

Chapter 3

Gaseous carbon emissions from rice and rice based cropping systems

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Rice paddies play an important role in the global budget of greenhouse gases (GHGs) *viz.* carbon dioxide (CO₂) and methane (CH₄), contributing to gaseous-C emissions to atmosphere (IPCC, 2007). Rice is flooded most of the times during its cultivation period. That's why many of the factors controlling gas exchange between rice paddies and atmosphere are unique and vary from other dryland agricultural practices. Net exchanges of gaseous-C (CO₂-C + CH₄-C) between rice paddies and atmosphere are regulated by various physico-biochemical processes. Methane and CO₂ budget in rice fields are both affected by structure and dynamics of anaerobic and/ or aerobic conditions in the soil, but specific impacts are often diverging for both gases.

Among the different GHGs, CO₂ is the largest contributor to the anthropogenic greenhouse effect, accounting 29 × 10¹² t CO₂ yr⁻¹, representing approximately 4% of global C fluxes involving the atmosphere. Industrial activity is the major source of atmospheric CO₂ including minor contribution from agriculture in the form of biomass burning associated with land-use change. On the contrary, CH₄ with an annual global budget of 5 × 10⁹ t CH₄ yr⁻¹ and N₂O with an annual global budget of 3 × 10⁹ t N₂O yr⁻¹, exert major influence on the global climate. In order to assess the total impact of the different GHGs, it is important to remember that each gas has a biological component and soils contribute to the budgets of many atmospheric trace gases by acting as either sources or sinks. The CO₂ release into the atmosphere is both chemically and biologically mediated processes. Conversely, both CH₄ production and its consumption are biologically mediated.

Rice, the most important cereal crop in India, is preferentially grown under submerged conditions due to better yields than in upland soil and positive response to modern agricultural practices. The dynamics of C and N in the submerged rice soil is different from that of aerobic soils because submerged rice soils are maintained at lower redox potentials. Predominantly anaerobic flooded soils promote the production of CH₄, a major end product of anaerobic decomposition of organic matter (native or added). Intermittent flooding and drainage, while retarding CH₄ emission promote the emission of CO₂, another important GHG from soils, especially when heavily fertilized with N fertilizers.

The existence of anaerobic soil due to overlying floodwater and the change in micrometeorological environment upon flooding influence photosynthesis, respiration as well as root activity of rice plants. Algae present in the floodwater may also affect CO₂ exchange between rice paddies and the atmosphere. During the daytime plant photosynthesis leads to uptake of CO₂ from the atmosphere while respiration at night leads to an efflux of CO₂ to the atmosphere. Net fluxes of soil-borne CO₂ in rice fields are associated with changes in agricultural management, e.g., tillage,

irrigation pattern, etc. However, most rice production systems indirectly entail emission of CO₂ from fossil fuel consumption due to farm operation and fertilizer production.

Although the CO₂ budget is almost in balance, CO₂ fluxes between agricultural lands and the atmosphere are large in both directions (120 Pg C yr⁻¹) (Denman et al., 2007). Part of the CO₂ efflux derives from decomposition of soil organic matter. Carbon storage in soils has been estimated to be 1500 Pg C, which is double that in the atmosphere (730 Pg C) (Prentice et al., 2001). Thus, to sustain soil carbon storage, it is important to reduce CO₂ emission from agricultural soils.

On the other hand paddy fields are one of the largest sources in the global budget of CH₄. The estimate of global CH₄ emissions from rice paddies is around 60 Tg year⁻¹, but with uncertainty ranging from 20 to 100 Tg year⁻¹ (IPCC, 1995). Actually CH₄ is released to the atmosphere by ebullition, diffusion across floodwater-air interface and by transport through aerenchyma. In undisturbed paddy fields upto 90% of CH₄ emission occurs through aerenchyma (Minami & Neue, 1994). Flooded soils planted to rice are conducive to the production and emission of CH₄ due to the presence of methanogenic bacteria that utilize readily decomposable organic compounds under anaerobic soil condition. Both CH₄ production and emission from flooded rice soils are strongly influenced by several soil processes including changes in soil redox status and pH, dynamics of substrate and nutrient availability and textural stratification (Bouwman, 1990). In addition, common cultivation practices such as application of agrochemicals also affect CH₄ efflux from flooded rice soils (Neue et al., 1997). While organic matter amendment generally increases CH₄ emission (Neue et al., 1997), CH₄ efflux is also strongly influenced by the type, method and rate of application of chemical fertilizer. With the intensification of rice cultivation to meet the needs for rising population, CH₄ emission from flooded rice paddy ecosystem is likely to increase.

A range of soil, climatic variables and agricultural management practices influence the production and emission of gaseous carbon from the rice and rice-based production systems. Among these soil temperature, soil moisture, pH, soil organic matter, organic manure and fertilizer application, rainfall, humidity, air temperature, solar radiation, high microbial activity and biomass turnover rate, water management, cultivar or variety, tillage practice, etc. are important factors. As there is considerable uncertainty regarding the magnitude of net fluxes of gaseous-C emissions from rice paddies, field studies to monitor and measure net fluxes and to understand the controlling factors behind this should be properly designed for quantification and budgeting of net carbon fluxes from rice-based production systems during cultivation and fallow periods.

Net ecosystem exchange

The most important processes affecting carbon balance of a terrestrial ecosystem are photosynthesis of above-ground vegetation and soil respiration. The net ecosystem exchange (NEE) of CO₂ between the biosphere and the atmosphere is the balance between fluxes associated with photosynthetic assimilation by the foliage (Gross ecosystem production, GEP) and respiratory effluxes from autotrophs (roots) and heterotrophs (microbial and soil fauna). The relationship between production and decomposition determines whether a system is a sink or a source of atmospheric CO₂. An accurate assessment of soil and plant respiration is crucial for understanding and predicting ecosystem responses to anthropogenic perturbations *viz.* climate change, pollution and agriculture. However, the seasonal variation in ecosystem CO₂ exchange with the atmosphere occurs in response to meteorological conditions and physiological activities of rice crop.

Soil respiration is the major pathway of C efflux from terrestrial systems and represents an integrated reporter of ecosystem functioning (Mills et al., 2011). Understanding controls on soil respiration is critical because relatively small changes in respiration rates may radically alter atmospheric concentrations of CO₂ and also soil C sequestration. Reducing CO₂ emissions from

soils may help to increase sequestration of atmospheric CO₂ in soil. Soil respiration includes root and microbial respiration, and bulk turnover of organic matter (OM) which all contributes to the release of CO₂ (Hill et al., 2004). Accurate quantification of gaseous CO₂-C fluxes from soil remains the main factor for furthering the understanding of soil C flow and ecosystem resilience (Davidson et al., 2002). Soil respiration seems to be one of the primary fluxes of C between soils and the atmosphere, with a global release of 75 Pg C year⁻¹. Soil and plant respiration is generally measured by the soil and or canopy chamber, enclosing the soil and or canopy for specified time and then measuring the liberated CO₂ due to respiration with the help of infrared gas analyzer.

