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Methanogenesis and Methane Oxidation in Paddy Fields under Organic Fertilization

Chungwoo Kim[1,3†], Denver I. Walitang[2,3†] and Tongmin Sa[3,4*]

[1]Chungcheongbuk-do Agricultural Research ang Extension Services, Cheongju 28130, Korea,
[2]College of Agriculture, Fisheries and Forestry, Romblon State University, Romblon 5505, Philippines,
[3]Department of Environmental and Biological Chemistry, Chungbuk National University, Cheongju 28644, Korea,
[4]The Korean Academy of Science and Technology, Seongnam 13630, Korea

ORCID

Chungwoo Kim
https://orcid.org/0000-0002-9209-9014

Denver I. Walitang
https://orcid.org/0000-0001-5469-5838

Tongmin Sa
https://orcid.org/0000-0001-7444-5852

Abstract

BACKGROUND: Global warming is one of the most pressing environmental issues which concomitantly complicates global climate change. Methane emission is a balance between methanogenesis and methane consumption, both of which are driven by microbial actions in different ecosystems producing methane, one of the major greenhouse gases. Paddy fields are major sources of anthropogenic methane emissions and could be compounded by organic fertilization.

METHODS AND RESULTS: Literature reviews were conducted to give an overview of the global warming conditions and to present the relationship of carbon and methane to greenhouse gas emissions, and the need to understand the underlying processes of methane emission. A more extensive review was done from studies on methane emission in paddy fields under organic fertilization with greater emphasis on long term amendments. Changes in paddy soils due to organic fertilization include alterations of the physicochemical properties and changes in biological components. There are diverse phylogenetic groups of methanogens and methane oxidizing bacteria involved in methane emission. Also, multiple factors influence methanogenesis and methane oxidation in rice paddy fields under organic fertilization and they should be greatly considered when developing mitigating steps in methane emission in paddy fields especially under long term organic fertilization.

CONCLUSION(S): This review showed that organic fertilization, particularly for long term management practices, influenced both physicochemical and biological components of the paddy fields which could ultimately affect methanogenesis, methane oxidation, and methane emission. Understanding interrelated factors affecting methane emission helps create ways to mitigate their impact on global warming and climate change.

Key words: Methane emission, Methane oxidation, Methanogenesis, Organic fertilization, Paddy fields

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Introduction

Global warming and climate change due to industrialization, fossil fuel utilization, forest destruction, and other anthropogenic activities bring environmental issues. The agricultural sector could not be an ex-

ception and soil management systems and indices aligned with sustainable development are to be considered with great importance[1]. Methane is a potent greenhouse gas with 28 times global warming potential compared to carbon dioxide with atmospheric methane concentration continuously increasing[2]. The average global concentration continues to rise with 600 Tg CH_4 yr^{-1} for global methane emissions, of which, 61% is attributed to anthropogenic sources recorded in the year 2020[3]. Methane emission varies under different soil types particularly those under aerobic and anaerobic conditions. It is dictated by the balance of methane production through methanogenesis and methane consumption through methanotrophy or methane oxidation and is influenced by multiple dynamic factors potentially compounded or stabilized under long term fertilization[4].

The implementation of organic and compost applications has been driven by interrelated environmental issues including soil degradation, unsustainable land use, and contamination of natural resources. The goal is to attain environmental beneficial impacts such as improved carbon sequestration, soil biological diversity, biogeochemical functions, soil fertility, and crop yield[5]. Organic fertilization plays a positive role in climate change mitigation via soil carbon sequestration but its application in paddy fields under submerged conditions becomes a potential source of methane emission[6, 7].

Rice paddies generate approximately 60 Tg CH_4 $year^{-1}$ of global methane emissions[8, 9]. In addition, fertilization with inorganic and organic fertilizers affects the physicochemical and biological components of soil paddy fields which ultimately reflect on the soil biogeochemical processes[10]. Therefore, agricultural input of compost or a combination of compost and inorganic fertilizers as short or long term fertilization in paddy fields influences methane-related processes mainly attributed to archaeal or bacterial paddy field communities. Methane emission is mainly mediated by methanogenic archaeal groups[2, 11, 12]. However, methanotrophy is carried out by type I and type II methanotrophs[2, 13], belonging mainly to γ-Proteobacteria and α-Proteobacteria, respectively. Additionally, the effects of fertilization on the soil properties, biotic components, and biologically-driven ecological processes are compounded by differing results[7, 11, 14]. These opposing studies could be linked and mechanistically be attributed to the composition,

community structure, diversity, abundance, and functional activity of microbial communities thriving in the paddy soils as they dynamically respond to the effects of fertilization regimes[11, 14].

Intensified global fertilizer application will be necessary to increase rice production but it is known that increased organic fertilization can enhance methane emission from rice agriculture. Long term compost fertilization can also lead to changes in soil factors and biotic components of the paddy fields related to methanogenesis, methane oxidation, and methanol oxidation[15-17]. Assessing contributing factors associated with methane production and consumption is essential to understand and formulate mitigating mechanisms to combat global warming.

This review gives an overview of global warming as a critical environmental issue and the goal of mitigating its impacts, along with the relationship of carbon and methane to greenhouse gas emissions potentially affecting not just agriculture but multiple aspects of human society. This review then focuses on the effects of organic fertilization, with emphasis on long term amendments, on the soil chemical properties and biological components related to methanogenesis and methane oxidation, the microbial diversity of methanogens and methanotrophs, and on the factors affecting the processes of methanogenesis and methane oxidation in paddy field agroecosystems. The scope of this review also extends to the mitigating steps that could be employed to regulate methane emission in paddy fields.

Global Warming

Global warming is the increase in the Earth's overall temperature causing climate change and environmental issues. Carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O) are the most important greenhouse gases which could be emitted from direct agricultural production but can be significantly reduced by improving soil management[1]. If the Earth's temperature rises above 2°C, more natural disasters will occur and disastrously lead to significantly reduced various risk factors such as biodiversity and food security[18]. The additive effects of global warming and climate change could also increase multifactorial stress combinations in plants, soils, and microbial communities driving a crucial decline in plant growth, soil conditions, and overall agricultural productivity[19].

The world's population will reach 9.8 billion by 2050, and more food production is needed up to 60%. If global warming continues due to abnormal climates such as unusually high temperatures, the range and number of environmental stresses that can have serious consequences to agricultural production will increase significantly[20]. Various stresses, including nutritional deficiencies and abnormal climates such as temperature and drought, reduce the average productivity and quality of crops, and these problems will become more serious in the future[21-23]. Current agriculture is facing the task of increasing production without further increasing agricultural land and is trying to reduce the damage to climate change by reducing environmental soil issues.

