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Production, oxidation, emission and consumption of methane by soils: A review

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Abstract − Methane emission by soils results from antagonistic but correlated microbial activities. Methane is produced in the anaerobic zones of submerged soils by methanogens and is oxidised into CO_2 by methanotrophs in the aerobic zones of wetland soils and in upland soils. Methanogens and methanotrophs are ubiquitous in soils where they remain viable under unfavourable conditions. Methane transfer from the soil to the atmosphere occurs mostly through the aerenchyma of aquatic plants, but also by diffusion and as bubbles escaping from wetland soils. Methane sources are mainly wetlands. However 60 to more than 90 % of CH_4 produced in the anaerobic zones of wetlands is reoxidised in their aerobic zones (rhizosphere and oxidised soil-water interface). Methane consumption occurs in most soils and exhibits a broad range of values. Highest consumption rates or potentials are observed in soils where methanogenesis is or has been effective and where CH_4 concentration is or has been much higher than in the atmosphere (ricefields, swamps, landfills, etc.). Aerobic soils consume atmospheric CH_4 but their activities are very low and the micro-organisms involved are largely unknown. Methane emissions by cultivated or natural wetlands are expressed in mg $CH_4 \cdot m^{-2} \cdot h^{-1}$ with a median lower than 10 mg $CH_4 \cdot m^{-2} \cdot h^{-1}$. Methanotrophy in wetlands is most often expressed with the same unit. Methane oxidation by aerobic upland soils is rarely higher than 0.1 mg $CH_4 \cdot m^{-2} \cdot h^{-1}$. Forest soils are the most active, followed by grasslands and cultivated soils. Factors that favour CH_4 emission from cultivated wetlands are mostly submersion and organic matter addition. Intermittent drainage and utilisation of the sulphate forms of N-fertilisers reduce CH_4 emission. Methane oxidation potential of upland soils is reduced by cultivation, especially by ammonium N-fertiliser application. © 2001 Éditions scientifiques et médicales Elsevier SAS

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1. INTRODUCTION

Methane is the main hydrocarbon present in the atmosphere, with an average concentration of 1.7 ppm. Variations between the northern and southern hemispheres average 0.14 ppm and exhibit seasonal variations of about 0.03 ppm [55].

Despite a short residence time in the atmosphere (about 10 years), the CH_4 ability to absorb infrared radiation makes it 20 to 30 times more efficient than CO_2 as a greenhouse gas [17, 169]. Methane is chemically very reactive and is therefore involved in changes in the chemical composition of the atmosphere [34]. In particular, it reacts with hydroxyl radicals in the troposphere, reducing its oxidative power and ability to eliminate pollutants such as chloro-fluoro carbons (CFCs), and leading to the production of other greenhouse gases (ozone, CO, CO_2). In the stratosphere, such reactions produce water vapour, which is involved in the destruction of the stratospheric ozone layer, the natural barrier against detrimental solar radiations. Methane is considered the second or the third greenhouse gas after CO_2 and CFCs [121, 138].

Annual CH_4 emission, estimated from the analysis of air trapped in polar ice, were 180 Tg·year^{-1} during the 15th century (1 Tg = 10^{12} g) and 200 Tg·year^{-1} at the beginning of the 18th century [102]. The recent estimates of the International Panel for Climate Changes (IPCC) [88] are around 300 Tg in 2000, and between 400 and 600 Tg in 2010.

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Atmospheric CH_4 is mainly (70–80 %) of biological origin. It is produced in anoxic environments, including submerged soils, by methanogenic bacteria during the anaerobic digestion of organic matter. Methane is mainly eliminated in the troposphere through oxidation by OH• radicals, according to the reaction: $CH_4 + OH• \rightarrow CH_3• + H_2O$. In the stratosphere, CH_4 also reacts with chlorine (originating from CFCs) according to the reaction: $CH_4 + Cl• \rightarrow HCl + CH_3•$. Methane is also eliminated in soils by microbial oxidation, which takes place in the aerobic zone of methanogenic soils (methanotrophy) and in upland soils, which oxidise atmospheric methane. Soils most efficient in methanotrophy are generally those from sites that are often submerged or water-saturated and where a significant methanogenic activity develops at intervals [146]. Ricefield soils, peat soils [204] and soils from landfills [238] often exhibit very high potential methanotrophic activities but in such environments, where anaerobiosis predominate, the balance between CH_4 production and oxidation is usually positive.

An environment is a CH_4 source when the balance between production by methanogenic bacteria and consumption by methanotrophic bacteria is positive, leading to CH_4 emission. When the balance is negative, the environment is a CH_4 sink.

Natural CH_4 sources are considered responsible for about 30 % of total emissions. Wetland soils (swamps, bogs, etc.) are the main natural source with an estimated emission of 100–200 $Tg \cdot year^{-1}$. Other sources are oceans, some forest soils, termites and wild ruminants (*table I*). About 70 % of CH_4 emissions are of human origin. Domesticated ruminants (65–100 $Tg \cdot year^{-1}$) and ricefields (25–150 $Tg \cdot year^{-1}$) are responsible for 15–40 % of total emissions, therefore agriculture is the main anthropic source of CH_4.

Because of their economical importance and high potential as CH_4 source, ricefields have been the most studied methanogenic ecosystems. They are also the most suitable model to study CH_4 emission because methanogenesis and methanotrophy are very active and all modes of CH_4 transfer occur in ricefields. Assuming an annual emission of 50 Tg CH_4 by ricefields, the production of 1 kg rice corresponds to the emission of 100 g CH_4.

As the sources of atmospheric CH_4 are closely related to human activities, it is theoretically possible to control them. According to Thompson et al. [208], the global temperature increase could be reduced by 25 % if CH_4 emissions could be stabilised.

Temperate and tropical oxic soils that are continuously emerged and exposed to atmospheric concentrations of CH_4 are CH_4 sinks. They usually exhibit low levels of atmospheric CH_4 oxidation but, because of the large areas they cover, they are estimated to consume about 10 % of the atmospheric CH_4 (*table I*). Among upland soils, forest soils are probably the most efficient CH_4 sink. Atmospheric CH_4 oxidation also occurs in extreme environments such as deserts and glaciers, in the floodwater of submerged soils and in river waters.

According to IPCC estimates [87], natural and cultivated submerged soils (landfills not included) contribute about 55 % of the CH_4 emitted into the atmosphere, corresponding to 175 $Tg \cdot year^{-1}$, while upland soils are responsible for 6 % of the CH_4 consumption, corresponding to 30 $Tg \cdot year^{-1}$ (*table I*). Soils are therefore a major actor of the global CH_4 cycle. New trends in atmospheric CH_4 studies deal with modelling the retroactive effect of global warming and atmospheric CO_2 increase on CH_4 emissions by terrestrial environments [138] with a special focus on ricefields [157, 183].

The role of soils as source and sink has been discussed before 1997 in general reviews [37, 145, 211], or in reviews dealing with specific environments such as ricefields [147, 230], forests and temperate cultivated soils [203]. Since then, in relation with the increasing scientific and political interest in greenhouse gases, numerous papers have been published on this topic. This review summarises current knowledge with emphasis on recent developments.

Table I. Soil contribution to atmospheric CH_4 ($Tg \cdot year^{-1}$) according to IPCC [87].

	Estimate	Uncertainty
Sources		
Submerged soils	115	55–150
Other natural sources	50	25–140
Ricefields	60	20–100
Enteric fermentation and animal waste	105	85–130
Energy production and use	100	70–120
Landfills	30	20–70
Biomass burning	40	20–80
Domestic sewage	25	
Total of sources	525	
Sinks		
Consumption in atmosphere	470	420–520
Oxidation in upland soils	30	15–45
Total of sinks	500	

2. MECHANISMS AND MICROFLORA INVOLVED

2.1. Methanogenesis

The complete mineralisation of organic matter in anaerobic environments where sulphate and nitrate concentrations are low occurs through methanogenic fermentation, which produces CH_4 and CO_2 according to the reaction: $C_6H_{12}O_6 \rightarrow 3\ CO_2 + 3\ CH_4$.

This transformation requires successive actions of four populations of micro-organisms that degrades complex molecules in simpler compounds:

– hydrolysis of biological polymers into monomers (glucides, fatty acids, amino acids) by an hydrolytic microflora that can be either aerobic, or facultatively, or strictly anaerobic;

Table II. Characteristics of trophic and morphological groups of methanogens.

Trophic groups and substrates	Cocci	Rods	Rods with a sheath*	Sarcinae
Hydrogenotrophs				
$H_2 + CO_2$	most	most	none	few
Formatotrophs (all formatotrophs are hydrogenotrophs)				
Formate	several	several	none	none
Acetotrophs				
Acetate	2 species	none	1 genus	all
Methylotrophs				
Methylated compounds	4 genera	none	none	all
Alcoholotrophs (no strict forms)				
Alcohols I, II	none	few	none	few

* Genus *Methanosaeta*.

– acidogenesis from monomeric compounds and intermediary compounds formed during fermentation (production of volatile fatty acids, organic acids, alcohols, H_2 and CO_2) by a fermentative microflora that can be either facultatively or strictly anaerobic;
– acetogenesis from the previous metabolites by a syntrophic or homoacetogenic microflora; and
– methanogenesis from the simple compounds that can be used by methanogens (in particular $H_2 + CO_2$ and acetate) which constitutes the last step of the methanogenic fermentation.

Methanogenesis, which requires strict anaerobiosis and low oxydo-reduction potentials (Eh < –200 mV), involves a specialised, strictly anaerobic microflora that can develop in synergy or in syntrophy with other anaerobic bacteria. Methanogens belong to the domain *Archaea* [242]. A review by Boone et al. [20] presents a detailed taxonomic treatment of methanogens based on the percentage of DNA/DNA hybridisation and the differences in sequences of the rRNA 16S gene. Currently, twenty-six genera and more than sixty species of methanogens have been recorded [67].

Methanogens have a limited trophic spectra comprised of a small number of simple substrates: $H_2 + CO_2$, acetate, formate, methylated compounds (methanol, methylamines, dimethylsulphur), and primary and secondary alcohols. This allows to distinguish five trophic groups of methanogens (*table II*). CO can be used by methanogens but is not an important substrate. The two major pathways of CH_4 production in most environments where organic matter decomposition is significant (digesters, freshwater sediments, submerged soils) are acetotrophy and CO_2 reduction by H_2 [41, 185, 205].