Soil CO₂ emission integrates all the components of soil CO₂ production, rhizospheric respiration as well as soil microbial respiration in rice and rice-based cropping systems. Variations in soil respiration i.e., soil CO₂ fluxes are influenced by agronomic management practices (*viz.* organic or inorganic fertilization). Agricultural operations affect soil CO₂ flux by changing the soil environment like soil pH, soil temperature, soil moisture, soil aeration, C/N ratio of substances, etc. These may have significant impact on soil microbial activities and the decomposition processes instrumental for transforming plant-derived C to soil organic matter and CO₂. The applications of chemical fertilizers alone or in combination with organic manures, soil and water management in rice paddies are crucial for predicting future trend of CO₂ emissions from rice paddy ecologies and for taking steps to mitigate climate changes due to agricultural practices.

Net ecosystem carbon dioxide exchange in rice field

In China, eddy covariance (EC) technique-based estimations revealed that the soil respiration rates at night times during the fallow periods were 52-398 mg m⁻² h⁻¹. Annual average soil respiration rates and total soil respiration of paddy soil in the subtropical region of China were estimated to be 178.5-259.9 mg m⁻² h⁻¹ and 1.56-2.28 kg m⁻² yr⁻¹, respectively (XiuE et al., 2007).

Diurnal variation of CO₂ fluxes during rice maturity period was noticed in Taiwan by eddy covariance measurements (Tseng et al., 2010). Fluxes of CO₂ were always positive during night hours, whereas during the daytime the flux was found to be negative. Thus the rice paddy ecosystem behaved as a CO₂ source during night hours and a CO₂ sink during the day. As a matter of fact the rice paddy ecosystem behaved as a potential CO₂ source with a daily average flux of 0.71 μmol CO₂ m⁻² s⁻¹.

At IRRI, Philippines, NEE was found to be negative during the daytime and positive during the night time for both flooded and aerobic rice fields. From active tillering to panicle initiation stage NEE was about -10 μmol CO₂ m⁻² s⁻¹ and it reached as low as -22 μmol CO₂ m⁻² s⁻¹ during heading to flowering stage in flooded rice fields. From tillering to ripening stage, the flooded rice fields behaved as net CO₂ sink on a daily basis and maximum uptake was noticed during heading to flowering stage with an average value of -5.98 g C m⁻² d⁻¹. Aerobic rice fields became net sink for CO₂ at reproductive stage and continued to behave as net CO₂ sink at harvest stage also with the mean value of -2.31 g C m⁻² d⁻¹. The total C budget integrated over the cropping period

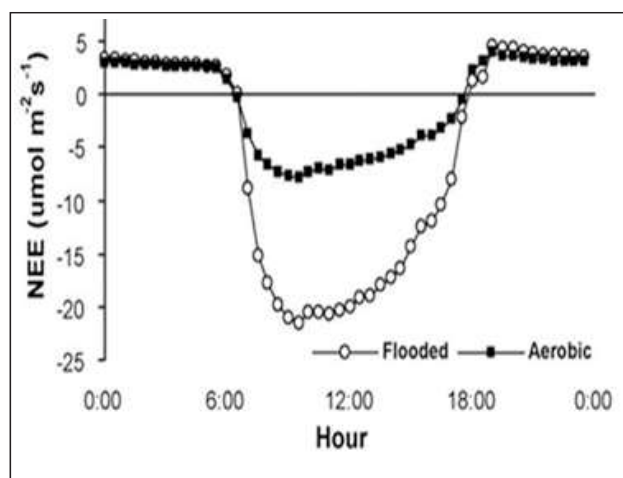


FIGURE 1. Diurnal variation of net ecosystem carbon dioxide exchange of aerobic and flooded rice field at heading stage at IRRI, Philippines

showed that in flooded rice fields NEE was about three times higher than that of aerobic rice fields NEE. The gross primary production (GPP) and ecosystem respiration (RE) values for flooded rice fields were 778 and 521 g C m⁻² and in case of aerobic rice fields the values of GPP and RE were 515 and 430 g C m⁻², respectively (Alberto et al., 2009).

Methane emissions from rice fields

Rice fields are considered to be an important anthropogenic source for CH₄ and contribute up to 20% or ~100 Tg CH₄ to the global budget on an annual basis (Houghton et al., 1996). With intensification of rice cultivation during the coming decades, CH₄ emission from this economically important but ecologically fragile ecosystem is anticipated to increase. Despite recent studies on identification of controlling variables (Neue et al., 1997), the uncertainty in the global CH₄ sources estimated for rice paddies are still very high (Houghton et al., 1996) due to large spatial differences. Such uncertainty in the sources estimated largely from different soil types as well as variations between crop management in space and time. Refinement in methodologies and more measurements incorporating site-specific practices are essential for an accurate assessment of the contribution of paddy ecosystem to global CH₄ budget. India produces annually 92.83 m t of rice on an area of 43.77 m ha (DOES, 2011). The rice growing areas of India can be broadly categorized into rainfed upland, rainfed lowland and irrigated medium land, representing about 15, 40 and 45% of total rice area of the country. In India, 48% of the country's rice area is irrigated while the rest is under rainfed situations. Flooded rice fields are the potent sources of CH₄ (Houghton et al., 1996) as well as can also act as sink for CH₄. The source and sink capacity entirely depends on field management practices. Methane predominantly escapes to the atmosphere

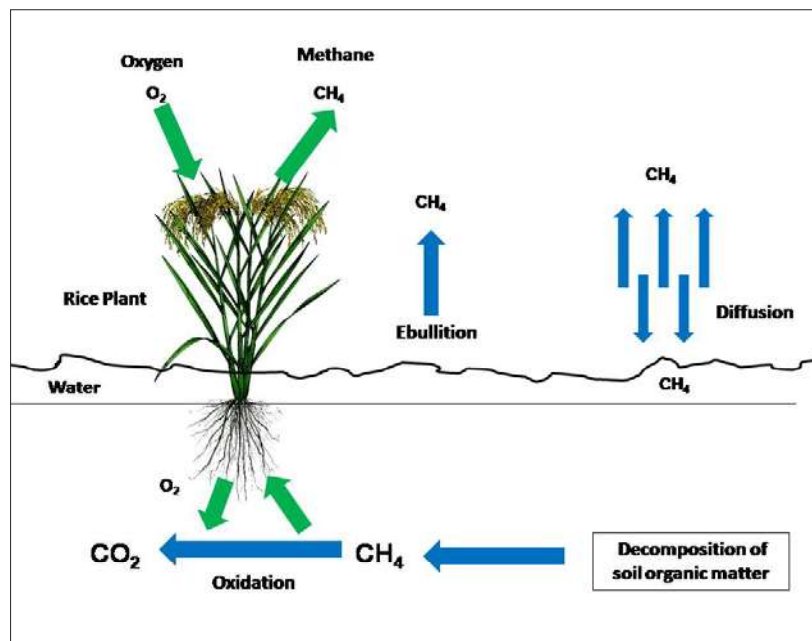


FIGURE 2. Methane emission from flooded rice field

through the aerenchyma of the rice plant (Fig. 2). The documented morphology of the aerenchyma allows the reconstruction of the vertical gas transfer including the speed-limiting passage from root to culm. Nutrient supply affects development of aerenchyma as well as root exudation and thus the budget of CH₄. Methane emission in rice fields is affected by the properties, structure and dynamics of the submerged soil. Its emission increases under continuous flooding in rice fields and it escapes to the atmosphere through the aerenchyma of the rice plant.