Active management of soil agriculture is essential to achieve the goal of decreasing global warming. Crops absorb CO_2 in the atmosphere to produce energy, and residues after harvest are decomposed by microorganisms and remain in the soil, making soils play important role in absorbing carbon. Therefore, soil microorganisms and plants can partially reduce CO_2 and methane in the atmosphere increasing the effectiveness of soil, including paddy soils, as an absorption sink of greenhouse gases[24]. Effective soil management can reduce greenhouse gases and strengthen soil carbon absorption functions, as well as enhance soil ecosystem diversity, soil fertility, and productivity as organic matter increases[25-28]. To cope with climate change and solve global warming, cost-effective methods are necessary such as optimizing compost fertilization and minimizing energy use while being feasible and eco-friendly.

Carbon and Methane in Relation to Agriculture and Greenhouse Gas Emission

Organic carbon and total nitrogen in the soil directly control the availability of soil carbon and nitrogen and play an important role in soil productivity indirectly by affecting the physicochemical conditions and biological properties of the soil[29]. In the agricultural environment, the carbon (C) sequestration of soil plays a very important role in alleviating emissions of carbon dioxide (CO_2) into the atmosphere and improving soil fertility[30, 31]. Carbon compounds in the soil not only improve productivity by making the soil fertile but also store billions of tons of carbon each year to reduce greenhouse gas concentrations in the atmosphere[32].

Carbon in the forms of CO_2 and CH_4 causes global warming. The global average methane concentration in the atmosphere reached 1,875 ppb at the end of 2019, which increased more than 2.5 times than the pre-industrial level. Therefore, continuous and long term monitoring of methane circulation is required to prepare for climate change and to confirm the reduction in methane emissions[33]. In the last decade, the global methane emission is 576 Tg CH_4 yr^{-1}, of which 60% or 358 Tg CH_4 yr^{-1} has been caused by human activity. In the agricultural field, intestinal fermentation and manure of livestock are the largest sources of emissions along with rice paddies. Rice is mostly grown in freshwater paddies under anaerobic conditions and accounts for about 10% of total methane emissions[3, 34, 35]. During the flooding period of the paddy soil, various organic matter is decomposed by methane generating archaea in an anaerobic state producing methane[36, 37]. It was reported that the main absorption source of methane was 90% of the oxidation reaction by hydroxyl radical (OH^{-1}) in the atmosphere, and the rest were absorbed into the soil within the range of 27~45 Tg CH_4 yr^{-1} by methane oxidizing bacteria[38]. Regionally, Mainland China and the Middle East saw a significant increase in methane emissions from 2000 to 2017, mainly due to coal mines, waste, and livestock. Europe, South Korea, and Japan decreased methane emissions due to reduced waste and fossil fuel use[39].

Studies related to methane production and emission [33, 39, 40] as well as methanogens and methanotrophic bacteria[41-46] and methane transformations in various environments such as wetlands are actively conducted[47-51]. To reduce greenhouse gas emissions, the carbon sequestration ability of the soil itself and CO_2 fixing and carbon sequestration in grassland or rice paddies have recently attracted attention[24, 52-54]. Paddy fields play the role of a carbon reservoir [55, 56] and are one of the best ways to prevent climate change.

The Importance of Understanding Long Term Organic Fertilization and Methane Emission on Rice Paddy Field Agroecosystems

The adoption of an organic management system in the rice agroecosystems influences rice grain yields and global greenhouse gas emissions, including carbon

dioxide, methane, and nitrous oxide[57]. The connections between methanogenesis, the process producing methane, and methane consumption or methanotrophy through methane oxidation then followed by methanol oxidation are controlled by microbial communities containing the *mcrA*, *pmoA*, and *mxaF* genes encoding their respective enzymes (Fig. 1). Recent uncertainties in global methane budgets push the need for research in the controls of sources and sinks of atmospheric methane. The production of methane by methanogenic archaea in wetlands and rice paddies is a major source while the consumption by methane oxidizing bacteria (MOB) in upland soils is a major sink [11]. It is essential then to evaluate methane emission from paddy fields, to further understand its impact on the greenhouse gas budget while optimizing organic fertilization as an efficient method to maintain rice yield and reduce fertilizer losses[12]. In addition, how nitrogen controls methane emission, consumption and underlying microbial processes have been designated as one of the key knowledge gaps in soil carbon–nitrogen interactions[11]. The dynamics of soil C and N also often vary with different rates of fertilization, hence, the change of soil labile C and N contents in relation to greenhouse gas emissions would be worth investigating under long term organic fertilization[10]. In order to estimate the contribution of paddy fields as a source of CH_4, it is important to understand the long term effects of fertilizer applications which are targets in strategies to combat global climate change [58]. Methane-consuming microbes play a vital role in global warming issues, as they are the only biological

sinks for methane[14]. These specific functional microbial populations play important roles in nutrient transformations in paddy ecosystems, revealing the composition and expression characteristics of specific functional genes concerning methanogenesis and methane oxidation[59].

Long Term Organic Fertilization and Its Impacts on the Soil Chemical Properties and Biological Components in Relation to Methanogenesis and Methane Oxidation

Long-term organic and N fertilization affect both edaphic and microbial communities in paddy fields involved in methane emission and consumption (Table 1). Studying how soil chemical parameters change as well as methanogenic (methanogens and methanogenesis) and methanotrophic communities respond to long term application of fertilizers could help us mitigate methane emission in paddy fields while allowing optimized fertilization and rice yields. Employing linear regression analysis based on the study of Zhang et al.[60], there is a predicted methane production potential based on the population sizes of methanogenic archaea population. This potential increases with the increase in the copy number of *mcrA* genes found in the soils of paddy fields.