Despite the low number of methanogenic species that can use acetate as C and energy source (14 %, corresponding to the genera *Methanosarcina* and *Methanosaeta*), acetotrophy is generally considered responsible for about two-thirds of the CH_4 produced. This reaction produces little energy in normalised conditions ($\Delta G'_0$),which results in a low growth rate of acetotrophic methanogens.

In ricefield soil, $H_2 + CO_2$-dependent methanogenesis contributed about 25–30 % of the CH_4 produced, as shown by CH_3F acetoclastic inhibition [38], and seemed to be driven by the decay and fermentation of root material [38, 39]. The H_2 inter-species transfer between fermentative and methanogenic bacteria is an important process in anaerobic fermentation. It detoxifies the medium by maintaining the H_2 partial pressure at a low level. About 77 % of methanogenic species are hydrogenotrophic; about 60 % also utilise formate. Formate, like H_2, is involved in inter-species transfers during the oxidation of the reduced compounds produced by the anaerobic decomposition of organic matter [57, 207]. The energy produced by these reactions is high, which results in a rapid growth of hydrogenotrophic and formatotrophic methanogens.

Methylated compounds are used by about 28 % of methanogens in specific environments such as marine sediments. Methanol, which mostly originates from pectin degradation during the decomposition of algae [180], could be a significant substrate for methanogens in ricefields where large biomasses of freshwater algae often develop [170]. However, the relative contribution of methanol to CH_4 production in submerged ecosystems has not yet been determined.

Methanogenic bacteria have been mostly studied in ricefield soils but they are probably ubiquitous in soils. Waterlogging upland soils, such as forest and cultivated soils, initiated methanogenesis and increased methanogenic populations [135].

Whereas twenty-six methanogenic genera have been currently described, strains isolated or evidenced in ricefield soils belong only to seven genera: *Methanobacterium*, *Methanosarcina*, *Methanobrevibacter*, *Methanoculleus*, *Methanogenium*, *Methanosaeta* and *Methanospirillum* [6, 7, 63, 93, 94, 117, 139, 163, 164]. The characterisation of *Archaea* populations in an Italian rice soil by molecular methods demonstrated the presence of representatives of *Methanosarcina*, *Methanosaeta*, *Methanobacter* and *Methanomicrobium*, together with euryarchaeotal and crenarchaeotal clusters [132]. The same study evidenced (i) clusters including known methanogens and uncultivable strains, and three new clusters of non-cultivable strains, all belonging to *Euryarchaeota* and (ii) two new clusters of *Crenarchaeota* [132]. The number of

non-cultivable strains belonging to clusters of known methanogens or new clusters inserted between clusters including known methanogens were much more numerous than cultivable identified strains. Assuming that most non-cultivable *Archaea* phylogenetically close to known methanogens are methanogens – as supported by the results of a study using cultivation and molecular methods [71] – it can be inferred that a very significant proportion of methanogens present in rice soils are currently uncultivable. Micro-organisms that have been isolated and most studied are not necessarily those that are the only or the most active in soil.

Very little data are available on methanogen abundance in soils other than ricefield soils. Values recorded in twenty-nine ricefield soils in Senegal ranged from 10^2 to 10^7 g^{-1} dry soil [68]. Apparently populations of cultivable methanogens show little variations during the rice crop cycle. In Italian ricefields, methanogen populations present in the soil before submersion (about 10^4 acetotrophs and 10^6 hydrogenotrophs·g^{-1} dry soil) were abundant enough to initiate CH_4 production after 100 h submersion without an increase of the population density [135]. In Japanese ricefields, populations of hydrogenotrophs (10^3–10^4), methylotrophs (10^4–10^5) and acetotrophs (10^4–10^5) remained approximately constant during 2 years cropping and were independent from the water management, the type of culture (rice or wheat), fertiliser application and sampling depth (0–1, 1–10 and 10–20 cm) [6]. Molecular methods confirmed the relative stability of *Archaea* in a ricefield soil studied for 17 d after flooding. *Methanomicrobiaceae* and *Methanosaetaceae* did not change in relative frequency. *Methanobacteriaceae* decreased over time; only the relative abundance of *Methanosarcinaceae* increased, roughly doubling from 15 to 29 % of total archaeal gene frequency within the first 11 d, which was positively correlated to the dynamics of acetate and formate concentrations [132].

2.2. Methanotrophy

Two forms of CH_4 oxidation are recognised in soils [12, 13, 75].

The first form, known as 'high affinity oxidation', occurs at CH_4 concentrations close to that of the atmosphere (< 12 ppm). This form is apparently ubiquitous in soils that have not been exposed to high NH_4^+ concentrations [210]. It is estimated to contribute 10 % of total CH_4 consumption [211]. The second form of oxidation, known as 'low affinity oxidation' occurs at CH_4 concentrations higher than 40 ppm. It is performed by bacteria called methanotrophs [92, 110, 238] and is considered as methanotrophic activity sensu stricto.

Bacterial population responsible for 'high affinity oxidation' are still largely unknown [12]. The study by denaturing gradient gel electrophoresis (DGGE) of *pmoA* genes from strains originating from forest and upland soils that exhibited high CH_4 consumption rates showed that their DGGE bands were only distantly related to those of known methanotrophs, which indicated the existence of unknown methanotrophs involved in atmospheric CH_4 consumption [77]. A similar conclusion arises from radioactive fingerprinting of micro-organisms that oxidise atmospheric CH_4 in different soils, which could only characterise strains as "an unknown group of the alpha *Proteobacteria*" [78].

Cultivable methanotrophs responsible for 'low affinity oxidation' occur in all soils with a pH higher than 4.4 [210]. Already in the 30s, enrichment in organic matter had been observed in soils surrounding leaking gas pipes [211, 214]. Methane oxidation in methanogenic environments (ricefields, peat soils, landfills, etc.) is a low affinity activity. Methane concentration in the water of the first centimetres of a ricefield soil may reach 110 ppm [40] and that in the air of a drained rice soil is often higher than the 11–45 ppm threshold established for a low affinity activity [12].

In wetlands, methanotrophs develop in the oxidised soil layer, in the aerobic rhizosphere of plants possessing an aerenchyma, and inside the roots and the submerged part of the leaf sheaths of the rice plants [21, 69].

Methanotrophs use CH_4 as only a C and energy source. Oxygen availability is the main factor limiting their activity. However, a partial CH_4 oxidation was reported in marine anoxic sediments [4] and was also suspected of occurring in submerged soils [144].

More than 90 % of the CH_4 produced in the anaerobic environments of ricefields can be reoxidised by methanotrophs in the aerobic zones [66, 158, 179]. Depending on the period of the crop cycle and the water management, the percentage of the CH_4 produced that is oxidised by methanotrophs varies from to 0 to 97. In a Texas ricefield, during maximum CH_4 production, under continuous irrigation, about 70 % of the CH_4 produced was reoxidised [179].

In ricefields, variations in CH_4 emission were mostly attributed to variations in methanotrophic activity [177, 185]. Similarly, in Florida swamps, an increase in CH_4 emission associated with a decrease of the environmental oxidation was not due to methanogenesis stimulation but to a decrease of the methanotrophic activity [110].

About 80 % of the CH_4 diffusing through the oxidised soil-water interface in ricefields is consumed by methanotrophs [40]. The use of methylfluoride as methanotrophy inhibitor showed that CH_4 emission would be five to ten times higher in the absence of oxidised soil [10]. But CH_4 oxidation in the rhizosphere is quantitatively the most important and varies according to the development stage of the rice plant [51]. Methanotrophs are also associated with roots and rhizomes of aquatic plants and their activity is correlated with the oxidising activity of the rhizosphere [110]. In oxic soils, maximum methanotrophy is usually observed in the lower soil layer [14].

Methanotroph counts deal mostly with ricefields. Very little data are available, probably because of methodological difficulties [61]. Estimates range from 10^4 g^{-1} in Japanese soil [232], 10^6 in Italian soils [12], $8{\cdot}10^5$ in surface soil planted or non-planted, and $1.4{\cdot}10^6$ in the rhizosphere [21]. Methanotrophs are also associated with the rice plant, with reported densities of 10^5–10^6 g^{-1} dry wt of root and 10^3–10^4 g^{-1} dry wt in the lower part of culms [232]. Methanotroph abundance increased with the age of the rice plant, whereas it remained approximately constant in submerged unplanted soil [69]. Methanotroph populations in twenty-two dry rice soils ranged from 10^2 to 10^4 g^{-1} soil dry wt [61]. Populations markedly increased when soils were incubated under an atmosphere enriched with CH_4 (10^7–10^9 g^{-1} soil dry wt). The enhancement of methanotrophic population by incubation under CH_4 was observed with soils from ricefields, forests and grasslands [12, 21, 232].

Methanotrophs isolated from ricefields belong to the genera *Methylocystis* [206] and *Methylosinus* [23, 122]. Type II methanotrophs are probably dominant in ricefields because they are the only type producing soluble methane-mono-oxygenase, which avoid the accumulation of NO_2 toxic to methanotrophs; they also possess resistance forms more efficient than those of type I [107, 122]. Phylogenetic analysis confirmed this hypothesis [53, 76].

Microcosm experiments demonstrated that methanotrophs significantly contributed to nitrification in the rhizosphere, while the contribution of nitrifiers to CH_4 oxidation was insignificant [18]. This indicate that the beneficial effect of methanotrophs on greenhouse gases balance could be reduced by the production of NO_x.

2.3. Relations between methanogens and methanotrophs

Counts of methanogens and methanotrophs have been currently performed mostly in ricefield soils. Results show that both groups are ubiquitous in these soils. Dynamic studies seem to indicate that methanogens and methanotrophs maintain their populations under unfavourable conditions, i.e. during drainage and drying-up for anaerobic methanogens and during submersion for aerobic methanotrophs [61, 63, 68, 94, 95]. A study where both populations were simultaneously counted in a range of ricefield soils, confirmed that methanogens and methanotrophs were present simultaneously in ricefield soils and showed that their densities were positively correlated. The densities of cultivable methanotrophs and potential methanotrophic activities were higher than the densities of cultivable methanogens and potential methanogenic activities [93].

2.4. Methane transfer from soil to atmosphere

Methane emission by wetland soils results from CH_4 production in anoxic zones, CH_4 consumption by methanotrophs in oxidised zones (rhizosphere, lower part of culms, soil-water interface and submersion water), and transfer to the atmosphere, mostly through rice aerenchyma and, at a lower level, through diffusion and ebullition (*figure 1*).