Rice ecosystems and methane emission

Cultivated rice, the major crop in tropical system is grown under flooded condition. In many rice-growing areas, wetlands may have at least one wet growing season, but may be dry, moist, or without water in other seasons. The accumulation and depletion of Fe and Mn, the redoximorphic features indicate the “aquic” soil conditions. A typical soil profile of a flooded rice soil has many horizons. The horizon, “Ofw” is well described as the layer of standing water that becomes the habitat of bacteria, phytoplankton, macrophytes, zooplankton, and aquatic invertebrates and vertebrates. The “Apox” horizon is the floodwater-soil interface while the “Apg” horizon is the reduced puddled layer. The “ApX” layer has increased bulk density, high mechanical strength and low permeability. The ‘B’ horizon depends highly on the water regime. Upon submergence, soils undergo characteristic physical, chemical and biological changes. Variations in the edaphic factors and hydrological conditions contribute more to the diverse nature of rice growing conditions.

Irrigated rice has by far the highest CH₄ source strength about 70-80% of all rice ecologies. It accounts for 97% of the CH₄ emission from rice fields in East Asia and for 60% of the CH₄ emitted from South and Southeast Asian rice fields, respectively. (Wassmann et al., 2000b). Rainfed rice ecologies contribute about 15% of CH₄ from the global rice area (Wassmann et al., 2000b). Wassmann et al. (2000a) reported that deepwater rice ecologies contribute about 10% of the global CH₄ from the rice source. The differences in crop calendars, season lengths, cultural practices, diverse cultivars and many other factors impede direct comparisons of CH₄ emissions from different rice ecologies. Though the irrigated rice is the largest source of CH₄, it also the most promising target for mitigating CH₄ emissions (Wassmann & Aulakh, 2000).

Mechanism of methane formation and transformation

The emission of CH₄ to environments from the field, whether terrestrial or aquatic, depend on a multitude of factors including the biological processes by which CH₄ is produced and consumed. The net emission from an agricultural system is the result of production (methanogenesis) and consumption (methanotrophy) and whether the net emission will be positive or negative, depends on the relative magnitudes of these processes. Though *Methanosarcina* and *Methanosaeta* are the smaller number in the ratio of methanogenic population, they account for two-thirds of CH₄ produced. However, the reaction provides little energy and the net result is low growth rate of acetotrophic methanogens. Using CH₃F, it has been clearly shown that about 70-77 % of the methanogenic population is H₂ and CO₂ utilizing methanogens and contributes only 25-30% of the CH₄ production. However, CH₄ production in rice fields depends on soil characteristics (organic carbon), rice varieties (especially root volume and exudation), cultural practices (fertilizer application, water management, pre-cultural practices) and methyloctrophy. It has been known that SO₄ and minerals like Mo, Fe, Mn and Ni play an important role in the methanogenic environments (Table 1).

TABLE 1. *Sequence of reduction reactions in submerged soil*

Element		After reduction	Redox potential (Eh)
O ₂	→	H ₂ O	
NO ₃ ⁻	→	N ₂ O	< 0.2 V
Mn ⁺⁴	→	Mn ⁺²	0.2 to 0.4 V
Fe ⁺³	→	Fe ⁺²	0.0 to -0.15 V
SO ₄ ⁻²	→	S ⁻²	< -0.15 V
CO ₂	→	CH ₄	< -0.2 V
H ⁺	→	H ₂	

Methanogenesis

Soils are the most important source in the atmospheric CH₄ budget, contributing about 60%. The active CH₄ emitting soils usually include all kinds of wetlands including flooded rice fields. In wetland soils, anoxic conditions establish in most of the soil because O₂ diffusion from the atmosphere is limiting. Mineralization of organic matter in such soils favoring the activities of fermenting and methanogenic bacteria produces CH₄ and CO₂ (Eq. 1).



The conversion of complex organic matter to CH₄ requires a microbial food web (consortium) composed of several interacting metabolic groups of anaerobic (facultative and strict) microorganisms:

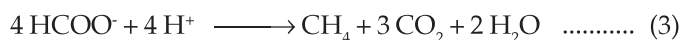
- (a) Hydrolysis of biological polymers into monomers (glycosides, fatty acids, amino acids) by an hydrolytic microflora that can be either aerobic or facultatively or strictly anaerobic.
- (b) Acidogenesis from monomeric compounds and intermediary compounds formed during fermentation (production of volatile fatty acids, organic acids, alcohols, H₂ and CO₂) by a fermentative microflora that can be either facultatively or strictly anaerobic.
- (c) Acetogenesis from the previous metabolites by a syntrophic or homoacetogenic microflora.
- (d) Methanogenesis from the simple compounds that can be used by methanogens (in particular H₂ + CO₂ and acetate) which constitutes the last step of the methanogenic fermentation.

About two thirds of the CH₄ produced in nature derives from the reduction of the methyl group of acetate and about one third from reduction of CO₂ with electrons from H₂ or formate (Ferry, 1992). Lesser amounts of CH₄ are produced by the oxidative and reductive dismutation of methanol or methylamines that are mostly encountered in marine sediments. Methanogenic organisms have also been described that produce CH₄ from dimethyl sulfide or reduce CO₂ with primary, secondary and cyclic alcohols as electron donors. All of the pathways of methyl group reduction to CH₄ are mentioned below:

I. Reduction of CO₂ to CH₄: The reduction of CO₂ to CH₄ with H₂ or formate as the electron donor (Eq. 2 and 3)



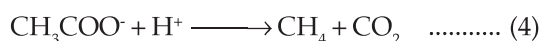
$$\Delta G^{\circ} = - 130.4 \text{ kJ mol}^{-1} \text{CH}_4$$



$$\Delta G^{\circ} = - 119.5 \text{ kJ mol}^{-1} \text{CH}_4$$

Carbon dioxide reduction pathway is derived mostly from studies with *Methanobacterium thermoautotrophicum* strains although they are classified as strains of the same species, the fact that they are only distantly related may explain some differences reported between them. Studies with these organisms have revealed several novel cofactors involved in the CO₂-reduction pathway and other pathways for methanogenesis.

II. Conversion of acetate to CO₂ and CH₄: The conversion (Eq. 4) is restricted to *Methanosarcina* and *Methanotherix*.



$$\Delta G^{\circ} = - 36 \text{ kJ mol}^{-1}$$

In both genera, acetate is activated to acetyl Co-A followed by decarboxylation and methyl transfer to HS-CoM. The reductive demethylation of CH₂-S-CoM to CH₄ is similar to that described for CO₂-reducing species that electrons for reduction of CoM-S-S-HTP derive from

oxidation of the carbonyl group of acetate to CO_2 . In nature, the major substrates for CH_4 production are acetate and $\text{H}_2 + \text{CO}_2$ and also a few other organic compounds (Table 2).

TABLE 2. Major substrates for methane production and the trophic groups

Trophic Group	Substrate utilized
Hydrogenotrophs	$\text{H}_2 + \text{CO}_2$
Formatotrophs	Formate
Acetotrophs	Acetate
Methylotrophs	Methylated compounds
Alcoholotrophs (no strict forms)	Alcohols I, II

Many of the anaerobic methanogens, utilizing acetate as a C source, use hydrogen as their electron donors. The consumption of H_2 by the methanogens is often important in maintaining low enough H_2 partial pressures to permit active growth of acetogenic bacteria that produce H_2 , yet are inhibited by its accumulation. This phenomenon of "interspecies H_2 transfer" is important in many anaerobic systems. It was observed that no H_2 accumulates during active methanogenesis, but if methanogens are inhibited by specific inhibitors, H_2 accumulates. This suggests that H_2 is an important and perhaps limiting energy source for the CH_4 -producing bacteria.