In general, organic fertilization in the paddy fields involves the use of composted or fresh manure (human, livestock, pigs, poultry) and plant residues (mainly rice straw). The input of different types of fertilization especially organic fertilizers changed the chemical pro-
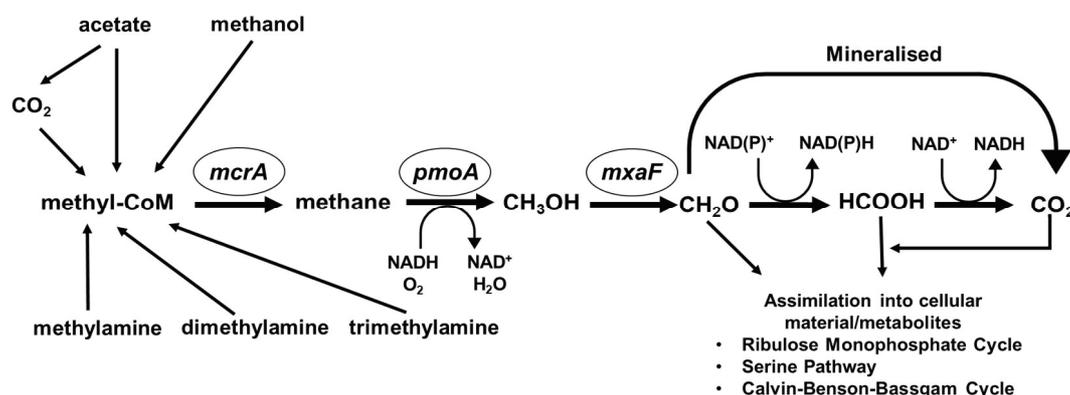

Fig. 1. Methanogenesis as modulated by the enzyme methyl-CoM reductase [76] and methane oxidation followed by methylotrophy as mainly controlled by methane monooxygenase and methanol dehydrogenase enzymes, respectively [77]. The functional genes *mcrA*, *pmoA*, and *mxaF* are molecular markers commonly employed to study methanogenesis, methane oxidation, and methanol oxidation, respectively.

perties of soils including organic matter content (OM) / soil organic carbon (SOC), total nitrogen (TN) content, macro and micronutrient content which in turn also influenced soluble and available levels of carbon, nitrogen, and other nutrients[10, 57, 61, 62]. Soil microbial biomass carbon and soil microbial biomass nitrogen also increased under manure fertilization[63]. Under organic manure and straw fertilization, the combined humus in the forms of humic acid and fulvic acid, also significantly increased with long term fertilization[62].

Table 1. Effects of long term organic and compost fertilization on the soil chemical properties and biological components in paddy field agroecosystem

Type of organic fertilizer	Effects on soil chemical property and biological components	Other effects and notes related to the current study	Citation
Manure, NPKM	The soil labile C, N pools and soil enzymatic activities increased in farmyard NPKM (manure). Microbial populations generally increased.	Annual cumulative GHGs emissions were significantly higher in NPKM treatments, including higher global warming potential (GWP) and carbon equivalent emission (CEE).	[10]
NPKC	NPK decreased Shannon Index and evenness; NPKC750 increased functional diversity. NPKC increased soil enzyme activity with increasing level of compost	Compost is made from 5-month composted rice straw.	[74]
Manure, NPKM	Manure and NPKM increased SOC, TN, SMBC, SMBN and WC. Strong increase in CO_2 emissions, potential mineralized C, and turnover rate constant in M and MNPK and microbial community.	Constant fertilization significantly altered soil properties and increased organic C accumulation mineralization, potential mineralized C content, and turnover rate constant.	[63]
Rice straw	Addition of straw immediately increased methanogen and methanotrophs population in soils with history of straw addition, while soils without history needed time to increase abundance.	Straw increased methanotrophs more strongly in soils with a history of straw incorporation. LT straw incorporation increased methanotrophic abundance and rice root size suggesting increased methane oxidation thus acclimation of methane emission from rice paddy fields.	[72]
NPKC	NPKC with 3x higher 16S rRNA abundance than NPK.; Shift in bacterial community;	Predicted functional genes related to PGP, development and decomposition.	[71]
Organic N	Chemical and organic N increased *mcrA* gene copy number. Methane fluxes were positively correlated with *mcrA* gene copy number and the ratio of *mcrA/pmoA*, while negatively correlated to *pmoA* gene copy numbers.	Chemical or organic N stimulated CH_4 emissions through improving soil C substrate and methanogenic activities. Abundance of *mcrA* and *pmoA* are mainly regulated by water irrigation regime.	[73]
Pig manure, straw	Manure plus straw increased SOC content of the topsoil. Cumulative mineralization was always higher in the manure treatments. Combined humus with humic acid and fulvic acid significantly increased.	LT application of fertilizers influenced only the loosely combined fraction of the humus, which was labile and highly active, whereas the whole organic C pool was relatively stable over time.	[62]
Organic	The promotion of soil EC, humic acid, available P, K, and N, TN, TC, and C: N in accelerating CH_4 emissions is very significant; drainage mitigates CH_4 production.	Methane emission was highest at the booting and filling stage. Methane emission was highest in organic, then in mixed then in chemical fertilizer.	[64]
Pig manure	Manure or NPKM increased yield, SOC, TN, TP, DOC, available P and K. It also increased methane production potential and *mcrA* abundance of soils.	The community structures of *mcrA* and *pmoA* were altered induced by changes in DOC, total P, available P and available K in the soil.	[60]
Manure	CEC, SOC and TN are higher in chemical fertilizer+manure.	C mineralization, CO_2 production, predominated over CH_4, but CH_4 has predominant role in global warming potential. Methane production is 3x higher in chemical fertilizer+manure.	[75]
NPKC	NPKC increased OM, TN, available P and available K. NPK+C increased copy number of type I and type II methanotrophs; Type II dominated all other treatments. Type I is more commonly detected.; LT fertilization, especially with NPK+C changed the soil methanotrophic community structure.	N, K, and crop residues could be important factors controlling abundance and community composition of the methanotrophs in the paddy fields.	[58]

LT – Long-term; NPK – Inorganic fertilizer containing N, P, and K; NPKM – NPK plus manure; NPKC – NPK plus compost; GHG – Green house gas; SMBC – Soil microbial biomass C; SMBN – Soil microbial biomass N; TN – Total nitrogen; WC – Water content; SOC – Soil organic carbon; DOC – Dissolved organic C; OM – Organic matter; CEC – Cationic exchange capacity; *mcrA* – gene encoding methyl coenzyme M reductase; *pmoA* – Gene encoding the particulate methane monooxygenase.

The labile forms of these soil nutrients became major components that drove soil biochemical transformations generally involving soil microorganisms[10]. Under organic fertilization, there was an increase in the available P, K, N, and DOC which accelerated methane emission[58, 60, 64]. Aside from the general increase in the nutritional content of the soil, other chemical parameters may also change under long term organic fertilization including pH, CEC, EC, and C:N[60, 64].