In planted ricefields, only a low percentage of the CH_4 produced escapes as bubbles through the soil and the submersion water. Rice plants with their aerenchyma act as pipes, allowing gaseous exchanges between soil and atmosphere [148]. Usually, planted ricefields emit more CH_4 than wet fallow fields because of a higher C availability for methanogenesis and an easier transfer to the atmosphere, both resulting from the larger aerenchymous plant biomass in planted fields than in fallow fields, as observed by Schütz et al. [185]. Methane emission is a passive transfer through the aerenchyma and micropores located on rice leaves [152]. Methane emission varies with rice varieties [1] probably because of morphological differences in the aerenchyma [27] and root porosity [193]. At the beginning of the crop cycle, when rice plants are little developed, bubble formation and vertical movement in the bulk of the soil is the main transfer mechanism. When rice plants develop, diffusion through the aerenchyma becomes the dominant process, responsible for more than 90 % of the CH_4 emitted during the reproductive phase of the rice plant [35, 185, 215].

Similarly, in temperate swamps, aquatic plants are responsible for about 90 % of the CH_4 transfer to the atmosphere [35, 185, 215, 240]. Nycthemeral variations in CH_4 emission can be related either to stomata opening (*Scirpus* sp.) or to a convection phenomenon related to temperature (*Phragmites* sp.) [218]. Plants possessing an aerenchyma are mostly herbaceous, but also include trees such as *Alnus* which favour CH_4 emission in wet areas [175].

3. METHODS FOR ESTIMATING ACTIVITIES

Methods to estimate CH_4 production, consumption, and emission by soils should be used with caution, while keeping in mind that they measure complex microbial activities, integrating a larger number of environmental parameters. To be significant, measurements must take into account the spatial and temporal variations as well as the low sensitivity of the methods, especially for CH_4 measurement at atmospheric concentration [211].

3.1. Flux measurements

The closed static chamber is the most frequently used field method to estimate positive (emission) or negative (consumption) CH_4 fluxes [184]. An alternative used to measure emission is the open chamber, where a continuous gaseous flux is circulated allowing to estimate CH_4 emission on a given area by difference. The major problem encountered with both methods is the very high variations of measurements in

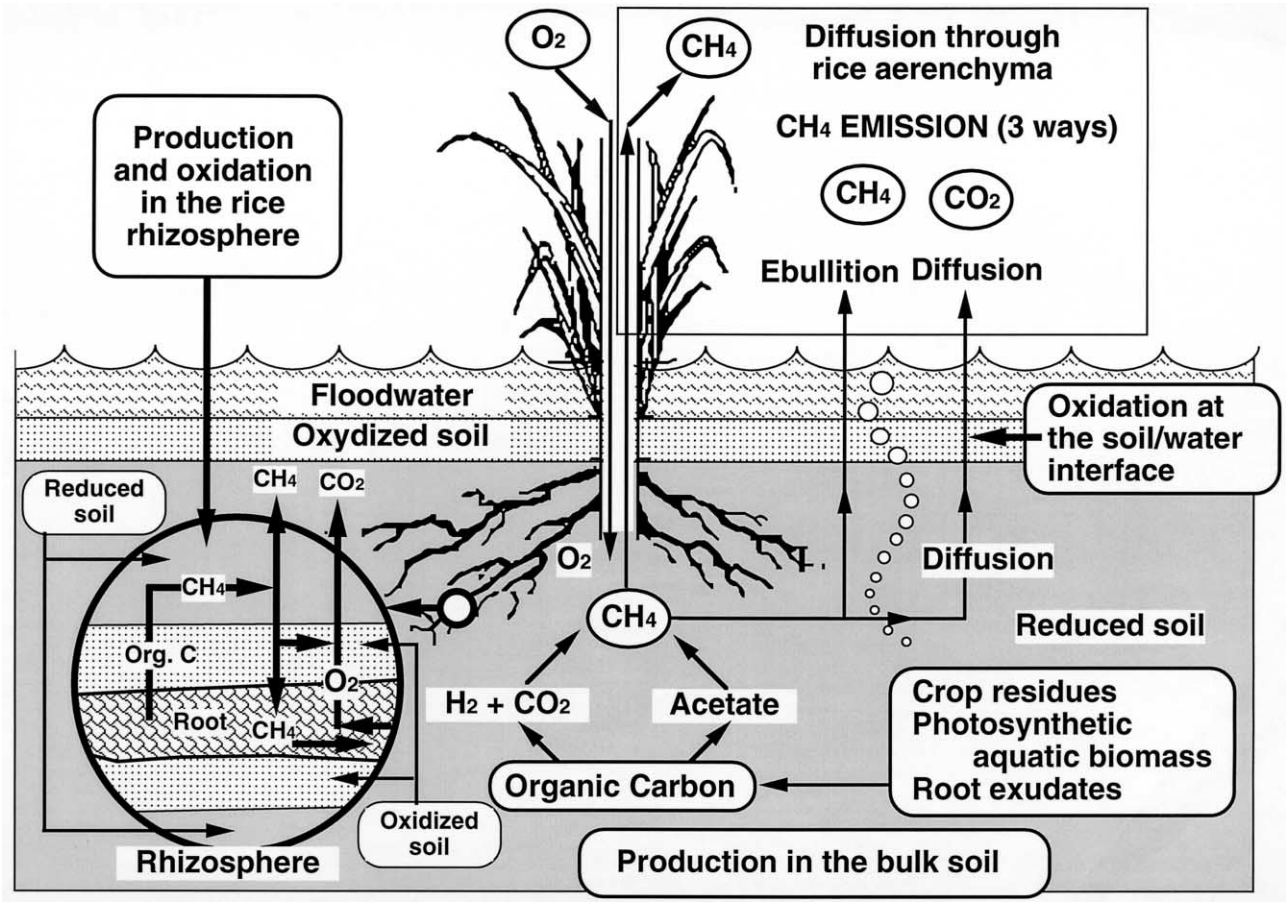

Figure 1. Production, consumption and transfer of CH_4 to the atmosphere in ricefields.

space and time [173]. Soil microbial activity usually exhibit very large variations in space. This was also observed with methanogens [173].

When measuring CH_4 emission, spatial variability is increased by the heterogeneity of the diffusion pathways. Methane emission measurements in Danish soils submitted to temporary flooding showed coefficients of variations ranging from 166 to 1 787 [5]. A bibliographic survey [140] presents 127 estimates of CH_4 emission by ricefields soils submitted to different treatments (36 references). Values range from 0 to 80 mg $CH_4 \cdot m^{-2} \cdot h^{-1}$. The study of the data shows a log-normal distribution (coefficient of variation = 94 %) for which the median is more representative than the mean. The median is 9.6 mg $CH_4 \cdot m^{-2} \cdot h^{-1}$ with a confidence interval at 95 % of –27 and +37 %.

Diurnal and seasonal variations of CH_4 emission can also be very high [191] (see also section 5.2.2). Methane concentration in the air over a ricefield may vary from 23 ppm·vol at the beginning of the day to an average value of 1.75 ppm·vol during the day [188].

Estimating CH_4 emission therefore requires a high number of replicates and integrated measurements at short time intervals. In a study of gaseous emission by cultivated and forest soils in Canada, between seven and 452 static chambers were needed, depending on the site, to obtain an accuracy of 10 % when measuring gaseous fluxes (CO_2 or CH_4) higher than 0.15 mg $\cdot m^{-2} \cdot d^{-1}$ [123].

Various mathematical models have been proposed to estimate CH_4 emission [64] and consumption [70, 168]. They were generally conceived for large scale evaluation and require the input of data that can be very expensive to acquire, such as a combination of Landsat Thematic Mapper, the Advanced Very High Resolution Radiometer satellite images [160] and stable isotope measurements [124]. The design of such models was urged by governments driven by international agreements [176]. They still require a realistic comparison with experimental results [157].

3.2. Specific activity measurements

Actual CH_4 production by a soil is generally estimated from soil cores incubated in anaerobiosis. The determination of dissolved CH_4 in soil solution is an alternative non-destructive method, which simplifies the sampling procedure [3]. The measurement of

potential methanogenesis requires the addition of various carbon substrates [93]. Using labelled substrates allows to follow, in vitro and in situ, CH_4 production from various substrates. Using this technique allowed to test an anaerobic digestion model used to describe biphasic kinetics of CH_4 formation in tundra soils. It fit the experimental data rather closely and provided the kinetic coefficients of acetogens, and hydrogenotrophic and acetoclastic methanogens [220].

Actual methanotrophy is estimated by using radon as a tracer [58] or inhibiting CH_4 oxidation by methylfluoride (CH_3F). The methanotrophic potential of a soil is estimated by incubation in a close device under an atmosphere enriched with CH_4 (20 % v/v) [122]. Interpreting potential methanotrophic activity data requires to know the incubation conditions because pre-incubating a soil under an atmosphere enriched with CH_4 induces an exponential increase of the activity, as compared with fresh soil, when the soil is exposed to CH_4 concentrations higher than 1 % for more than 12 h [146]. In rice soils submerged after a dry fallow, the ratios between the activities of soils pre-incubated under CH_4 concentrations higher than a few ppm (low affinity) and those pre-incubated under lower concentrations (high affinity) ranged from 10 to 200 [12]. This indicates that soil methanotrophs are more often in a resting cell status than in a stage of maximum activity [122, 133].

Combining methods allowed to estimate simultaneously CH_4 production and consumption and to elucidate the functioning of the ecosystem. Inhibiting CH_4 oxidation by methylfluoride (CH_3F). has been used in situ to quantify CH_4 production and consumption and has shown that methanotrophs may sometimes consume more than 90 % of the CH_4 available in submerged soils [158]. An experiment utilising simultaneously seven methods and four taiga soils [237] showed that (i) at atmospheric concentration of CH_4, oxidation rates where lower than 2 mg $CH_4 \cdot m^{-2} \cdot d^{-1}$, (ii) oxidation occurred in the sixty first centimetres of the soil, (iii) oxidation was maximum in the 10–20 cm zone, (iv) oxidation occurred at CH_4 concentrations lower than 0.9 ppm, (v) 60 % of CH_4 was oxidised into CO_2 and 40 % was incorporated into the biomass, and (vi) exposure to high CH_4 concentrations induced a methanotrophic activity reaching 867 mg $CH_4 \cdot m^{-2} \cdot d^{-1}$.