Methanotrophy

Like nitrification-denitrification and sulfur oxidation - sulfate reduction, methanotrophy is the other part of the coupled reaction of methanogenesis and involves the conversion of methyl group to CO_2 , using either oxygen or other compounds of higher oxidation status as electron acceptors. Bacteria that are able to grow using CH_4 are referred to as methanotrophs and are part of a larger grouping of organisms that can utilize one-carbon (1-C) compounds having no C-C bonds. Methanotrophic bacteria isolated and investigated so far uses molecular oxygen as the terminal electron acceptor and therefore are obligate aerobes, although there is evidence that certain, mostly SO_4^{2-} -reducing habitats exist in which anaerobic CH_4 oxidation occurs.

Aerobic methane oxidation

The enzyme responsible for the initial step in CH_4 oxidation is a monooxygenase enzyme that requires molecular O_2 . The product of this reaction, methanol, is further successively oxidized via formaldehyde to formate and then CO_2 . There is some evidence that some of these intermediates may leak or be excreted from cell and perhaps support growth of other bacteria. The use of enzymes known as methane monooxygenases to catalyze the oxidation of CH_4 to methanol is a defining characteristic of methanotrophs. The common metabolic pathway, branches off, depending upon the type of methanotrophs, the monooxygenase involved, the metabolism of substrates by methanotrophs, the central role of formaldehyde as an intermediate in catabolism and anabolism and the unique pathways employed for the synthesis of intermediates of central metabolic route. Formaldehyde is usually assimilated further either through RuMP pathway or Serine pathway. Yeast strains that grow on methanol utilize another pathway known as the dihydroxyacetate pathway for formaldehyde assimilation. Methane monooxygenases present in aerobic methanotrophic bacteria exhibit a striking lack of substrate specificity, resulting in the fortuitous metabolism of a very large number of compounds including xenobiotic chemicals. Because of the ability of methanotrophs to catalyze a large number of biotransformations, they have attracted the interest of scientists involved in the development of bioremediation technologies and in the use of bacteria containing methane monooxygenases for the production of chemicals with commercial value.

Anaerobic methane oxidation

Several studies have confirmed that CH₄ is also consumed in other anaerobic environments, including anoxic marine water, sediments of soda lakes and freshwater sediments. In vertical profiles of marine sediments, methane oxidation and sulfate reduction occur coincidentally. Although repeated attempts to isolate CH₄-oxidizing anaerobes in pure culture have failed, sulfate dependent methane oxidation (SDMO) has been accepted to occur in nature. Coupled with the poor thermodynamic yield of SDMO, this has led to the idea that CH₄ oxidation under anaerobic conditions is a co-metabolic activity and that the responsible organism(s) do not conserve energy from the process. Anaerobic CH₄ oxidation has frequently been determined by measuring the conversion of ¹⁴CH₄ to ¹⁴CO₂ which is trapped in alkaline solutions. In nearly all cases, net CH₄ consumption was not demonstrated in culture studies.

Methane oxidation and rice plants

Methane emission is the net balance of two opposite processes i.e. CH₄ production and its oxidation. In soil 58-80% of locally produced CH₄ is oxidized. The rate of CH₄ oxidation is often higher in rice-planted soil than in unplanted one. Such oxidation rate varies with rice growing stages. For example, about 36.5 and 54.7% of CH₄ is oxidized at tillering and panicle initiation stages respectively. Oxidation at harvesting and ripening stage is, however, negligible.

Root oxidation power as measured by oxidation of alpha-naphthylamine decreases when the roots grow older. It differs greatly among cultivars. If rice cultivars have similar root weights, those with high oxidative capacity are ideal for mitigating CH₄ emission.

Rice plants influence CH₄ oxidation in 2 ways, i.e. by diffusion of atmospheric O₂ via aerenchyma into the rhizosphere, and by enzymatic oxidation as measured by N flush inhibition technique and alpha-naphthylamine oxidation method. The pore size of aerenchyma is the main plant parameter that controls O₂ transport through the plant to the rhizosphere, and it's often shows a positive correlation with O₂ concentration in the rhizosphere. Several factors have been reported to affect the O₂ release from the rice roots. For instance, metabolic inhibitors such as DNP, NaN₃ and KCN could increase the O₂ release rate. The soil redox potential (Eh) could also influence the process.

The development of aerenchyma is determined by the intensity of anaerobiosis. For example, the development of aerenchyma in plants at a soil Eh of -250 ± 10 mV as compared to plants under well-aerated conditions (515 ± 25 mV). As results of enlarged aerenchyma, the root porosity was increased to 41.4% in the flooded plants as compared to only 13.3% in non-flooded or drained plants. Increased porosity enhance the transport of O₂ from the atmosphere to the roots; O₂ loss from the roots increased to 4.6 mmol O₂ g⁻¹day⁻¹ in the flooded plants as compared to only 1.4 mmol g⁻¹day⁻¹ in drained plants. The supply of O₂ by the plants to the rhizosphere often stimulates high activities of CH₄-oxidizing bacteria in the vicinity of rice roots.

Different rice cultivars can support different rates of CH₄ oxidation by developing variable root porosity and oxidation powers. It was found that at the tillering stage, the root air spaces were small and did not vary among the rice cultivars. But at later stage they varied greatly. Several experiments indicated that up to 40% of the potential CH₄ flux could be oxidized in the rhizosphere. Indirect assessments suggested that 50-90% of the CH₄ transported to the rhizosphere of the rice plants is oxidized. Even though recent results indicate the presence of methanotrophic activity associated with roots and to a lesser extent lower parts of the stem, the significance of CH₄ oxidation during the passage through the rice plants is still unknown.

Aerenchyma and mechanisms of methane transport through rice plants

The primary function of aerenchyma formation in hydrophilic plants, including rice, is the delivery of O₂ to the roots, but several gases are also transferred through them in the reverse direction. They are predominantly responsible for plant-mediated transfer of CH₄ from paddy fields to the atmosphere. Aerenchyma in rice plants is composed of small, medium and large size

lacunae. Both amount and density of large aerenchyma lacunae exhibited highly significant correlation suggesting that they control methane transport capacity (MTC) of rice plants.

Aerenchyma formation in rice plants is a varietal character - in some varieties it is well developed while in others it is not so. It develops with the advancement of plant growth. Its development is also affected by the Eh of the rhizosphere; large aerenchyma develops in response to highly reduced conditions. Wide difference in gas transport capabilities of different cultivars is mainly due to variations in type and amount of aerenchyma.