Long term fertilization not only modifies soil physicochemical properties but may also influence microbial population, community structure, and diversity (Table 1). These in turn change the potential functional attributes found in the paddy soils including enzyme activities and biogeochemical processes such as carbon mineralization, decomposition, methanogenesis, and methane oxidation. In general, the effects of fertilization resulted in changes in the microbial communities and related biological attributes of paddy soils which may stabilize under long term fertilization management schemes. The most usual change observed is in the abundance of the population measured directly or through molecular markers most commonly the 16S rRNA gene. On the other hand, primers for functional genes were also developed to assess gene abundance and indirectly, the abundance of microorganisms related to them[65-69]. Long term organic fertilization or in combination with inorganic fertilizers generally causes changes in community dynamics. In paddy fields, the abundance of cultivable microorganisms has generally increased significantly[10, 70]. This increase in the general population of bacteria was also observed in the 16S rRNA gene universal markers[71]. In terms of specific communities of microorganisms related to the methane cycle, the methanogens or the *mcrA* gene abundance generally increased under organic fertilization[60, 72, 73]. The abundance of *pmoA* genes or methanotrophic communities generally increased under compost fertilization or in combination with NPK[58, 72]. However, the effect of compost fertilization especially in combination with different nitrogen fertilizers could have varying effects on specific communities of methanotrophic bacteria. These differences created varying results across studies even in similar soil types or environmental conditions[4]. However, patterns could still be seen especially when looking at more specific groups of methanotrophs. The changes in community abundance, structure, and di-

versity could also influence the functionality of the soils. Islam et al.[74] showed that substrate evenness, community level functional diversity, and soil enzyme activities increased under long term compost fertilization. Soil enzyme activities, as well as microbial populations, also increased under long term farmyard fertilization[10]. In some cases, predicted functional activities in compost fertilization treatment were deduced to significantly contain higher functional genes related to plant growth promotion, development, and decomposition[71].

Microbial Ecology of Methanogens and Methanotrophs in Paddy Fields: Phylogeny, Diversity, and Ecological Niches

Culture-independent analyses of archaeal and bacterial genes involved in methane emission and consumption allow robust studies of diverse yet specific microbial communities[65-69] in rice paddies. The difficulty of isolating methanogens resulted in the development of primers amplifying the *mcrA* gene that codes for the α-subunit of the methyl coenzyme M reductase. It catalyzes the final step in the production of methane and is conserved among all methanogens. The particulate methane monooxygenase is an important enzyme for the conversion of methane to methanol and could be detected by primers designed for *pmoA* gene amplification[66]. Methanol dehydrogenase is also an important enzyme found in methylotrophic bacteria that catalyzes the conversion of methanol to formaldehyde. Primers designed to amplify the *mxaF* gene that codes for methanol dehydrogenase allow the detection of diverse methylotrophic communities[65, 67]. Microorganisms involved in methanogenesis and methanotrophy in paddy fields under different fertilization are presented below(Table 2).

Methanogenesis is modulated by the enzyme methyl-CoM reductase, which is coded by the *mcrA* gene, a highly conserved gene found in all methanogens [76]. In addition, methanotrophy through the enzyme methane monooxygenase is coded by the *pmoA* gene, while methylotrophy through the enzyme methanol dehydrogenase is coded by the *mxaF* gene[77]. All methanogens belong to the domain Archaea[2]. A summary of the most dominant groups of methanogens in paddy fields was presented by Yuan et al.[37]. The most dominant families are represented by *Methanobacteriaceae*, *Methanocellaceae*, *Methanomicrobiaceae*,

Table 2. Microbial ecology of methanogens and methanotrophs in paddy soils: phylogeny, diversity, and ecological niches

Methanogens and Methanotrophs	Notes on ecology	Citation
Type I: *Methylococcaceae, Methylomicrobium album, Methylobacter,* Type II: *Methylocystis, Methylosinus*	Urea (200 μg N/g.d.w.s. and above) inhibit CH_4 oxidation; ammonium sulfate (200 μg N/g.d.w.s) inhibited CH_4 oxidation activity. Type I increased abundance with N fertilizers, type II MOB in the native soil.	[80]
Type I: *Methylococcus*; Type II: *Methylosinus; Methylocystis*	The number of type I MOB increased relative to type II MOB upon fertilization. The dominance was most pronounced in unplanted and unfertilized samples where the type II biomarker was 7 times more abundant than type I.	[78]
Alphaproteobacteria MOB unified in *Methylocystaceae, Beijerinckiaceae.* Type II: *Methylocystis, Methylosinus. Methylocella; Methyloferula;*	Type I methanotrophs use the ribulose monophosphate pathway for assimilation of carbon into cells. Type II uses the serine pathway. Type I MOB were thought to be obligate 1-C user, but some are shown to be facultative methanotrophs which can also use acetate.	[83]
Type I: *Methylobacter;* Type II: *Methylocystis, Methylosinus*	High methane stimulated type I and type II. There was shift in bacterial community between methane incubated soils and without methane, but *pmoA* diversity is much lower. However, populations of methanotrophs seemed to persist and still may be active in anoxic microniches in drained soils.	[67]
Methanogen: *Methanosaeta harundinacea* (acetoclastic) was discovered in manure-applied treatments. *Methylosinus* (type II) and *Methylocaldum* (type I) were the dominant T-RFs. The relative abundance of type I methanotrophs tended to increase, while the abundance of type II decreased in the M and NPKM treatments.	Chemical or organic N input stimulated CH_4 emissions mainly through improving soil C substrate and methanogenic activities. Abundance of *mcrA* and *pmoA* are mainly regulated by water irrigation regime. The abundance of *mcrA* and *pmoA* had trade-off relationship over the rice growing season. N fertilized treatment enhanced CH_4 emission through increased *mcrA* abundance rather than reduced *pmoA*-dominated methanotrophic CH_4 oxidation. N fertilization showed no effect on *pmoA* abundance. Methane fluxes were positively correlated with *mcrA* gene copy number and the ratio of *mcrA*/*pmoA*, while negatively correlated to *pmoA* gene copy numbers.	[73]
Type I: *Methylobacter, Methylocaldum, Methylococcus, Methylomicrobium, Methylomonas, Methylosphaera, Methylosarcina;* Type II: *Methylocapsa, Methylocella, Methylocystis, Methylosinus*	Type I methanotrophs active in forest soils (*Methylomicrobium / Methylosarcina* related) differed from the active species in rice field soils (*Methylobacter, Methylomonas* related). Growth rates and methane incorporation were generally stimulated in type I MOB, but inhibited in type II.	[14]
Methanotrophs: *Methylocystis, Methylosinus, Methylobacter, Methylomicrobium, Methylomonas, Methylococcus, Methylocaldum,*	Populations on roots were dominated by type I methanotrophs, whereas populations in the rhizosphere soils were dominated by type II methanotrophs, irrespective of growth stages and fertilizer treatment. Type I predominate in both PK and UPK and in the rhizospheric soils. Type II were relatively more dominant under unfavorable conditions such as APK treatment.	[79]
Methanogens: *Methanobacteriaceae, Methanocellaceae, Methanomicrobiaceae, Methanosaetaceae, Methanosarcinaceae; Methanobacterium, Methanobrevibacter, Methanocella, Methanoculleus, Methanoregula, Methanosaeta, Methanosarcina, Methanothrix*	In different rice stages, *mcrA* abundance fluctuated. Both *mcrA* and *pmoA* increased abundance at the beginning of tillering stage. The *mcrA* gene increased again at the end of heading stage while *pmoA* increased at the filling stage. The *mcrA* and *pmoA* abundance are significantly and positively correlated. Methanotroph: The *pmoA* abundance varied significantly between different treatments and different plant stages.	[37]
Methanogen: Methanomicrobiales; Methanotroph *Methylocaldum* and *Methylococcus capsulatus; Methylomarinovum caldicuralii.*	Manure application plus NPK stimulated CH_4 production significantly by increasing methanogenic abundance and changing the composition of methanogen communities. Pig manure significantly changed the *pmoA* profiles.	[60]
Type I: *Methylocaldum, Methylococcacea, Methylosarcina, Methylomicrobium;* Type II: *Methylocystis*	Long term flooded paddy fields fertilized with human/animal feces with NPK; Type I is enriched in the surface layers while type II in the deeper layers of paddy fields.	[81]
Type I: *Methylobacter, Methylomicrobium, Methylomonas, Methylocaldum;* Type II: *Methylocystis, Methylosinus*	Their qPCR data indicated higher abundance of type II methanotrophs indicating dominance, however, their DGGE and cloning data showed type I methanotrophs to be more common especially in the NPK+Com treatment. Their data showed different responses of methanotrophs to fertilizer treatment at the community level.	[58]