The kinetic isotope effect for carbon within recent unconsolidated sediments and soils, used in geological studies, allowed to differentiate the various bacterial CH_4 generation and consumption pathways, and elucidated the cycling of labile sedimentary carbon, including a possible anaerobic oxidation [136].

4. ESTIMATION OF ACTIVITIES IN VARIOUS ENVIRONMENTS

As already indicated, flux and activity measurements present a very large variability that may partly refrain interpretation or comparisons. However, using large sets of data allows to draw general conclusions. Estimates presented in this section are from a data base we established from 57 references presenting individual or aggregated data [56, 58, 73, 79, 80, 84, 86, 90, 93, 100, 103, 105, 110, 115, 116, 120, 123, 126, 133, 137, 150, 153, 156, 161, 162, 165, 178, 179, 181, 185, 189, 192, 193, 197, 200, 201, 204, 224, 230, 238, 240, 244, 245]. Twenty-eight different units have been used by authors to express fluxes and activities. In order to allow rough comparisons and analysis of the data, values have been converted in g $CH_4 \cdot ha^{-1} \cdot d^{-1}$ on the basis of 1 200 t soil per hectare and a constant activity during the day.

4.1. Methanogenesis

Data of CH_4 production by soils, mostly obtained from small samples of ricefields soils incubated in anaerobiosis ($n = 45$) range from 0 to 78 kg $CH_4 \cdot ha^{-1} \cdot d^{-1}$. In rice soils enriched with straw ($n = 22$), values may reach 128 kg $CH_4 \cdot ha^{-1} \cdot d^{-1}$. Data dealing with swamps and peat soils ($n = 5$) range from 0 to 50 kg $CH_4 \cdot ha^{-1} \cdot d^{-1}$. The larger range of CH_4 production in rice soils, as compared to uncultivated soils, can at least partly be attributed to an usually higher content in easily mineralisable carbon.

4.2. Methanotrophy

Values are distributed within two large groups. Those corresponding to methanotrophy of high affinity, measured in upland soils, range from 0 to 1.7 kg $CH_4 \cdot ha^{-1} \cdot d^{-1}$. Higher values were obtained in forest soils, lower values were obtained in cultivated soils (*table III*). Among upland soils, forest soils are probably the most efficient CH_4 sink. Their higher methanotrophic activity may partly be attributed to a stimulation by a significant methanogenic activity of the litters [99, 187, 202]. Methane concentration in the ten first centimetres of forest soils in New York state was about 500 ppm [249]. Atmospheric CH_4 oxidation also occurs in extreme environments such as deserts and glaciers, in the floodwater of submerged soils and in the water of the rivers. However, less than 2 % of the CH_4 produced in river sediments is reoxidised in water [250].

Values corresponding to methanotrophic activities of low affinity measured either in situ in methanogenic environment, or in soil samples incubated under an atmosphere enriched with CH_4, range from 0 to 1.7 t $\cdot ha^{-1} \cdot d^{-1}$. The extremely high maximum value was observed in a sandy soil at the top of a landfill [105].

Results confirm the positive correlation between methanotrophy and methanogenesis, the highest methanotrophic activities being observed in methanogenic environments.

Table III. Methanotrophy in various soil types (g $CH_4 \cdot ha^{-1} \cdot d^{-1}$).

Environment	No. of data	Minimum	Maximum	Median
Cultivated soils	13	0.00	866	5.5
Grassland soils	7	1.75	485	6.5
Non-cultivated upland soils	6	0.10	228	8.3
Forest soils	17	0.16	1 659	9.9
Wetland soils	9	0	$7 \cdot 10^5$	172
Upper soil layer in covered landfills	3	$7 \cdot 10^4$	$1.7 \cdot 10^6$	$4.5 \cdot 10^5$

4.3. Methane emission

Methane emission in unplanted upland soils temporarily submerged is around a few $g \cdot ha^{-1} \cdot d^{-1}$. In submerged soils, highest emissions (median: 3 kg $CH_4 \cdot ha^{-1} \cdot d^{-1}$) are observed in ricefields, where the plant biomass provides substrates for methanogenesis and favours CH_4 transfer to the atmosphere, and in freshwater ecosystem without vegetation, which leads to a low methanotrophic activity and high emission by ebullition. In swamps, the median is 700 $g \cdot ha^{-1} \cdot d^{-1}$. Emissions are lower in acidic peat bogs (median: 433 $g \cdot ha^{-1} \cdot d^{-1}$) (*table IV*).

5. ENVIRONMENTAL FACTORS THAT AFFECT METHANE EMISSION

Factors that affect CH_4 emission by soils are those that affect:
– gas diffusion in relation with the oxydo-reduction level and CH_4 transfer, in particular the water content, the nature of the clays and the type of vegetation;
– microbial activities in general: temperature, pH, Eh, substrate availability, physicochemical properties of soils, etc.;
– methanogenesis and in particular the competition with denitrification and sulphate-reduction;
– methane-mono-oxygenase activity: content in H_2, CH_4, ammonium, nitrate, nitrite, and Cu, etc.

Competition and predation may probably affect methanogenic and methanotrophic populations but have not yet been studied [134].

5.1. Physicochemical properties of soils

Little data is available on correlations between soil physicochemical properties and CH_4 emission. They mostly deal with potential methanogenic and methanotrophic activities in ricefield soils for which major physicochemical properties were presented [93, 150, 227]. Results show that interactions are often complex. The study of twenty-nine rice soils in Senegal showed negative correlations between (i) methanogenic potential and (ii) soil conductivity, chlorine content, clay content and C/N ratio [68]. In a study of sixty ricefield soils, no correlation was found between CH_4 production and soil pH in aerobiosis, N-content, organic matter content, soluble C content and cation exchange capacity [227]. Significant correlations may be obtain when grouping soils according to their level of CH_4 production in the absence of organic manuring [227]. Principal component analysis of methanotroph and methanogen counts, potential methanogenic and methanotrophic activities and physicochemical properties in twenty-two ricefield soils [93] indicated that (i) the ratio between potential methanotrophy and potential methanogenesis was mostly governed by methanotrophy, (ii) soils prone to methanotrophy were above neutrality, rich in available P and had a lower clay content, (iii) soil content in active Mn was positively correlated with methanogen and methanotroph densities, and (iv) no correlation was found between soil texture and populations or potential activities [93].

5.1.1. Water content

Soil submersion allows the development of the methanogenic activity and reduces methanotrophic activity by reducing the size of the oxidised zones.

In wet zones in northern USA, variations in CH_4 emission were related with the depth of the water table and the abundance of rooted plants with aerenchyma, both factors being correlated [112, 189]. Laboratory studies with soil cores from swamps and peat bogs

Table IV. Methane emission in different soil types (g $CH_4 \cdot ha^{-1} \cdot d^{-1}$).

Environments	No. of data	Minimum	Maximum	Median
Upland soils temporarily submerged	5	0	216	3
Freshwater environments without plants	5	0	$10 \cdot 10^3$	$3 \cdot 10^3$
Swamps	11	0	$17 \cdot 10^3$	720
Peatlands	4	6	$2 \cdot 10^3$	433
Ricefields	23	1	$29 \cdot 10^3$	10^3

showed that CH_4 emission exhibited a negative logarithmic correlation with the depth of the water table (0 to –60 cm) whereas CO_2 emission exhibited a positive linear correlation with this depth [143]. Upland soils, when temporarily submerged, may become CH_4 sources. This was observed in Canada in grasslands and in well drained cultivated soils when snow was melting or during heavy storms in summer [224].

Soil methanotrophic activity is related to its water content. It increases to a value close to field capacity, then decreases when the water content increases [44, 122]. In poorly drained soils around Canadian forests, CH_4 consumption was negatively correlated with soil water content [123]. In Massachusetts forests, a negative correlation was observed between methanotrophy and soil water content when 60 to 100 % of soil porosity was filled and gaseous transfer was reduced; at low water content (22 to 60 %), methanotrophy depended upon soil fertility and was two to three times higher in most fertile soils [32]. In Norwegian forest soils, a small increase in the water content over the field capacity markedly reduced methanotrophy [198].

Methanotrophs remain viable in anaerobiosis and, in the absence of carbon source, are more preserved in anaerobiosis than in aerobiosis. This explains why soils submitted to alternate desiccation and submersion maintain a high methanotrophic potential when environmental conditions allow its expression [171, 172]. In Danish soils temporarily submerged, CH_4 emission and consumption were maximum during the drying-up of the soil, probably because of increased CH_4 diffusion and oxygenation of the soil [5].

5.1.2. Oxygen availability and soil Eh

In methanogenic environments, O_2 availability is the major factor limiting methanotrophy. Methanotrophs are ubiquitous in ricefield soils, where their densities were not strongly affected by the oxidation status of the soil [93]. In ricefields, CH_4 oxidation was higher in the rhizosphere followed by surface soil (0.1 cm) and the bulk of the soil (10–20 cm) [118]. The importance of O_2 availability was also evidenced in Florida swamps where methanotrophy was significant in peat, where gas diffusion is easy, whereas methanotrophy was negligible in compact clay soils [110]. In submerged soils and freshwater ecosystems, light availability, which allows benthic photosynthetic activity, increases the thickness of the oxidised soil layer and thus CH_4 oxidation.

Laboratory experiments with submerged soils planted with *Spartina patens* and rice and maintained at Eh values of 100, 0, –100, and –200 mV show that Eh affects not only methanogesis but also gas transfer through the plant [113]. At lower Eh, aerenchyma formation increased and the size of the roots decreased. A decrease in Eh from –200 to –300 mV induced a ten-fold increase in CH_4 production and a 17-fold increase in its emission [114].

5.1.3. Organic matter content

The intensity of reduction processes in submerged soils depends upon the content and nature of organic matter (OM), the ability of the microflora to decompose this OM, and the availability and nature of electron acceptors. The Eh of ricefield soils rich in active Fe and organic matter may reach values lower than –200 mV in less than 2 weeks [148]. A positive correlation may therefore be observed between the methanogenic potential and the OM content in soils. In five rice soils in Japan, CH_4 emission ranged from 0.6 to 8.2 g $CH_4 \cdot m^{-2}$ and was maximum in a peat soil where mineralisable C was highest. However, such a correlation was not invariably observed. The study of twenty-nine ricefield soils comprising eighteen saline soils showed a positive correlation between methanogenesis and OM content only in non-saline soils [68], which was explained by the inhibitory effect of salinity on methanogenesis. Similarly, a positive correlation between CH_4 production and OM content was observed only in soils exhibiting a high methanogenic activity [227].