At the seedling stage (plant age 25 days), MTC is lowest; it increases by a factor of about 6 and 8 at the early tillering stage (35 days old) and maximum tillering (50 days old), respectively. Plants at panicle initiation (60 days old) show maximum MTC and further growth to the flowering stage (80 days old) does not change the MTC. However, there is a significant decrease in MTC at maturing. Such decrease at maturity appears to be due to collapse of large aerenchyma lacunae and a concomitant blockage of aerenchyma channels. The path of CH_4 through the rice plant involves the following steps: diffusion into the root, conversion to gaseous CH_4 in the root cortex, diffusion through cortex and aerenchyma, and release to the atmosphere through microspores in the leaf sheaths. The dissolved CH_4 in soil water diffuses into surface water of roots and cell-wall water of root cortex. Such transfer is driven by concentration gradient. Cracks in the junction point of the main root and root hairs are, however, the predominant entrance ports for CH_4 from surrounding soil solution to the aerenchyma. The roots can also absorb as much in gaseous form.

Methane is released to the atmosphere mainly through micropores in the leaf sheaths in the lower leaves but not from stomata. Use of ^{13}C labeled CH_4 demonstrated that although CH_4 is transported by the rice plants predominantly via molecular diffusion, a small component is also due to transpiration - induced flow.

Most of the CH_4 released is channeled through the culm, which is an aggregation of leaf sheaths. The aerenchyma channels of primary roots showed direct connection with those of culms and are the main conduit for CH_4 emission. About 50% of the CH_4 is released from leaf blades before shoot elongation, whereas only a small amount is emitted through leaves, as plants grow older. In addition to the presence of micropores on the leaf sheaths, cracks at the junction of internodes are also found sometimes to facilitate CH_4 transport. Methane can also be released from panicles particularly when vegetative parts are submerged. Root-shoot transition zone is, however, the main site of resistance to plant-mediated CH_4 exchange. Relative difference in CH_4 flux between two varieties of rice is mainly due to variation in their transfer capacity through pore diameter of the root-shoot zone, rather than to production of CH_4 or its oxidation.

Rice cultivars having higher number of tillers increases the CH_4 emission rate. It is presumably due to the proportional enhancement in channels/outlets of aerenchyma for the upstream transport of CH_4 . Tiller number can thus, become a major controlling factor of plant-mediated CH_4 transport in widely different cultivars. Therefore, plants with less number of tillers would minimize the CH_4 transport from the soil to the atmosphere. Rice cultivars with few unproductive tillers, small root system, high root oxidative activity and high harvest index are ideal for mitigating CH_4 emission in rice fields.

Factors for methane production

Methane emission from rice fields

Methane emission show pronounced variations among the rice growing sites of world, even under identical crop management. Continuous flooding, pure mineral fertilizer and cultivar types have pronounced influence on CH_4 emission (Wassmann et al., 2000b) (Table 3).

Methane emission varied from 14 to 375 $\text{mg m}^{-2} \text{d}^{-1}$ in most rice growing areas in the world. It is affected by water regimes, soil amendments, cultivars and type of fertilizers used. In India the mean CH_4 emission from rice field ranged from 3.5 to 4.2 Tg yr^{-1} (Mitra, 1992; Parashar, 1996). The

TABLE 3. Contribution of plant-mediated methane emission under different treatments

Fertilizer/ Cultivar	Plant age or interval	Overall CH ₄ emission rate (mg CH ₄ m ⁻² h ⁻¹)	Plant mediated CH ₄ emission (% of overall emission)
Urea/Roma	25 days	7.8	0
Urea/Roma	54 days	17.0	48
Urea/Roma	76-103 days	23-28	90-97
Unfertilized/Roma	Single season	11.0	88
Unfertilized/Lido	Single season	8.1	90
Urea/IR 72	Dry season	1.1	85
Straw/IR 72	Dry season	9.4	65
Urea/IR 72	Wet season	1.3	82
Straw/IR 72	Wet season	6.3	48

average CH₄ emission from rainfed tropical rice ecosystem in India was reported as 32 kg ha⁻¹ yr⁻¹ (Adhya et al., 2000). As the systems with high GWP are restricted to rice field with long flooding periods and considerable amount of organic inputs, the GWP of these systems are driven by CH₄ emission. Irrigated continuously-flooded rice paddy showed a CH₄ flux value of 4-26 mg m⁻² hr⁻¹ and 0.7-4.7 Gg ha⁻¹ per cropping season of 75 days (Adhya et al., 1994). Bhatia et al. (2004) estimated the CH₄ flux from different states of India using the IPCC default value and concluded with an emission of 4.7 Tg yr⁻¹.

Effect of soil amendments on methane emission

Seasonal flux of CH₄ was high following the application of fertilizer-N and organic amend-

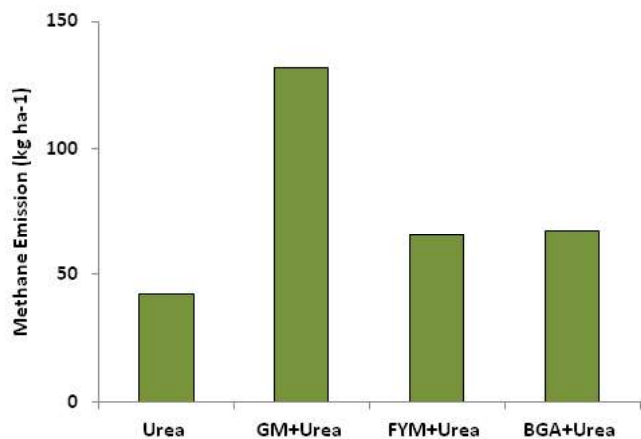


FIGURE 3. Methane emission from a rainfed alluvial field planted to rice (cv. CR 749-20-2) under the influence of urea N in combination with different organic amendments

ments (Fig. 3). All the organic treatments in combination with urea affected higher CH₄ flux over that of chemical-N (urea) alone. Over the season, the ranking in emission from the four treatments was green manure (GM) (212% increase as compared to urea alone) > blue green algae (BGA) (61% increase) > FYM (54% increase) > urea (Adhya et al., 2000). Organic matter amendment enhanced the readily mineralizable soil organic carbon which is the main source of fermentation products in flooded soils and sediments that are driven to CH₄ by strict anaerobic bacteria (methano-gens).

Effect of water regime on methane emission

Flooding the soil creates anaerobiosis and conditions favourable for CH₄ production

and emission. Thus flood-water regime can have a strong influence on CH_4 emission rates from rice fields and a single mid season drainage is considered to reduce seasonal CH_4 emission rates by about 50%. Mean CH_4 emission was lowest in field plots that were alternately flooded as to continuously flooded (Fig. 4) field plots leading to a 15% reduction in seasonal CH_4 flux. Amendments with rice straw at 2 t ha^{-1} significantly increased CH_4 production under both continuously flooded and intermittently flooded fields.

Cultivar variation

Rice plants serve as the major conduit for the transfer of CH_4 from the reduced soil layer to the atmosphere and more than 90% of the CH_4 fluxes from paddy soils are mediated by the rice plants. There are inherent variability in plant architecture, metabolic activity and gas transport potential among different rice cultivars. Among the four high yielding varieties tested, the degree of CH_4 efflux followed the order of Lalat > IR72 > Gayatri > Tulasi (Fig. 5) (Adhya et al., 2000). Cultivar Gayatri and Tulasi had lower CH_4 flux, there by producing -13% and 22% lesser CH_4 than that of IR72. Wide variations among rice cultivars with regard to CH_4 flux opens up possibilities for breeding rice cultivars with low CH_4 emission potential.