Methanosaetaceae, and *Methanosarcinaceae.* In addition, the most dominant groups of methanogens at the genus level include *Methanobacterium, Methanobrevibacter, Methanocella, Methanoculleus, Methanoregula,* *Methanosaeta, Methanosarcina,* and *Methanothrix.*

The methanotrophic communities usually detected in paddy fields are grouped into type I and type II MOB. They come from phylogenetically different classes

under Proteobacteria and show different biochemical characteristics. Type I belongs to the Gammaproteobacteria employing the ribulose monophosphate pathway for carbon assimilation, while type II belongs to the Alphaproteobacteria and assimilates carbon through the serine pathway[4]. Type I MOB generally observed in rice paddies include *Methylobacter, Methylocaldum, Methylococcus, Methylomicrobium, Methylomonas, Methylosphaera,* and *Methylosarcina*[14, 58, 60, 67, 73, 78-81]. Type II MOB generally observed in rice paddies belong to the genus *Methylocapsa, Methylocella, Methylocystis,* and *Methylosinus*[14, 58, 73, 78-82]. Aside from the phylogenetic and biochemical differences of type I and type II MOB, it seems that there are some general deductions on their responses and ecological microniches in paddy fields under long term organic. Under long term fertilization, type I MOB was generally stimulated while type II was generally inhibited or with a slower response[14, 58, 78]. In flooded conditions with NPK+manure, type I was enriched on the surface layers while type II was more dominant in the deeper layers[81]. MOB populations on roots were dominated by type I methanotrophs, whereas populations in the rhizosphere soils were dominated by type II, irrespective of growth stages and fertilizer treatment. Type I predominated in both phosphorus-potassium treatment (PK), UreaPK, and the rhizosphere soils while Type II was relatively more dominant under unfavorable conditions such as AmmoniaPK treatment[79]. Type I MOB displayed an increased abundance in soil amended with fertilizers, whereas type II MOB dominated the native soil[80]. In general, type I MOB responds more positively through increased dominance under fertilization while type II MOB responds less, neutral, or inhibited under fertilization.

Methanogenesis and Methane Oxidation and Factors Affecting the Processes in Paddy Fields

Along with potential alteration of the soil physicochemical properties of paddy fields, complex microbial responses were also observed due to different fertilization. These responses are categorized as either stimulation, inhibition, or no response[84]. The changes in physicochemical and biological components of the paddy soils concurrently affect soil biochemistry and function. Methanogenesis and methane oxidation, are

influenced by multiple factors which are potentially facilitated when paddy soils undergo long term organic fertilization. However, in general, the most important variables that control methane production include soil type, rice variety, temperature, soil redox potential (E_h), water management, and fertilization with organic carbon and nitrogen[4]. The factors affecting methane oxidation include concentrations of acetate, CH_4, O_2, type of fertilization, the availability of nitrogen and copper, pH, and temperature[4]. Since methane emission is a balance between production and consumption, factors that affect methane diffusion, microbial activities in general, methanogenesis, and methane monooxygenase activity all integrate into the equation [2]. Effects of long term organic fertilization on methanogenesis, methane oxidation, and related processes are presented in Table 3.

Long term compost fertilization in paddy field agroecosystems is a critical scenario in relation to methane source, methane sink, methane emission, and global warming potential. In most studies, methane emission seemed to increase as the amount of organic or compost increased especially observed in treatments with low, moderate, and high manure[59, 60]. This was also observed when organic or compost is in combination with any other chemical fertilization[10, 37, 59, 64, 75]. All of these studies unify to present that organic fertilization, in any form, generally enhances methane emission in paddy fields. However, differences in the degree of methane emission can be observed in different types of organic fertilization, with a generalization that manure usually enhances a greater methane flux than crop residues, with the same generalization for fresh manure or crop residue against composted fertilizers[59, 87]. In a wider perspective, different types of N can also impact methane production, albeit, with different effects. Complete chemical fertilizer in combination with compost generally has positive effects on methanogen abundance or the *mcrA* gene abundance, and in turn, methanogenesis.[37, 59, 64]. Other forms of N such as urea, ammonium, or nitrate, and their concentration, when used as chemical fertilizers may stimulate or inhibit methanogenesis[6, 7, 12, 78].