In peat soils, the nature of the OM determined both CH_4 production and consumption, both activities being correlated [143]. In the wet peat soils, significant CH_4 production only occurred from organic matter fractions with a large particle size; the fraction > 2.0 mm contributed 90 % of the total CH_4 production capacity. Methane production capacity strongly decreased with depth; the layer 0–5 cm contributed 70 % of the total CH_4 produced, indicating that recent plant residues are a major substrate for methanogens [217]. Atmospheric CH_4 consumption by a tundra soil increased four times when glucose was added to the soil [234].

5.1.4. pH

The activity of methanogens is usually optimum around neutrality or under slightly alkaline conditions [67] and is very sensitive to variations in soil pH [226]. The minimum pH allowing the growth of 68 methanogenic species was 5.6 [67]. Studies in clay soils in Texas showed that CH_4 emission was four times lower in the most acidic soil with low structural stability [177]. However, methanogens can adapt to acidic environment. Methane production and consumption in peat soils in temperate and subarctic areas (pH 3.5–6.3) was optimum between 5.5 and 7.0 for methanogenesis and between 5.0 and 6.5 for methanotrophy [60]. Methanotrophs are more tolerant to pH variations than methanogens [60]. They are, however sensitive to the acidification of the environment. In non-fertilised permanent grassland at the Rothamsted experimental station, methanotrophy decreased from –67 to –35 nL $CH_4 \cdot L^{-1} \cdot h^{-1}$ when pH decreased from 6.3 to 5.6 and was fully refrained at lower pH [86]. Molecular ecological methods have however evidenced acidophilic methanotroph, non-cultivable on classical media, in peat soils at pH < 4.7 [133].

5.1.5. Soil texture and mineralogy

In submerged soils, texture is involved in (i) the establishment of the anaerobiosis needed for methanogenesis, (ii) protecting organic matter from decomposition, (iii) the transfer and trapping of CH_4 produced in the reduced soil, and (iv) affecting the depth of the oxidised soil layer hosting methanotrophs.

One could expect clay soils, which are poorly drained and prone to anaerobiosis, to favour methanogenesis. The study of 132 ricefield soils in Japan showed CH_4 emissions higher in gley soils than in the other types of soils. On the other hand, a negative correlation was observed between the methanogenic potential and the clay content in ricefield soils in Senegal [68]. More than clay content, the nature of the clay affects CH_4 emission because some clay types protect organic matter from mineralisation [155], which delays methanogenesis. Soils rich in swelling clays are usually more favourable to methanogenesis than sandy soils, silty soils or soils rich in kaolinite, where density increases after submersion, slowing down pH and Eh variations and organic matter decomposition [149]. A field study in two Thailand soils showed that rice straw decomposition was slower in soil rich in kaolinite [149]. However, in Indian ricefields, higher CH_4 emission was reported in inceptisols (8–21 $g \cdot m^{-2}$) than in swelling vertisols (1.5–11 $g \cdot m^{-2}$) [194].

A high clay content can also favour trapping of CH_4 bubbles in soils [178] and decreases emission. In the Philippines, CH_4 emission and production during three crop cycles were markedly higher in a calcareous sandy silt than in a clay soil [52]. In calcareous soils, CH_4 production seems to be partly stimulated by a buffering effect of carbonates [148]. In sandy ricefield soils in Texas, a positive correlation was observed between sand content (18.8 to 32.5 %) and the average CH_4 emission during the crop (15.1 to 36.3 $g \cdot m^{-2}$) [178].

Methane production in different textured model soils demonstrated that a high amount of negative surface charges increased CH_4 production under both oxic and anoxic conditions. Methane production rates in marshland soils increased in the following order: sand < gravel < clayey silt < clay. Indigenous microflora in combination with the sorptive quality of soil particles (clay, silt, organic matter) enabled methanogenic activity in the presence of oxygen, promoting micro-scale anoxia within the slurries [221].

5.1.6. Chemical properties

Nitrate reducers, ferric iron reducers and sulphate reducers constitute a sequence of competitors of methanogens for acetate and electrons [33]. A high Fe content of the soils, which allows a fast Eh decrease after submersion, favours methanogenesis [93, 226]. Ferric iron can have both a chemical impact, because of its reoxidation by root O_2, and a biological impact, by increasing C oxidation into CO_2 [65, 248]. Fe(III) may reduce CH_4 production in ricefield soils by maintaining the activity of the micro-organism implied in its reduction, thus delaying substrate availability for methanogenic bacteria [230].

Methane emission is usually lower in sulphate [245] and acid-sulphate soils [91] than in the other soil types. This mainly results from the competition for H_2 between methanogens and sulphate reducers, but the lower rice productivity in sulphate soils may also contribute to the decrease in CH_4 production. In Thailand, CH_4 emission was ten times lower in sulphate soils (2–4 $mg \cdot m^{-2} \cdot h^{-1}$) than in non-sulphate soils (20–30 $mg \cdot m^{-2} \cdot h^{-1}$) [245]. However, thermodynamical experiments using sixteen ricefields soils showed that CH_4 production depended mainly on the availability of degradable organic substrates rather than the amount of reducible sulphate and ferric iron [247, 248].

Experiments in ricefields showed that an artificial increase in salinity (0.66 $kg \cdot m^{-2}$) decreased CH_4 production by three to four times and its emission by 25 %, which indicated a higher sensitivity of methanotrophy to salinity as compared to methanogenesis [50]. Phosphorus addition on planted rice soils significantly decreased CH_4 emission [131] probably by increasing methanotrophic potential [95]. Heavy metal impact on CH_4 production is complex and generally seems to be inhibitory [142].

5.2. Climatic factors

5.2.1. Temperature

Methanogenesis is optimum between 30 and 40 °C. Low soil temperatures reduce CH_4 production by decreasing the activity of methanogens but also that of other bacteria implied in methanogenic fermentation. The latter seems to be more sensitive than methanogens to temperature variations [42]. Variations in CH_4 production in waterlogged soils in relation with temperature may partly be due to a variation of Q_{10} (relative increase in activity after an increase in temperature of 10 °C) in time for methanogens [219] and different values of Q_{10} for populations which compete with methanogens for H_2: 2.4 for iron reduction, 1.6 for sulphate reduction, and 4.6 for CH_4 production [216].

Laboratory studies with soil cores from swamps and peatlands in Canada showed that CH_4 emission increased by 6.6 times when incubation temperature increased from 10 to 23 °C [143]. In temperate or cold regions, seasonal variations of CH_4 emission were correlated with soil temperature [112]. These were also observed in subtropical zone [19, 161]. However, significant CH_4 emissions were still observed in swamps in winter. Emission rates of 3 to 49 mg $CH_4 \cdot m^{-2} \cdot d^{-1}$ were measured in various wetlands under the snow in northern Minnesota [54].

Methanotrophy seems to be less sensitive to temperature than methanogenesis. Methane production and consumption in temperate and subarctic peats was optimum around 20–30 °C for both activities, with a

broader tolerance for methanotrophy than for methanogenesis [60]. Methanotrophy by soil cores from temperate forest did not show large variation between –1 and 30 °C [108]. Observation in Massachusetts forests showed that methanotrophy was affected between –5 and 10 °C but not between 10 and 20 °C [31]. Significant methanotrophy was still observed in forest soil in Norway at average temperatures lower than 1 °C [198].

Temperature also affect CH_4 transport through the rice plant [152] as shown by a positive correlation between soil temperature at –5 cm and plant conductance for CH_4 [81].

Daily variations of CH_4 emission in ricefields were related with temperature variations during the day [178, 186]. In the Philippines, they followed a consistent pattern, with the highest rates observed in the early afternoon and lowest rates in the early morning [229]. Nycthemeral variations showed emission peaks at night [223] that could be due to a lower activity of methanotrophic bacteria when O_2 was limiting (< 2 ppm) because no photosynthetic activity occurred [170].

5.2.2. Seasonal variations

In methanogenic environments of temperate regions, seasonal variations of CH_4 emission were related to temperature and insolation [201]. At high latitudes such variations were especially marked [137]. In river sediments in Australia, CH_4 emission ranged from < 0.01 in winter to 2.75 $mmol \cdot m^{-2} \cdot h^{-1}$ in summer [19]. However, in temperate ricefields, variation in CH_4 emission during the crop cycle did not correlate with soil temperature whereas nycthemeral variation did [186].

In addition to a direct effect of the temperature, seasonal variation of CH_4 emission by wetlands in temperate climate was also related to the vegetative cycles of plants possessing an aerenchyma, and non-rooted floating vegetation, which may play an important role in CH_4 oxidation, as observed in North Carolina swamps [100].

5.3. Role of the vegetation in submerged soils

5.3.1. In ricefields

The presence of rice strongly increased CH_4 emission by providing C sources [46] and by favouring CH_4 transfer to the atmosphere. In a Louisiana soil, CH_4 emission in 77 d was 50 $kg \cdot ha^{-1}$ in unplanted control and 220 $kg \cdot ha^{-1}$ in planted field [126]. The quantity of CH_4 emitted during the crop cycle was positively correlated ($r^2 = 0.845$, $n = 11$) with the aerial vegetative biomass of rice. Daily production was correlated with the aerial biomass ($r^2 = 0.887$, $n = 93$) and root biomass ($r^2 = 0.816$, $n = 33$). Carbon emitted as CH_4 corresponded to 3 and 4.5 % of the photosynthetic carbon in rice varieties with low or high potential for CH_4 emission, respectively [82]. All yield parameters, including the number of tillers, were correlated with CH_4 emission [193]. As rice yield is usually higher during the dry season than during the rainy season, CH_4 emission is higher during the dry season. In the Philippines, a rice yield of 5.2–6.3 $t \cdot ha^{-1}$ during the dry season corresponded to an average emission of 190 mg $CH_4 \cdot m^{-2} \cdot d^{-1}$ and a yield of 2.4–3.3 $t \cdot ha^{-1}$ during the wet season to 79 mg $CH_4 \cdot m^{-2} \cdot d^{-1}$ [229].