Root exudates of rice plants and methane production

Rice plants can influence soil Eh and thus CH_4 production by consuming O_2 from the rhizosphere (root respiration) and by enhancing the supply of electron donors i.e. easily decomposable organic substrate through root exudates, sloughed-off tissues and debris. On average, 30-60% photosynthesised C is allocated by plants to the roots and a substantial portion of this C is released or secreted by the roots in the form of organic compounds in the rhizosphere. These compounds constitute good food/energy materials for CH_4 producing organisms, methanogens.

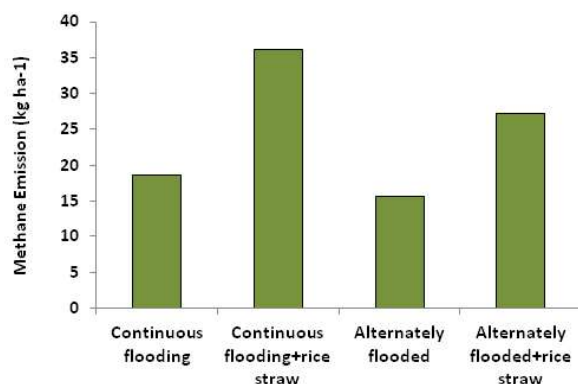


FIGURE 4. Methane emission from a rainfed alluvial field planted to rice (cv. CR 749-20-2) as affected by water regime and straw amendments

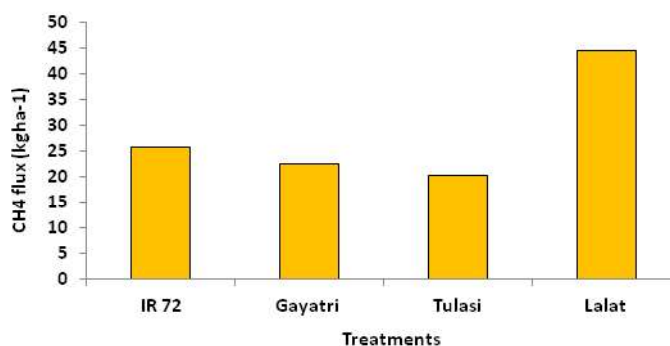


FIGURE 5. Methane emission from a rainfed alluvial field planted to different rice cultivars under uniform conditions

Considering the enormous genotypic and phenotypic variations in the species *Oryza sativa*, large variation in the quantity (exudation rate) and quality (composition) of root exudates is observed (Table 4) (Aulakh et al., 2001)

TABLE 4. Total organic carbon and organic acids added through root exudates of different rice cultivars

Cultivar	Total organic C				Total organic acids ^a			
	Seedling	Panicle initiation	Flowering	Maturity	Seedling	Panicle initiation	Flowering	Maturity
	mg C g ⁻¹ soil ^b							
Dular	3.8	7.2	7.8	5.8	1.3	4.0	4.3	3.9
IR 72	2.9	9.7	9.2	4.9	1.1	5.6	5.5	2.9
IR 65598	1.9	4.4	5.3	3.4	0.8	2.9	3.8	2.4
B 40	1.8	7.6	c	c	0.7	4.6	c	c
IR 65600	2.0	3.8	c	c	0.8	1.9	c	c

a= total of lactic, formic, acetic, tartaric, malic, oxalic, succinic and citric acid; b = on dry weight basis; c = treatment was not included

Root exudates contain both high-molecular-weight substances mainly mucilage and ectoenzymes, as well as low-molecular-weight substances consisting of organic acids, phenols and amino acids. Total amounts as well as the proportion of different compounds in root exudates vary considerably due to various endogenous and exogenous factors such as growth stages of rice, mechanical impedance to its roots, presence of toxic elements, nutrient deficiencies and water status of growing medium (soil), etc. The exudation rates, in general, are lowest at seedling stage; increase until flowering but decreased at maturity (Table 4). Plants increase their exudation to improve their ability to tolerate toxic elements such as Pb, Cd, Al. Increased exudation is also associated with nutrient deficiencies and dry soil conditions for mobilizing soil nutrients. Among the organic acids released by rice roots, malic acid showed the highest concentration followed by tartaric, succinic, citric and lactic acids. With advancement of plant growth, exudation of organic acids substituted exudation of sugars (Aulakh et al., 2001).

Methane production and CH₄ emission are more closely related to the release pattern of root exudates C than its individual components. The proportion of exudates C converted to CH₄ ranged between 61 and 83% (Aulakh et al., 2001) (Table 5). The plant-derived CH₄ production

TABLE 5. Proportion of added root exudate- carbon converted to methane in rhizosphere

Cultivar	Proportion of added root exudate-C converted to CH ₄ (%)			
	Seedling	Panicle initiation	Flowering	Maturity
21-d incubation				
Dular	65	65	72	73
IR 72	73	62	62	75
IR 65598	79	61	65	69
7-d incubation				
B 40	76	70	a	a
IR 65600	83	67	a	a

a = treatment was not included

rates corresponded to 17-40% of the CH₄ emission rates at flowering and maturity. Such plant-derived organic C would produce 3-4 fold greater amount of CH₄ during panicle initiation to flowering as compared to the seedling stages. It is, therefore, reasonable to speculate that plant-derived C possibly determines CH₄ production during later growth stage of rice.

An understanding of the quality and quantity of root exudates of rice during different growth stages and of widely used cultivars may thus help in selecting and breeding cultivars that have low root exudation and, as a consequence, results in reduced CH₄ emission from paddy fields. Since root exudation represents a possible loss of photosynthates from the plants, minimizing this process may also result in increased rice yield.

Mitigation options

Mitigation of carbon dioxide emissions

The increasing concentration of GHGs in the atmosphere, such as those of CO₂, CH₄, and N₂O are expected to contribute to global warming. Reducing the content of these gases has become a “global commons” issue (Ingram & Fernandes, 2001; Lal, 2004). The increase in the storage capacity of carbon (C) in agricultural soils through judicious land-use and appropriate management practices can mitigate the process of climate change (Wright et al., 2004).

On the other hand, CO₂ emission depends on the soil management, water management and cultivation methods and other agricultural management practices. No tillage or minimum tillage reduces CO₂ efflux from soil to the atmosphere rather than conventional tillage resulting into more C sequestration in soil. Prolonged existence floodwater in rice soil creates anaerobic environment which helps in slow decomposition of soil organic matter and the overlying water acts as a diffusion barrier to liberated CO₂ from soil to the atmosphere, thereby storing more carbon as compared to aerobic rice system. In a rice-maize-legume cropping system, legume cultivation reduces CO₂ emission from soil as compared to maize cultivation, which, in turn, helps to store more soil-C leading to soil-C sequestration. The aerobic rice cultivation system in upland condition is responsible for higher CO₂ emissions than lowland flooded rice soils and in case of CH₄ emission the scenario is just opposite.