Another central feature of methanogenesis is its usual correlation with the abundance of methanogens, *mcrA* gene, or the transcriptional activities of methanogens[10, 12, 60, 73, 88]. In extension, the ratio between the abundance of *mcrA* and *pmoA* (*mcrA*/

Table 3. Methanogenesis, methane oxidation and factors affecting the processes in paddy fields

Factors affecting methanogenesis (methane production and emission) and methane consumption (methanotrophy and methane oxidation)	Notes on the factors	Citation
Methanogenesis: NPKM enhances GHG emissions. Methane flux is dependent on fluorescein diacetate, readily mineralizable carbon and methanogen abundance.	CH_4, CO_2-C, and N_2O-N fluxes were lowest in fallow period; CH_4 flux highest in wet season. CO_2 and N_2O showed fluctuations in fluxes.	[10]
Methane oxidation: The non-inhibition by ammonium may be by the high methane availability in paddies that counterbalances competitive inhibition. Both type I and II MOB need ammonium to grow in the rice rhizosphere. Type I MOB abundance increased to a greater extent relative to type II MOB upon fertilization. The dominance was most pronounced in unplanted and unfertilized samples where type II biomarker was 7X more abundant than type I.	Ammonium-based fertilization does not necessarily inhibit methane consumption. Fertilization resulted in 9X growth of type I methane oxidizers in microcosms fertilized with 400 kg N ha^{-1} of urea or $(NH_4)_2HPO_4$. The type-II-specific marker increased only 2–3X after fertilization.	[78]
Methanogenesis: inhibited by stimulating competing nitrate-reducing bacteria, which lower organic carbon availability on one hand but which can also produce toxic compounds (NO_2, NO, N_2O). Stimulation of plant growth by fertilizers can enhance methane production by increased organic carbon availability for fermenting microbes. Direct effect of plants includes root exudates and indirect effect through oxygen excretion and organic acid secretions. Methane oxidation: Effect of N on methane oxidation include type, dose and history shown on type I and type II MOB responses. Nitrogen can indirectly affect methane oxidation by enhancing competing microbes especially nitrifiers, AOB/AOA. Nitrogen can also indirectly influence methane oxidation by affecting plants (diversity, biomass, traits).	Fertilization of paddy fields resulted to contradictory results among studies without mechanistic explanations. These contrasting results could be attributed to the community composition, diversity and nature of the microbes involved in methane cycling.	[11]
Methane oxidation: High affinity methane oxidation activity was quickly induced during the low-affinity oxidation of high-concentration methane. The induction occurred only after the rapid growth of methanotrophs catalyzed by known methanotrophs	High levels of methane induced methane oxidation. Periodically draining of paddy fields could induce atmospheric methane uptake in paddy fields.	[85]
Methanogenesis: When grown on rice field soil, the methanogenic community of the different rice cultivars was always dominated by RC-1 methanogens. In contrast, roots were colonized by *Methanomicrobiales* when grown on riverbank soil where RC-1 methanogens were absent, resulting in lower CH_4 production and CH_4 emission rates.	Physicochemically similar soil type but different microbial communities drive and affect methanogenesis. Differences in initial community had major influence in rice colonization and methane cycling.	[86]
Methanogenesis: Soil available K, *mcrA* gene abundance, and available P were key factors for methane emission in reduced N+no-P and sulfur-coated urea fertilization. Soil available K, available P, SOC are key factors for methane emissions in NPK+organic and organic fertilization. Methane oxidation: The *pmoA* gene abundance seems to be the same though all the treatments and does not mainly influence methane emission.	The best strategy they recommended was to use the sulfur-coated urea combined with uncoated urea since it maintained rice yield and reduce methane emission.	[12]
Methanogenesis: Methane fluxes were positively correlated with *mcrA* gene copy number and the ratio of *mcrA*/*pmoA*, while negatively correlated to *pmoA* gene copy numbers. The *mcrA* gene abundance is positively correlated with CH_4 flux, DOC, water layer, ammonium-nitrogen and soil temperature. Methane oxidation: The *pmoA* gene abundance is negatively correlated with DOC and water layer.	Chemical or organic N input stimulated CH_4 emissions through improving soil C substrate and methanogenic activities. Abundance of *mcrA* and *pmoA* are mainly regulated by water irrigation. The abundance of *mcrA* and *pmoA* had trade-off relationship over the rice growing season. N fertilized treatment enhanced the source strength of CH_4 emission through increased *mcrA* abundance rather than reduced *pmoA* abundance. N fertilization showed no effect on *pmoA* abundance.	[73]
Methanogenesis: N addition increased CH_4 emission by 97% and SOC by an average of 2%. Methane oxidation: N addition reduced CH_4 methane uptake by 38 %. However, at low N-application levels (<100 kg N ha^{-1} yr^{-1}), methane consumption was stimulated while at higher levels, inhibitions were observed.	Overall conclusion was that N-enrichment of ecosystems in general would lead to enhanced methane emission because of lowering of consumption and increase of production.	[6]
Methane oxidation: Fertilizer application stimulated type I and type II was inhibited. Type I methanotrophs active in forest soils (*Methylomicrobium*/*Methylosarcina* related) differed from the active species in rice field soils (*Methylobacter*, *Methylomonas* related).	Impact of environmental perturbations on the methane fluxes is poorly understood and results with fertilizer studies are contradictory which could be due to the composition and diversity of microbial communities.	[14]