5.3.2. In swamps

In swamps, plants with an aerenchyma favour CH_4 emission by allowing its transfer to the atmosphere [200], whereas plants without aerenchyma reduce its emission, partly because of rhizospheric oxidation. In swamp areas with no vegetation, CH_4 emission by ebullition was higher than that in areas with rooted plants; in the presence of rooted plants, the percentage of CH_4 in the biogas was lower (42–45 %) than in the bare areas (60 %), which confirmed the major role of the rhizosphere in CH_4 oxidation [201]. Methane emission in Hudson Bay peatlands was three to thirty times higher in areas with no vegetation than in the adjacent zones colonised by plants [73].

In Michigan peatlands with a water table at –20 cm, a slight CH_4 consumption (–0.2 to –1.5 mg $CH_4 \cdot m^{-2} \cdot d^{-1}$) was observed in bush zones, whereas emission was observed in areas colonised by plants with aerenchyma [189]. Similarly, in wet tundra soils, no CH_4 emission was observed in the absence of vascular vegetation, indicating that in the absence of CH_4 transport through plants, the upper layer of such soils behaved as an efficient biofilter [111, 212].

Usually, CH_4 emission and the net productivity of cultivated or non-cultivated submerged soils are positively correlated. About 3 % of the daily productivity is emitted as CH_4. The increase in atmospheric CO_2, which increases ecosystem productivity should also increase CH_4 emission by wetlands [45, 239].

Variations of CH_4 flux in a given area might appear as related to vegetation, but relationships are often more complex. In an alpine tundra ecosystem [235], CH_4 production was observed in *Carex* sites. A significantly higher value (seasonal mean: +8.45 mg $CH_4 \cdot m^{-2} \cdot d^{-1}$) in one site as compared with other similar sites (seasonal means: –0.06 and +0.05 mg $CH_4 \cdot m^{-2} \cdot d^{-1}$) was attributed to a shallower snowpack during winter. In *Acomastylis* meadows, which had an intermediate moisture regime, CH_4 oxidation dominated (seasonal mean: 0.43 mg $CH_4 \cdot m^{-2} \cdot d^{-1}$). In a windswept *Kobresia* meadow plant community, which received the least amount of moisture from snowmelt, only CH_4 oxidation was observed (seasonal mean: –0.77 mg $CH_4 \cdot m^{-2} \cdot d^{-1}$). Methane fluxes correlated with a different set of environmental factors within each plant community. In *Carex* plant community, CH_4 emission was limited by soil temperature. In *Acomastylis* meadows, CH_4 oxidation rates correlated positively with soil temperature and negatively with soil moisture. In the *Kobresia* community, CH_4 oxidation was stimulated by precipitation [235].

5.4. Role of soil fauna

In waterlogged ricefields, soil and water fauna, especially aquatic *Oligochaetes*, significantly affect soil texture and Eh, and microbiological activities [170]. One could expect a resulting effect on CH_4 emission but no data is available. A study of the effect of chironomid larvae on CH_4 production, oxidation, and fluxes in a rice soil concluded that they had no effect on CH_4 flux across the sediment surface either by diffusion or by ebullition, but that chironomid tubes were microsites with an intensified microbial activity, where CH_4 production and oxidation might be tightly coupled [97].

6. EFFECTS OF CULTURAL PRACTICES IN WETLANDS

Cultural practices in wetlands (planted mostly with rice but also with other aquatic plants such as jute or waterchestnut) affect CH_4 emission through their effects on methanogenesis, methanotrophy and CH_4 transfer.

6.1. Effect of submersion and water management

Rice is mostly cultivated in submerged conditions because wetland rice has a higher yield (up to 10 $t \cdot ha^{-1}$) than upland rice (0.5 to 4 $t \cdot ha^{-1}$) [47]. The physicochemical processes and successive steps of the establishment of anaerobiosis in ricefield soils that allow methanogenesis after submersion are well known [148]. When the soil is submerged, dissolved O_2 concentration rapidly decreases and facultative anaerobic, then microaerophilic, and finally strict anaerobic micro-organisms develop. They use successively various electron acceptors for their respiration: NO_3^- at Eh values lower than 350 mV, Mn^{4+} at Eh < 200 mV, Fe^{3+} at Eh < 100 mV and SO_4^{2-} at Eh around –150 mV [159]. Strict thiosulphate reduction, which was recently shown to be as important as sulphate reduction in rice soils [62] may develop at an Eh between –150 and –200 mV. Thiosulphate being more reduced than sulphate should be the last electron acceptor before methanogenesis. This succession of reductive reactions may rapidly lead to an Eh around –200 mV, favourable to the reduction of CO_2 into CH_4. Simultaneously, concentrations in CO_2 and HCO_3^- increase, which stabilises soil pH around neutrality. The shift of soil pH toward neutrality after submersion is observed for both acidic and alkaline soils [148]. The depth of the submersion water affects anaerobiosis but also water temperature, which in turn affects microbial activities and CH_4 transfer [83].

Numerous in situ studies report a significant decrease (60 to > 90 %) of CH_4 emission by ricefields that are drained one or several times during the crop cycle [26, 98, 141, 151]. In Texas ricefields, average CH_4 emission expressed in $mg \cdot m^{-2} \cdot d^{-1}$ were 106 for classical continuous irrigation, 56 when the field was drained in the middle of the crop cycle, 13 when the field was drained three times, and 151 for a late continuous irrigation [179]. However, in Indonesia, CH_4 emissions were reportedly similar in fields continuously submerged or weekly drained [153]. Short drainage induce the formation of sulphate and ferric iron, which allows the development of competition for H_2 between methanogens and sulphate reducers + ferro-reducers, which in turn induces an inhibition of methanogenesis that persists after soil reflooding [166]. Water management between crops is also an important factor. A dry fallow emitted less CH_4 during the next crop cycle than a wet fallow [213]. Increasing water percolation in soil might also reduce CH_4 emission [230] but the economic feasibility of this method is doubtful.

A number of water management strategies have been tested to produce more rice with less water [72]. They are based on reduced water depth and reduced time of submersion by maintaining the soil saturated without standing water. For example, a minimum irrigation technology has been developed in China for two decades. It involves the following water management stages: thin water layer at transplanting and during seedling recovery, wet soil without standing water before tillering, drying-up of the soil during tillering (until crack formation on the soil surface), thin water layer from panicle initiation to grain milky stage, and wet soil for the end of the maturation stage. On average, this technique saved 21 % of irrigation water and increased yield by 11.4 %. It has been popularised over 950 000 ha [243]. Such techniques may reduce CH_4 emission but their effect has not yet been determined [230].

6.2. Effect of fertilisers

Rice demand is increasing, whereas the area available to grow rice is already almost fully utilised. Increasing yield requires to increase fertilisation. In most rice producing countries, the use of organic fertiliser has been highly recommended to reduce chemical fertiliser use and maintain soil fertility in the long term. But organic fertilisers (rice straw, green manure or farmyard manure) rich in carbon favour CH_4 production much more than chemical fertilisers do. The nature of fertilisers used, organic or chemical, mainly depend upon the agro-economical conditions, but a right balance should be found to maintain fertility in the long term and mitigate CH_4 emissions.

6.2.1. Organic fertilisers

All in situ studies have shown that organic matter incorporation markedly increased CH_4 emission [26, 98, 126]. As an example, incorporating rice straw (5–12 $t \cdot ha^{-1}$; C/N about 60) increased CH_4 emission by two to nine times in ricefields in Italy [185], Texas [177], Japan [244] and the Philippines [228]. Emission increased linearly with the quantity (0 to 3 %) of straw incorporated [225]. Organic matter incorporation

favoured more CH_4 emission during the dry season when rice biomass is higher, than during the wet season [244]. Methane production and emission decrease when the C content and the C/N ratio of the incorporated material decrease. A high C/N, as in rice straw, usually corresponds to an organic material rich in labile C and thus easily usable by the microflora. Incorporation of *Sesbania* green manure with a lower C/N ratio than straw, increased CH_4 emission by two to five times, according to the quantity incorporated [49, 120]. Incorporating straw compost with low C/N increased CH_4 emission by less than two times. Field experiments showed that the Nouchi model [152] may predict the effect of straw incorporation on CH_4 emission in ricefield soils [22].

Growing *Azolla* (an aquatic fern used as green manure) had a moderating effect on CH_4 efflux from flooded soil that was attributed to an increase in the dissolved oxygen concentration at the soil/floodwater interface [16].

6.2.2. Chemical fertilisers

The reported effects of chemical N-fertilisers on CH_4 emission are complex and sometimes contradictory. They depend on the nature of the fertiliser, the quantity applied [125] and the method of application. By increasing rice productivity, fertilisation may increase CH_4 emission. This was observed with urea applied in continuously flooded ricefields [126]. An increase in soil pH resulting from urea hydrolysis might also have favoured CH_4 production [225]. On the other hand, in intermittently drained ricefields, urea application (100 and 300 kg $N \cdot ha^{-1}$) resulted in a 7 and 14 % decrease (respectively) in CH_4 emission as well as in an increase in N_2O emission [29].

Electron acceptors other than CO_2, especially nitrate and sulphate, may cause bacterial competition unfavourable to methanogens and decrease CH_4 production/emission. As H_2 and acetate are preferentially used by sulphate-reducing bacteria, sulphate application generally reduces methanogen activity. Ammonium sulphate was frequently reported to significantly (30 to 60 %) reduce CH_4 flux from ricefields [26, 29, 185]. When $(NH_4)_2SO_4$ was applied, the inhibition of CH_4 production was not associated with an increase in soil Eh, which did not change significantly; a direct inhibitory effect of sulphate on methanogenesis was assumed [225]. Despite some contradictory results showing an increase in CH_4 emission after ammonium sulphate application [35], most data support the idea that ammonium sulphate use is a possible way to reduce CH_4 emission from ricefields. Gypsum (calcium sulphate) is used to restore the fertility of saline and/or alkaline rice soils. An additional effect is a significant decrease of CH_4 emission (–29 to –46 % with applications of 1 and 2 $t \cdot ha^{-1}$ gypsum [127], 50 to 70 % with application of 6.6 $t \cdot ha^{-1}$ [48], 47, 46 and 51 % with applications of 2.5, 5 and 10 $t \cdot ha^{-1}$ [130]). This inhibitory effect seems to be independent from the nature of the N-fertiliser used: the application of 6.7 $t \cdot ha^{-1}$ gypsum reduced CH_4 emission by 50 and 70 % in ricefields fertilised with urea or green manure, respectively [48]. However, sulphate addition might be detrimental to rice by favouring rhizospheric sulphate-reduction [47].