Mitigation of methane emissions

The increase in CH₄ contributes to the global warming and effects the atmospheric chemical changes. Rice plants are implicated in CH₄ production, oxidation and transportation. In order to reduce the CH₄ emissions from rice fields various researchers suggested options for mitigation. Large number of studies from various countries indicated the possibility of substantial reductions in CH₄ emissions from actual field situations. The options available differ from the practices that are followed which include management of the crop, soil and irrigation requirements, varietal choice, and agrochemical usage. The contributions of options that are available towards the reduction of CH₄ emission largely depend upon the situations and component factors. Mitigation options are broadly related to the following activities:

- adoption of different rice cultivars
- field management
- applications of different agrochemicals
- organic residue management
- irrigation schedules
- crop protection and microbial manipulations

Mid-season drainage substantially reduced CH₄ emissions by about 30-50% as compared to continuous flooding or waterlogging. The practice of intermittent irrigation or cycles of alternate flooding and drying as occur in rainfed rice situations led to significant reductions in the CH₄ emissions from rice fields. Acid sulphate soils had minimum emission rates compared to other

soils. Methane emission rates were higher from transplanted rice than from direct sown. Direct seeding on dry soil had least CH₄ emission, followed dry direct seeding on wet soil. The age of seedlings at the time of transplanting also had significant impact on subsequent CH₄ emission (8 day old seedling had higher CH₄ than the 30 day old seedlings) probably because of the larger cultivation period of the former treatment. Thus, methane emissions from 30-day old transplanted seedlings, direct seeding on wetland soil and direct seeding on dry soil were reduced by 5%, 13% and 37%, respectively (Ko & Kang, 2000).

The proper selection of rice cultivars is a potential mitigation option of methane emission. Rice cultivars with low CH₄ emission potential may be selected. Land management in the winter crop season significantly influenced CH₄ fluxes during the following flooded and rice growing period (Knox et al., 2000). Methane flux from plots planted to alfalfa (legumes) in the winter crop season was significantly higher than those obtained with treatments involving winter wheat or dry fallow. Land management practices in the winter crop season also affected temporal variation patterns of CH₄ fluxes and soil Eh after flooding.

Water management in the preceding crop season becomes crucial factor in influencing CH₄ emission from rice fields. The application of rice straw, which undergoes aerobic decomposition during winter crop season after incorporation, greatly reduces the subsequent CH₄ emission during following flooded and rice growing period. Rice straw and possibly green manure application at a suitable application time not only sustains soil fertility but also prevents the emission of large amounts of methane.

The influence of crop on seasonal CH₄ emissions is considerable and large part of this originating from the rhizodeposition of the current crop. The adoption of new varieties with reduced CH₄ emission could be a more profitable mitigation option. As rhizodeposition contributes about 37% of the total substrate (Cao et al., 1996), reduction of the rates of rhizodeposition, therefore, would be beneficial to both yield and reduced CH₄ emissions. Seasonal emissions could be decreased with the increase in the temperatures and shortened crop production. The diurnal variations in emissions are strongly correlated to temperature and moisture. The seasonal CH₄ emission in the wet season was about 2-3 times as much as that in the dry season. This is particularly explained by the higher daily mean temperatures in the wet season.

Application of rice straw has enhanced CH₄ emission. Rice straw compost resulted in a six fold reduction in CH₄ emission compared with uncomposted rice straw. The application of green manure rather than rice straw would be desirable to improve fertility status on one hand and decrease CH₄ emissions on comparable basis. The application of sulphate fertilizers has been suggested as a suitable option to reduce CH₄ emissions by increasing the size of the soil pool of alternative electron acceptors. Emission reductions to the tune of 50% were observed when SO₄⁻² was applied to soil systems. The partial competition of the sulphate-reducing bacteria with methanogens for C substrate plays an important role. Seasonal methane emissions are sensitive to percolation rates in the range of 0 to 4 mm d⁻¹. High percolation rates and the necessary high frequency of irrigation could influence CH₄ emissions either by increasing the flux of O₂ dissolved in the irrigation water into the soil or by transport of CH₄ produced downward into groundwater, preventing it from being emitted. Possibly, the methanogenic substrates also move away from being acted upon by the methanogens.

Application of single super phosphate and potassium fertilizer led to the decrease cumulative seasonal CH₄ emissions. Results clearly indicated the role of sulphur content in the single super phosphate decreasing the CH₄ emissions. Also, potassium has a role in maintaining higher levels of oxidation status in the top soil profile encouraging oxidation processes in the rhizosphere and other regions affected by plants.

Several pesticides are reported to have influence on CH₄ production in soils systems. Though these agrochemicals are applied to the system as plant protection measures, studies indicate their role in mitigating the CH₄ production and its resultant emission (Sethunathan et al., 2000).

Compounds like carbofuran, hexachlorocyclo-hexane, butachlor, etc. had proven potential to reduce CH₄ production. Also some of the nitrification inhibitors have been shown to have potential to reduce CH₄ emissions. Methane emission from rice fields and the possible mitigation options should be evaluated within the perspective of overall context of rice cultivation of the region and ecosystem. The practices, depending upon their suitability and adoption, should be an integral part of the rice production system. This would, in the long run, serve to protect the environment through reduced emission as well as improve the crop yield.

Conclusions

World climate is not only a function of atmospheric physics but of atmospheric chemistry as well. In fact, the composition of the atmosphere is presently changing in a direction that ultimately may alter the global and regional climate. There is considerable concern over the increasing concentrations of atmospheric trace gases, such as CO₂, CH₄ and N₂O in view of their acknowledged role in atmospheric chemistry, both in the troposphere and stratosphere, through various photochemical interactions and the consequential climate change. With the intensification of agriculture and industry to sustain the demands of the growing billions, the contribution of greenhouse gases to global change is anticipated to increase. Atmospheric scientists predict that changes in the concentrations of these gases will have dramatic consequences for the habitability of our planet. Rice paddies are an important man-made ecosystem for the global C budget. The various controls of CH₄ emission from this ecosystem depend on the structure of plant and microbial communities and their interactions within the physical and chemical limits of soil environments. Further research is warranted to characterize these ecologies in relation to microbial- and other organismal communities and to identify the soil management options for manipulating the activities of methanogenic - and methanotrophic communities with dual objectives of increasing productivity and environmental quality.

References

- Adhya, T.K., Bharati, K., Mohanty, S.R., Ramakrishnan, B., Rao, V.R., Sethunathan, N., & Wassmann, R. (2000). Methane emission from rice fields at Cuttack, India. *Nutrient Cycling in Agroecosystems*, 58, 95-105.
- Adhya, T.K., Rath, A.K., Gupta, P.K., Rao, V.R., Das, S.N., Parida, K., Parashar, D.C., & Sethunathan, N. (1994). Methane emission from flooded rice paddy fields under irrigated condition. *Biology and Fertility of Soils*, 18, 245-248.
- Alberto, R., Carmelita, Ma., Wassmann, R., Hirano, T., Miyata, A., Kumar, A., Padre, A., & Amante, M. (2009). CO₂/heat fluxes in rice fields: Comparative assessment of flooded and non-flooded fields in the Philippines. *Agricultural and Forest Meteorology*, 149, 1737-1750.
- Aulakh. (2001). Impact of root exudates of different cultivars and plant development stages of rice (*Oryza sativa* L.) on methane production in a paddy soil. *Plant and Soil*, 230, 77-86.
- Bhatia, A., Pathak, H., & Aggarwal, P.K. (2004). Inventory of methane and nitrous oxide emissions from agriculture soils of India and their global warming potential. *Current Science*, 87, 317-324.
- Bouwman, A.F. (1990). Exchange of greenhouse gases between terrestrial ecosystems and the atmosphere. In A.F. Bouwman (Ed.), *Soil and greenhouse effect*. (pp. 61-127). New York, USA: John Wiley & Sons.
- Cao, M., Gregson, M.S., Dent, B., & Heal, O.W. (1996). Global methane emission from rice paddies. *Chemosphere*, 55, 879-897.
- Davidson, E.A., Savage, K., Verchot, L.V., Navarro, R. (2002). Minimizing artifacts and biases in chamber-based measurements of soil respiration. *Agricultural and Forest Meteorology*, 113, 21-37.
- Denman, K.L., Brasseur, G., & Chidthaisong, A. (2007). Coupling between changes in the climate system and biogeochemistry. In S. Solomon, D. Qin, M. Manning, Z. Chen (Eds.), *Climate change 2007: The physical science basis*. (pp. 499-587). Cambridge and New York: Cambridge University Press.

- Directorate of economics and statistics (DOES), Department of agriculture and cooperation, Ministry of agriculture (MOA), Government of India (GOI), (2011). <http://agricoop.nic.in/agristatistics.htm>
- Ferry, J.G. (1992). Biochemistry of methanogenesis. *Critical Reviews in Biochemistry and Molecular Biology*, 27, 473-503.
- Hill, P.W., Marshall, C., Harmens, H., Jones, D.L., & Farrar, J. (2004). Carbon sequestration: Do N inputs and elevated atmospheric CO₂ alter soil solution chemistry and respiratory C losses?. *Water Air and Soil Pollution*, 4, 177-186.
- Houghton, J.T., Meir-Filho, L.G., Callander, B.A., Harris, N., Katerberg, A., & Maskel, K. (1996). *IPCC report on climate change: The science of climate change. WG I contribution to the IPCC second assessment report on methane emission from rice cultivation*. Cambridge, UK: Cambridge University Press.
- Ingram, J.S.I., & Fernandes, E.C.M. (2001). Managing carbon sequestration in soils: Concepts and terminology. *Agriculture Ecosystem and Environment*, 87, 111-117.
- Intergovernmental Panel on Climate Change (IPCC). (1995). *Climate change 1995: The science of climate change*. In J.T. Houghton, L.G. Meira Filho, B.A. Callander, N. Harris, A. Kattenberg, K. Maskell (Eds.), Cambridge: Cambridge Univ. Press.
- Intergovernmental Panel on Climate Change (IPCC). (2007). Climate change-synthesis report. In *An assessment of the Intergovernmental Panel on Climate Change*. Plenary XXVII. 12-17, November, Valencia, Spain, pp. 52.
- Knox, J.W., Matthews, R.B., & Wassmann, R. (2000). Using a crop/soil simulation model and GIS techniques to assess methane emissions from rice fields in Asia. III. databases. *Nutrient Cycling in Agroecosystems*, 58, 179-199.
- Ko, J.Y., & Kang, H.W. (2000). The effects of cultural practices on methane emissions from rice fields. *Nutrient Cycling in Agroecosystems*, 58, 311-314.
- Lal, R. (2004). Soil carbon sequestration impacts on global climate change and food security. *Science*, 304, 1623-1627.
- Mills, R., Glanville, H., McGovern, S., & Emmett, B. (2011). Soil respiration across three contrasting ecosystem types: Comparison of two portable IRGA systems. *Agricultural and Forest Meteorology*, 174, 532-535.
- Minami, K., & Neue, H.U. (1994). Rice paddies a methane source. *Climate Change*, 27, 13-26.
- Mitra, A.P. (1992). Greenhouse gas emission in India. 1991 - Methane Campaign. Scientific Report No. 2. Council of Scientific and Industrial Research (CSIR) and Ministry of Environment and Forest (MoEF), New Delhi.
- Neue, H.U. (1997). Rice growing soils: Constraints, utilization and research needs. In *Classification and management of rice growing soils*. Proceedings of the fifth International soil management workshop, Taiwan. p. 1-14.
- Parashar, D.C., Mitra, A.P., Gupta, P.K., Rai, J., Sharma, R.C., Singh, N., Kaul, S., Lal, G., Chaudhay, A., Ray, H.S., Das, S.N., Parida, K.M., Rao, S.B., Kanungo, S.P., Ramasami, T., Nair, B.U., Swamy, M., Singh, G., Gupta, S.K., Singh, A.R., Saikia, B.K., Barua, A.K.S., Pathak, M.G., Iyar, C.P.S., Gopalkrishnan, M., Sane, P.V., Singh, S.N., Banerjee, R., Sethunathan, N., Adhya, T.K., Rao, V.R., Palit, P., Saha, A.K., Purkait, N.N., Chaturvedi, G.S., Sen, S.P., Sen, M., Sarkar, B., Banik, A., Subbaraya, B.H., Lal, S., Venkataramani, S., & Sinha, S.K. (1996). Methane budget from paddy fields in India. *Chemosphere*, 33, 737-757.
- Prentice, I.C., Farquhar, G.D., Fasham, M.J.R. (2001). The carbon cycle and atmospheric carbon dioxide. In J.T. Houghton, Y. Ding, D.J. Griggs (Eds.), *Climate change 2001: The scientific basis*. (pp. 183-238). Cambridge and NY: Cambridge University Press.
- Sethunathan, N., Kumaraswamy, S., Rath, A.K., Ramakrishnan, B., Satpathy, S.N., Adhya, T.K., & Rao, V.R. (2000). Methane production, oxidation, and emission from Indian rice soils. *Nutrient Cycling in Agroecosystems*, 58, 377-388.

- Tseng, H.K., Tsai, L.J., Alagesan, A., Tsuang, J.B., Yao, H.M., & Kuo, H.P. (2010). Determination of methane and carbon dioxide fluxes during the rice maturity period in Taiwan by combining profile and eddy covariance measurements. *Agricultural and Forest Meteorology*, 150, 852-859.
- Wassman, R., Neue, H.U., Lantin, R.S., Makarim, K., Chareonsilp, N., Buendia, L.V., & Rennenberg, H. (2000a). Characterization of methane emissions from rice fields in Asia. II. Differences among irrigated, rainfed, and deepwater rice. *Nutrient Cycling in Agroecosystems*, 58, 13-22.
- Wassmann, R., & Aulakh. (2000). The role of rice plants in regulating mechanisms of methane emissions. *Biology and Fertility of Soils*, 31, 20-29.
- Wassmann, R., Neue, H.U., Lantin, R.S., Buendia, L.V., & Renneberg, H. (2000b). Characterization of methane emissions from rice fields in Asia. I. Comparison among fields sites in five countries. *Nutrient Cycling in Agroecosystems*, 58, 1-12.
- Wright, A.L., Hons, F.M., & Rouquette, F.M. (2004). Long-term management impacts on soil carbon and nitrogen dynamics of grazed Bermuda grass pastures. *Soil Biology and Biochemistry*, 36, 1809-1816.
- XiuE, R., QinXue, W., ChengLi, T., JinShui, W., KeLin, W., YongLi, Z., ZeJian, L., Masataka, W., & GuoYoung, T. (2007). Estimation of soil respiration in a paddy ecosystem in the subtropical region of China. *Chinese Science Bulletin*, 52, 2722-2730.