Factors affecting methanogenesis (methane production and emission) and methane consumption (methanotrophy and methane oxidation)	Notes on the factors	Citation
Methane oxidation rates in PK and UreaPK treatments were similar during most of the rice-growing season, revealing no effect of urea. Ammonium sulfate strongly suppressed methane oxidation. Populations on roots were dominated by type I; rhizosphere soils were dominated by type II, irrespective of growth stages and fertilizer treatment. Type I predominate in both PK and UPK and in the rhizospheric soils. Type II were relatively more dominant under unfavorable conditions such as APK treatment.	Different fertilizers had different effects on methanotrophic communities, but it was stronger in roots than in the rhizosphere soils.	[79]
Methanogenesis: The responses of CH_4 emissions to N application in rice paddies were highly variable and overall, no effects were found. CH_4 emissions were stimulated at low N application rates (<100 kg N ha^{-1}) but inhibited at high N rates (>200 kg N ha^{-1}) as compared to no N fertilizer (control). Methane oxidation: The critical factors that affected CH_4 uptake and N_2O emission were N fertilizer application rate and the controls of CH_4 uptake and N_2O emission.	N addition overall increased GWP of CH_4 and N_2O emissions by 78 %. Response of CH_4 emission to N input might depend on the CH_4 concentration in rice paddy.	[7]
Methanogenesis: High manure plus chemical fertilizer had the highest CH_4 emissions associated with soil redox and soil temperature.	GWP, CH_4, and N_2O were ranked from high manure+NPK> low manure+NPK> rice residue + NPK > NPK > no fertilizer.	[59]
Methanogenesis: CH_4 emitted most in organic treatment, followed by mixed treatment, chemical and no fertilization. Soil nutrients or fertility (humid acid, carbon, nitrogen, phosphorus, potassium and C:N) may perhaps speed up CH_4 emissions. CH_4 fluxes and emissions from organic fertilizer field significantly increase, in comparison to no-fertilizer or chemical counterpart. The production of CH_4 was higher in booting as compared to other stages. Drainage could alleviate methane production.	Fertilizer affected emissions of CH_4, N_2O and CO_2. CH_4 emitted most in organic treatment, followed by mixed, chemical and no fertilization. Applying substantial organic fertilizer at once might accelerate sudden and huge release of N_2O. Despite the inconsistencies among different years observed, the trend is that organic fertilizer made the biggest amount of contribution to GWP.	[64]
Methanogenesis: Methane fluxes increased from tillering to jointing and at filling. Organic > mixed (NPKC) > Urea affected methane emission. Soil K, oxalate, acetate and succinate significantly affect methanogens. Methane emission was significantly related to $mcrA/pmoA$. Methane oxidation: The $pmoA$ abundance correlated significantly with $mcrA$ abundance. Correlation analysis showed it has significant and negative correlation with methane flux, methane emission, and $mcrA/pmoA$.	Organic fertilizer increased the relative abundance of *Methanosaeta* and decreased the relative abundance of hydrogenotrophic *Methanocella*.	[37]
Methanogenesis: The abundance of methanogens ($mcrA$) increased significantly especially in higher manure content, while the abundance of methanotrophs ($pmoA$) is the same in all treatments. Methane production potential were positively correlated with the $mcrA$ gene abundance. Long term manure application can affect both the abundance and composition of methanogens, and thus, enhance methane production and is largely dependent on soil nutritional status. Methane oxidation: The abundance of methanotrophs ($pmoA$) is the same in all treatments.	The community structures of $mcrA$ and $pmoA$ were distinctly altered by continuous manure application, and their variations were closely associated with fertilizer induced changes in dissolved organic C, total P, available P and available K in the soil.	[60]
Methane production was 3x higher under manure+chemical fertilizer and 27x higher in chemical alone compared to unfertilized paddy soils. Mineralization favors methane production under submerged conditions.	Methane and carbon dioxide production varied according to different particle size where labile organic C is more associated to larger particle size.	[75]

NPK – Inorganic fertilizer containing N, P, and K; NPKM – NPK plus manure; NPKC – NPK plus compost; GHG – Greenhouse gas; MOB – methane oxidizing bacteria; GWP – Global warming potential; SOC – soil organic carbon.

$pmoA$) also generally positively correlated with methanogenesis[37, 73]. Other prominent features of the paddy field agroecosystems related to methane emission are the effects of submergence and drainage and rice-stage-related fluxes in methane emissions. Methanogenesis by methanogenic archaea mainly occurs under anoxic conditions favored during submergence and flooding, or even in water-saturated soils[2, 4]. Paddy fields are flooded throughout most of the rice-growing season. Methane emission was promoted when the paddy fields were flooded and inhibited when drained, similar to the effects of wet and dry

seasons[10, 73, 89]. Methane flux was also observed in the different rice growing stages. Production of methane was higher during the booting stage[64] and tillering to jointing and at the filling stage[37].

One of the major drivers of methanogenesis, exemplified by long term organic or compost fertilization, is the direct or indirect increase in the substrates necessary for the production of methane. Organic fertilization directly provides the carbon compounds or indirectly enhances plant growth that will eventually release carbon in the paddy soils. The increase in SOC, DOC, labile and soluble C, readily mineralizable C, and other forms of carbon are major factors enhancing methane production[10-12, 60, 73, 75].

Other factors driving methanogenesis in the paddy field provide interesting areas of research. Perhaps one of the most complicated, yet still understudied, are the responses of different groups of methanogens and how these affect methane emission on a global scale. Interactions of methanogens with other competing or synergistic microbial communities add to the complications. A glimpse of such complexity has been shown where interacting microorganisms were crucial factors to methane emission[11, 86, 87].

Under long term organic fertilization, some generalizations could be drawn in relation to methane consumption. Overall, the high concentration of methane in paddy field soils generally enhanced the population, $pmoA$ gene abundance, or the activity of MOB [37, 67, 78, 85]. Aerobic environmental condition is also generally essential for methane oxidation. Flooding enhanced methanogenesis while drainage promoted methane oxidation[10, 64, 73, 85]. The presence of oxygen explained the differences observed between the root rhizosphere and the bulk paddy soils[78, 81]. When organic or compost fertilization were in combination with different inorganic nitrogen fertilizers, there were differences in the results owing to the responses of the specific groups of MOB to different forms of nitrogen[11, 78, 79]. High and low levels of nitrogen, as well as the rate of application, can also be an important factor in methane consumption[6, 7, 80].

To understand methane consumption through methane oxidation, we have to greatly consider the different responses of Type I and II MOB. Type I generally responded well to fertilization[78]. For organic fertilization, Type I tended to increase while type II decreased[14, 58, 73]. Type I predominated in normal conditions in paddy soils while type II is generally dominant in unfavorable conditions such as APK treatment[79]. As a generalization, type I MOB seems to flourish under fertilization, especially surrounding the roots and the rhizosphere while type II MOB seems to favor unfertilized bulk paddy fields.

Ultimately, changes in soil physicochemical and microbial components of the rice agroecosystems also lead to alteration of the microbial functions[10, 90] which could affect global-scale processes such as greenhouse gas methane emission, carbon, and nitrogen cycling. Different fertilization schemes should be assessed in order to optimize potential yield while maintaining soil health and function and mitigating environmental issues such as greenhouse gas emissions especially in long term and on the global scale.

Mitigating Methane Emission in Paddy Field Agroecosystems under Long Term Organic Fertilization

Paddy field, with rice as a major crop, is a distinct agroecosystem as it mainly needs soil submergence for at least part of the growing season. This leads to potential enhanced methane emissions. However, rice is a major commodity that is consumed by many people around the world, and rice production is in parallel with the increasing world population. In addition, long term compost fertilization or in combination with chemical fertilizers try to mitigate the unsustainable rice farming system but are also faced with potential issues including enhanced methane emission. As methane emission is a balance between methanogenesis and methane consumption, factors and processes that affect these two interacting processes would also affect the net methane emission and could be exploited for mitigating steps (Fig. 2).