Similarly, nitrate application causes a competition for H_2 between denitrifying bacteria and methanogens, that favours denitrifying bacteria. Nitrate is also an oxidant that reduces CH_4 emission by increasing soil Eh [96, 174]. This inhibitory effect was reported to be short-termed: addition of 300 $mg \cdot kg^{-1}$ NO_3^--N increased soil Eh by 220 mV and almost completely inhibited CH_4 production, but soon after, the applied NO_3^- was reduced through denitrification and CH_4 production increased [225].

A number of experiments have compared different fertilisers and modes of application. They confirm the advantage of ammonium sulphate which may reduce CH_4 emission by 50–60 % as compared with urea [106, 125]. In Louisiana ricefields, the control without N-fertiliser emitted 60 kg $CH_4 \cdot ha^{-1} \cdot$crop $cycle^{-1}$. Applying 60 kg $N \cdot ha^{-1}$ increased emission by 10 kg with ammonium sulphate, 20 kg with potassium nitrate, and 50 kg with urea. Applying 120 kg $N \cdot ha^{-1}$ increased emission by 40 kg with ammonium sulphate, 30 kg with potassium nitrate, and 160 kg with urea. Ammonium itself might also indirectly inhibit CH_4 production, nitrates produced by its nitrification being inhibitory for methanogenesis [40, 96]. On the other hand, ammonium being inhibitory for methanotrophy, may reduce CH_4 reoxidation and increase its emission [40].

Methane emission seems to be reduced when N-fertiliser is incorporated, as compared with surface application [185]. In a rain-fed lowland ricefield, deep placement of urea super-granules reduced CH_4 emissions as compared with prilled urea broadcasting [167]. A higher emission when N-fertiliser was surface-applied might be due to an inhibitory effect of ammonium on methanotrophy, which was observed in oxic soils [134] but also at the soil-water interface in a submerged soil [40].

The increased CH_4 emission due to organic manure can be mitigated by combining organic and mineral fertilisation. Ammonium sulphate combined with organic manure reduced emission by 58 % as compared with organic manure alone and increased yield by 32%. Emission peaks were suppressed at tillering and during the reproductive stages of rice [190]. Experiments in Indonesia also showed a significant decrease in CH_4 emission when organic manure was combined with ammonium sulphate and even urea [154].

6.3. Effect of pesticides and microbial inhibitors

Little data are available on the impact of pesticides on CH_4 emission under laboratory conditions. Herbicide bromoxynil and insecticide methomyl inhibited CH_4 oxidation in soil slurries [209]. A commercial formulation of fungicide tridemorph to a tropical flooded rice soil stimulated CH_4 production at low levels (5–20 $\mu g \cdot g^{-1}$) but inhibited the process at

50–100 $\mu g \cdot g^{-1}$. Oxidation of CH_4 was progressively inhibited with increasing concentrations of the fungicide [15].

Acetylene inhibits nitrification and methanogenesis. When applied as encapsulated calcium carbide, it was slowly liberated and decreased by 90 % CH_4 emission and N_2O emission, which reduced N-losses [24]. In situ, calcium carbide application reduced CH_4 emission by 35 % [129] and increased rice yield by 30 % [9]. Dicyandiamide, another nitrification inhibitor, also reduced CH_4 emission [129].

In both upland and wetland soil, methanotrophy was inhibited by nitrification inhibitors (thiourea, sodium thiosulphate, dicyandiamide, nitrapyrine, calcium carbide). This was attributed to the structural similarity between methanotrophic and nitrifying bacteria. The urease inhibitor N-(*n*-butyl) thiophosphoric triamide (NBPT) also inhibited methanotrophy [25, 118].

Bacterial inhibitors are still at the experimental level and adoption by farmers is strongly refrained by technical and economical constraints. In particular, the application of urease or nitrification inhibitors is not common in rice cultivation. However, as calcium carbide significantly reduces CH_4 emission and increases rice yield through its inhibitory effect on nitrification, it has a potential for adoption.

6.4. Effect of rice varieties

The increasing demand for rice has led to the selection of rice varieties with a high productivity (high grain/straw ratio), efficient in utilising soil nitrogen, and resistant to parasites and diseases. Some recent studies deal with the selection of varieties with an aerenchyma that reduces CH_4 transfer.

Varietal differences in CH_4 emission have been demonstrated. Under continuous irrigation, average emission was 20 mg $CH_4 \cdot m^{-2} \cdot h^{-1}$ for IR64 and 14 mg $CH_4 \cdot m^{-2} \cdot h^{-1}$ for Cisadane variety [83]. Varietal differences of almost 500 % were observed for Chinese rice varieties [190]. Watanabe et al. [231] have shown that CH_4 emission differed among varieties but could not evidence correlations with rice type (japonica, indica), the number of tillers, the height and the biomass of the plant, or the root biomass. Rice variety IR65597 emitted about 30 % less CH_4 than the traditional variety Dular, whose stems and roots are more developed [151, 222]. Short varieties tested in Louisiana emitted less CH_4 (185 $kg \cdot ha^{-1}$) than those with high stems (300 $kg \cdot ha^{-1}$) [128].

Root exudation, which produces organic substrates directly or indirectly utilised for CH_4 production, varies qualitatively and quantitatively with rice varieties [119, 135]. This allows to select varieties that produce less exudates and root exfoliations. However, such characteristics reduce the plant's ability to favour associative N_2-fixation and efficiently use soil nitrogen [119].

6.5. Dynamics of methane emission during the crop cycle

Methane emission during the rice crop cycle varies with substrate availability, soil Eh, and cultural practices. Different dynamics were reported [150, 178, 196, 245]. Three emission peaks may occur during the crop cycle. The first peak, observed shortly after submersion, is attributed to the decomposition of the easily mineralisable organic matter; it is usually observed in soil where organic manure was applied [150, 231]. A second peak is usually observed during the reproducing phase of the crop and seems to be related to an increased rhizospheric exudation. The incorporation into the soil of the photosynthetic aquatic biomass by weeding and by the activity of the soil fauna also provides organic matter to the soil [170] and may contribute to the anaerobic fermentation process at this stage. A third peak observed at the end of the crop cycle could result from an input of organic matter due to root exfoliation and plant senescence. Variations during the crop cycle cannot generally be attributed to temperature variations [186] and depend mostly on substrate availability for CH_4 production. A last peak of emission is observed after rice harvest, when discontinuing irrigation leads to the formation of soil cracks through which trapped CH_4 escapes [28]. This peak was reported to provide about 10 [52] to 20 % [229] of the CH_4 emitted during the whole cycle.

Dominant activities of the trophic groups of methanogens vary during the crop cycle. Acetotrophy contribution to CH_4 produced decreased from 67–80 % at the beginning of the crop cycle to 29–60 % during the crop cycle [215].

In most cases, CH_4 emission by ricefields was higher during the second half of the crop cycle. In California, CH_4 emission was 5 g $CH_4 \cdot m^{-2}$ during the two to three last weeks before harvest while average emission during the crop was 0.25 g $CH_4 \cdot m^{-2}$ [36]. In Texas more than 75 % of total CH_4 was emitted during the last 5 weeks of the crop cycle [82]. Maximum emission values were observed during flowering [79, 193] and maturation stages [82, 229], which corresponded to about 50 % of the total rice biomass [82]. The percentage of carbon from the photosynthetic production emitted as CH_4 increased from 0.9–2.0 during the vegetative phase to 3.6–5.0 during the reproductive phase and to 7.9–8.3 during the maturation phase [82]. However a maximum emission was reported during the first half of the crop cycle in three types of ricefield soils in Thailand [91].

7. EFFECTS OF CULTURAL PRACTICES IN UPLANDS AND FORESTS

Cultural practices in upland soils mostly affect their potential to oxidise atmospheric CH_4. Nitrogen fertilisation that lead directly or indirectly to an increase in the NH_4 content of the soil has an inhibitory effect on CH_4 oxidation, through competition at the level of the

methane-mono-oxygenase towards nitrification [30, 146] and the toxicity of NO_2 produced. Cultural practices that destroy micro-aerophilic niches suitable for CH_4 oxidisers also reduces atmospheric CH_4 oxidation [86, 199].

7.1. Fertilisers

7.1.1. Organic fertilisers

Green manure incorporation (clover residues) in upland cultivated and forest soils in Louisiana reduced methanotrophy by an average 42 % [146]. On the other hand, long-term experiments (140 year) at Rothamsted Experimental station (UK) did not show any inhibitory effect of organic manure on the soil potential to oxidise atmospheric CH_4 [85]. Most probably, the difference between both treatments was a greater release of ammonium by green manure as compared with farmyard manure with a lower C/N ratio.

7.1.2. Chemical fertilisers

In upland soils, the effect of N-fertilisation on soil potential to oxidise atmospheric CH_4 markedly varies with the nature and the quantity of fertilisers applied. Ammonium and urea usually inhibit atmospheric CH_4 oxidation and nitrate does not. In particular, the inhibitory effect of ammonium is well demonstrated [25, 40, 59, 105, 118, 134, 146, 199]. Long-term experiments at Rothamsted in a 1-km^2 area have classified the CH_4 oxidising potential of soils in the following order: forest > pastures > cultivated soils [241], which indirectly demonstrates a relationship between the quantity of fertiliser applied and the level of CH_4 oxidation in soils. Similarly, the comparison of thirteen soils of same origin, in Scotland, Denmark and Poland, either planted with trees or cultivated, showed that putting a soil under culture reduced its CH_4 oxidation activity by about 60 % [156].

In cultivated soils of the Rothamsted Experimental Station, mineral N-fertiliser ($(NH_4)_2$ SO_4 and KNO_3), inhibited atmospheric CH_4 oxidation whereas organic fertilisation did not [85]. Mineral N applied annually as $(NH_4)_2SO_4$, at 96 or 144 kg $N{\cdot}ha^{-1}$ for 130 years, completely inhibited CH_4 oxidation, even where lime was applied to maintain a soil pH of about 6. By contrast, the long-term application of N as $NaNO_3$ (96 kg $N{\cdot}ha^{-1}$) caused no decline in CH_4 oxidation as compared to unfertilised grassland at the same pH; in some cases, it caused a small increase. Withholding NH_4-N for 3 years caused no significant recovery of CH_4 oxidation; withholding NO_3-N caused a slight decline [86]. In the pasture, the CH_4 oxidation potential significantly decreased in plots fertilised for 138 years with ammonium fertiliser whereas it was not affected by nitrate fertiliser [241]. The inhibitory effect of N-fertilisation was also observed in soils under dryland rice [195] and in peat soils that were drained and fertilised, inhibition being faster with NH_4Cl as compared to KNO_3 and urea [43]. The inhibitory of mineral N observed in upland agricultural soils was also reported in landfill soils (sixty-four inhibition by NH_4NO_3) [105].

In fertilised forest soils, ammonium had a partial inhibitory effect on atmospheric CH_4 oxidation. The level of inhibition (15–40 %) was positively correlated either with the quantity of fertiliser applied or the content of the soil in available N [198]. An inverse relationship between N-availability and CH_4 uptake was also observed in temperate forest soils [202]. In forest soils of Massachusetts, applying 50 and 150 kg NH_4NO_3-$N{\cdot}ha^{-1}{\cdot}year^{-1}$ reduced atmospheric CH_4 oxidation by 15 and 64 % respectively [31]. Urea application in pine forest soils in Florida reduced it by five to twenty times [30].

The inhibition of CH_4 oxidation in soils by NH_4 is attributed to a competition at the level of the methane-mono-oxygenase, a transfer of the CH_4 oxidising activity towards nitrification [30, 146] and the toxicity of NO_2 produced. Observations with forest soils showed that nitrite, the end product of methanotrophic ammonia oxidation, was a more effective inhibitor of CH_4 consumption than ammonium [182]. This inhibition only affected atmospheric CH_4 oxidation and could persist after nitrification of the added NH_4^+ [146] and become irreversible [109]. The inhibition can be released at CH_4 concentrations higher than 100 ppm [109].

On the other hand, N-fertiliser application in infertile environments such as acidic meadows, where atmospheric CH_4 oxidation is negligible, can significantly increase this activity. Methane oxidation activity in a *Calluna* meadow increased from 0.01 to 0.28 mg $CH_4{\cdot}m^{-2}{\cdot}d^{-1}$ after applying 112 kg $N{\cdot}ha^{-1}{\cdot}year^{-1}$ for 6 years, which allowed a significant growth of grasses in the ecosystem [116].

Upland soils are generally behaving as CH_4 sinks, however some can also behave as CH_4 sources as observed in a sugarcane soil where chemical fertilisers had effects similar to those observed in wetlands: CH_4 emission (297 to 1 005 g CH_4-$C{\cdot}ha^{-1}$) occurred from plots fertilised with urea whereas CH_4 consumption (442 to 467 g CH_4-$C{\cdot}ha^{-1}$) was measured in plots fertilised with ammonium sulphate only [233].

7.2. Other cultural practices

In upland soils, soil compaction by agricultural equipment may reduce CH_4 oxidation by half [74]. In cultivated soils in Germany, direct seeding with no ploughing of the soil increased CH_4 oxidation by six to eight times as compared with ploughed soil [84]. A possible cause of the reduction of CH_4 oxidising activity in ploughed soils is the destruction of micro-aerophilic niches and the organic matter enriched layer that develops at the top of uncultivated soils [86, 199]. The gas exchange response of different soil types to tillage, particularly CH_4 oxidation rate, which is affected by long-term soil structural damage, is a potentially useful aspect of soil quality when taken in conjunction with other qualities [8].

8. CONCLUSION

8.1. Potential ways for mitigation

8.1.1. Cultivated methanogenic soils: ricefields

Cultivated wetlands are mostly ricefields. Strategies to reduce CH_4 emission by ricefields may be oriented toward (i) reducing CH_4 production, (ii) increasing CH_4 oxidation, and (iii) reducing CH_4 transport through the plant. Potential techniques include water, fertiliser management, cropping pattern, varietal selection, and, possibly, the use of selective inhibitors.

8.1.1.1. Water management

Introducing drainage periods during the crop cycle appears to be the most efficient management practice to reduce CH_4 emission from ricefields. Irrigated rice is susceptible to water deficiency during the flowering and grain formation stages [47]; therefore, long drainage period should be avoided during theses stages. However, when intermittent drainage is properly used, it does not reduce grain yield [179]. A drainage of a few days at the beginning of the crop cycle favours the anchorage of the young seedling, their growth during tillering and soil N-mineralisation. Drainage also reduces the accumulation of toxic organic acids in the soil and help control vectors of human diseases [170]. It was extrapolated that introducing intermittent drainage periods in 33 % of the poorly drained ricefields in China could reduce by 10 % the agricultural CH_4 emissions (9.9 ± 3.0 Tg) in this country [101]. However, intermittent drainage has also some disadvantages. It may consume two to three times more water than continuous flooding [179]. It may also increase nitrification and N-losses by denitrification and the emission of N_2O, another greenhouse gas, during resubmersion of the soil [26, 29, 166]. Finally, intermittent drainage requires a good soil levelling and water management facilities that are available only in a small percentage of wetland ricefields [101, 246].

8.1.1.2. Fertilisation and nitrification inhibitors

The methods of fertilisation known to reduce CH_4 emission include: (i) combining organic fertilisers with mineral N-fertiliser; (ii) preferential utilisation of sulphate-containing fertilisers in environments not prone to toxicities due to sulphate reduction; and (iii) deep placement or incorporation of N-fertiliser, which has also additional advantages such as decreasing N-loss by volatilisation, favouring photodependent biological N_2-fixation, and decreasing the incidence of the vectors of human diseases [170]. Acetylene, brought as encapsulated calcium carbide, increased rice yield by 30 % through its inhibitory effect on nitrification [9] but also decreased CH_4 emission by 35 %. Calcium carbide has therefore a significant potential for adoption.

8.1.1.3. Varietal selection

Rice varietal differences in CH_4 emission of almost 500 % have been reported. Shao and Li [190] defined suitable traits for reducing CH_4 emission as a low level exudation, a large root biomass growing preferentially in the oxidised soil layer, tillers with a structure reducing CH_4 transportation. However such characteristics are the opposite of those required to favour biological N_2 fixation and a high ability to utilise soil N.

8.1.1.4. Crop successions

The cumulative CH_4 emission from tropical rice ecosystems can indeed be lowered by growing suitable upland crops to reduce the submersion period during the annual cropping cycle. Field experiments in India have shown cumulative CH_4 flux of 12–13 g $CH_4 \cdot m^2$ from an upland crop followed by a lowland rice crop and 40 g $CH_4 \cdot m^2$ in a rice-rice rotation. The seasonal CH_4 emission from the lowland rice grown in the wet season was lower after an upland dry season crop than after a dry season flooded rice [2]. Ratoon rice, which already possesses a developed root biomass, emitted much more CH_4 (540–830 kg $CH_4 \cdot ha^{-1}$) than the initial crop (185–300 kg $CH_4 \cdot ha^{-1}$) [128].

8.1.1.5. Techniques suitable for adoption in rice cultivation

According to the International Rice Research Institute [89], high emission rates are associated with specific management practices, some of which can be modified to reduce emissions without affecting yield. Mitigation strategies that may improve rice productivity can be derived from the following findings [89]:

– Temporary soil aeration reduces CH_4 emission while maintaining rice yields. Temporary soil aeration can also reduce water demand in fields that have an impermeable subsoil. A number of water management strategies have been tested to produce more rice with less water [72]. They rely on reduced water depth and time of submersion. They may also reduce CH_4 emission.

– Modern rice plants are characterised by low root exudation leading to relatively low CH_4 emission rates. Plants grown under sufficient nutrient supply have less root exudation than those grown under nutrient deficiencies, e.g. for phosphorus.

– The increment in CH_4 emission rates triggered by organic manure can be greatly reduced by applying compost residues, which in turn improve soil fertility.

– Methane production and denitrification, the main mechanism for N-losses, are inhibited by a largely identical set of factors. The use of nitrification inhibitors reduces both N-losses and CH_4 emission.

– Direct seeding, instead of transplanting, reduces CH_4 emission with no negative impact on yield.

8.1.2. Cultivated upland soils and forests

Upland cultivated soils are CH_4 sinks whose efficiency is markedly reduced by cultural practices.

Methods identified as non or less detrimental for the CH_4 oxidising potential of such soils are (i) using organic [85] and/or nitrate N-fertilisers [241] and (ii) direct seeding with no ploughing [84]. Forest soils are usually efficient CH_4 sinks. When fertilised, they are often treated with urea in the form of super-granules or briquettes of a few grams. Urea application is known to decrease methanotrophy by five to twenty times [30]. This inhibitory effect was avoided when fertilisation was brought as $(NH_4)_2SO_4$ in solution [236].

Ammonium fertilisation of cultivated fields, grasslands and forests causes an irreversible inhibition of the atmospheric CH_4 oxidation potential of these soils. The use of nitrate fertiliser and/or organic fertilisers should be encouraged in such soils.

Obviously, techniques that may contribute to reduced atmospheric CH_4 concentration through the management of cultivated wetland and upland soils must, to be adopted, have a significant advantage for farmers. This reduces the applicability of identified potential methods. Further studies to verify the mitigation options should focus on feasibility for local farmers [146].

8.1.3. Non-cultivated soils

Uncultivated soils are in most cases 'orphan sites' with regard to the mitigation of CH_4 emission. Management practices that reduce emission in wetlands and oxidation in uplands will be financed only if they have a significant economical impact in the short term. For example the drainage of malaria-prone swamps or that of peat areas to allow cultivation will contribute to reduce CH_4 emissions. Improving the fertility of acid meadows to allow sheep raising will increase soil methanotrophic activity through the growth of grass [116].

8.2. Gaps in knowledge

The main gap in basic knowledge deals with the microflora involved, which is still very imperfectly understood. Recent studies demonstrate the implication of numerous uncultivable strains in the CH_4 cycle. In particular CH_4-oxidising bacteria responsible for the consumption of atmospheric CH_4 are largely unknown. Micro-organisms that have been isolated and most studied are not necessarily those that are the only or the most active in soil.

The development of methods to establish global and regional budgets of greenhouse gases has been for a significant part driven by international agreements requiring governments to establish emission inventories and to develop means to stabilise or reduce national emissions. Although techniques and models for quantifying gas fluxes have improved considerably for some gases and sources, large uncertainties remain at the national, regional and global budgets [176]. Estimating CH_4 emission in a region or a broad type of environment (i.e. ricefields) requires the measurement of emission rates under a representative set of environmental conditions. However, identifying the factors that control emissions rates is difficult, and there are uncertainties in determining how many different environmental combinations have to be studied to characterise the source. