggest that by switching to high-yielding cultivars, CH_4 emissions from rice agriculture can be reduced substantially. Greenhouse gas emissions from rice paddies will likely be exacerbated because of rising levels of atmospheric CO_2 and climate change (van Groenigen, Osenberg, & Hungate, 2011; van Groenigen et al., 2013), further underlining the importance of mitigation measures. However, it is still unclear whether rice cultivar improvement interacts with other agronomic practices (e.g., irrigation, tillage, and fertilizer management) to influence CH_4 emissions. These interactions represent a knowledge gap that needs to be addressed to determine the effectiveness of adopting high-yielding cultivars to mitigate CH_4 emissions.

Two limitations of our study must be noted. First, our experiments lasted for one growing season. However, some of the effects of high-yielding cultivars on soil C input will only become apparent in long-term experiments, when biomass produced in one season contributes to soil C input in the next season. Indeed, numerous studies (e.g., Feng et al., 2013; our study) show that rice straw incorporation strongly stimulate CH_4 emissions; increased biomass and straw production with high-yielding cultivars would enhance these effects. On the other hand, increased straw input will increase soil C availability, and the mitigation effect of high-yielding cultivars on CH_4 emissions become more pronounced in high C soils. Clearly, long-term studies are needed to confirm whether the mitigation effects of high-yielding cultivars persist over time.

Second, the microbiological analyses in our study are all based on single measurements in time. Microbial communities are dynamic, so the microbiological data presented here should be viewed accordingly. The data support our hypothesis that high-yielding cultivars reduce CH_4 emissions by stimulating oxygen transport into the soil, but future studies should include a time series component to confirm whether effects of high-yielding rice cultivars on methanotrophs and methanogens persist throughout the growing season.

Maintaining food security in the face of population growth and climate change is one of great challenges facing mankind today (Alexandratos & Bruinsma, 2012). Food security can be enhanced through agricultural intensification, but measures that increase crop yields often increase greenhouse gas emissions too (Tilman, 1999). Here, we show that agricultural intensification can go hand in hand with greenhouse gas mitigation. Other mitigation practices advocated to curb CH_4 emissions from rice paddies include mid-season drainage, intermittent irrigation, no-till, and the use of alternative fertilizers (Hussain et al., 2015; Linquist et al., 2015; Zhao et al., 2016). However, these practices can result in yield losses (Pittelkow et al., 2015), are labor-intensive, and their applicability varies among rice cropping systems and countries (Bodelier, 2015). In contrast, rice cultivar improvement may be a win-win strategy, as it simultaneously decreases CH_4 emissions and increases grain yield. Although seeds of higher yielding cultivars will be more expensive, farmers benefit where an increase in grain yield exceeds extra cost and society benefits through the reduction in greenhouse gases. Considering the dominance of small households in most rice production areas (Zhang et al., 2016), the use of high-yielding cultivars may therefore be accepted sooner and implemented more efficiently than other mitigation practices. Along with other mitigation efforts, future policy measures aimed at reducing CH_4 emissions from rice cultivation should consider the use of high-yielding cultivars.

ACKNOWLEDGEMENTS

This work was supported by the National Key Research and Development Program China (2016YFD0300903, 2016YFD0300501, and 2015BAC02B02), Special Fund for Agro-scientific Research in the Public Interest (201503122), Central Public interest Scientific Institution Basal Research Fund of Institute of Crop Science, the Innovation Program of CAAS (Y2016PT12, Y2016XT01), and the China Scholarship Council.

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SUPPORTING INFORMATION

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How to cite this article: Jiang Y, van Groenigen KJ, Huang S, et al. Higher yields and lower methane emissions with new rice cultivars. *Glob Change Biol*. 2017;23:4728–4738. https://doi.org/10.1111/gcb.13737