Fertilization, especially forms of nitrogen, has been one of the most studied areas concerning methane emission. However, conflicting results even in paddy fields with the same physicochemical soil occur across studies [78]. For long term organic fertilization, the different types, doses, and rates are crucial factors and need to be investigated in order to optimize rice production while limiting environmental problems. Across studies, the addition of organic fertilizers has always increased methane emission, especially in higher dosages[59, 64]. Thus, the input of the optimized dosage of the required organic fertilizer is essential. Organic fertilization should also concentrate on composted ma-
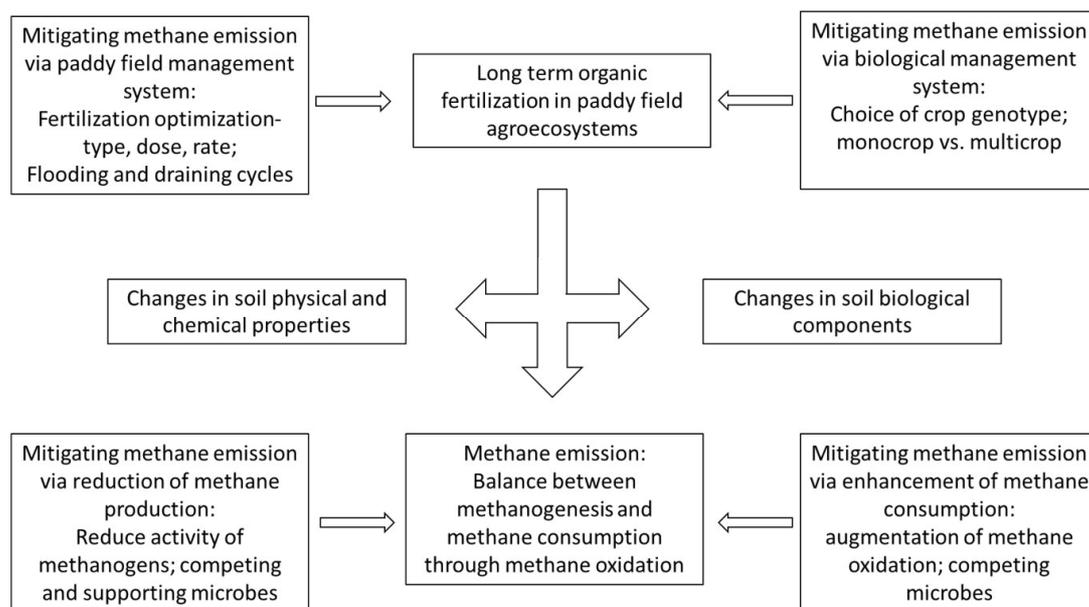
Fig. 2. Potential and hypothetical mitigation schemes of methane emission from paddy fields in combination with long term organic fertilization.

terial rather than fresh materials as enhancement of methane emission is greater in uncomposted materials [87]. Combination of organic and chemical fertilizers should also be optimized as some studies showed synergistic enhancement of methane emission with NPK and organic/compost fertilization[6, 12, 59, 75] or reduction of methane emission[37, 64].

Water regime is also one of the most important factors that could enhance or reduce methane emission. Flooding generally enhances methane emission as it provides an ideal anoxic condition especially in the deeper layers of paddy soils. Draining, on the other hand, oxygenates soils and allows methane oxidation [64, 73]. Therefore, repeated or controlled paddy field drainage without affecting rice yield should be applied. Activation of high-affinity methane oxidation has also been observed in drained paddies enhancing them as methane sinks[85]. However, nitrous oxide emission when paddy fields are drained should also be considered.

Crops used in paddy fields also directly and indirectly affect methane emission through enhancement of methane production or methane oxidation. Monocrop systems using rice as the only crop or in alternation with other crops in a multicrop system could affect methane emission, with rice monocrop showing a lower response to methane emission compared to different rice multicrop system[7]. The plant type (genotype,

cultivar, diversity, etc.) could directly affect methane emission through root exudations or when they are left in the paddy fields after harvest[11]. Rice plants also act as transport systems for methane through the aerenchyma system. The root and the rhizosphere are also the major sites of methane oxidation as the rice aerates the paddy soils[4]. Thus, rice varieties that provide maximum yield with minimal impact on methanogenesis could be used over other rice varieties.

Theoretically, anything that affects the activity of methanogens or methane oxidizing bacteria could also affect methane emission. Competing and supporting microbes, such as fermenting microorganisms for methanogens and competing nitrifiers for methane oxidation have also complicated the process but are equally important. On the microbial level, stress tolerance, substrate affinity, growth rate, diversity, temperature, pH, soil redox potential, presence of salts, and other interacting factors cumulatively interact to either enhance or reduce methane emission through methanogenesis and methane oxidation[11, 86, 87]. This is greatly observed in the different responses between type I and type II MOB which also influenced the overall methane emission process[14, 58, 67, 73, 78-81].

Conclusion and Future Perspective

This review mainly focused on the effects of long

term compost fertilization on the soil chemical properties and biotic components especially related to methane cycling in the paddy field agroecosystems. Organic fertilization alters soil physicochemical properties and biotic components of the soil potentially influencing the dynamics of methane cycling through the balance between methanogenesis and methane consumption. These processes are affected by multiple factors in paddy fields under organic fertilization which could be assessed and targeted to develop mitigating steps in the contribution of methane to global warming and climate change.

However, to fully comprehend methane emission, there are some other interacting variables and processes that need to be considered and an overall global study and consensus should be elucidated. For instance, there are many other types of organic matter amendments. Temporal fluxes related to rice growth responses and management practices should also be considered together with short-term perturbation and long-term estimation of their contributions to methane emission. Most of the studies on methane emission were also conducted during the rice/crop growing period but changes observed during the fallow period potentially dictate the responses and processes during the rice growing period.

Although paddy fields could be a major source of methane emission, it is also a major sink for methane consumption. Therefore, it is necessary to incorporate the trade-offs under short and long-term organic fertilization. For example, compost fertilization may increase methane emission, but beneficial effects such as enhanced soil fertility, soil productivity, and sustainability are equally important. Furthermore, long term fertilization trials could help us understand the effects of such management systems, assessing and balancing positive and negative impacts which help up design and implement better mitigating steps to reduce agricultural environmental impacts.

Note

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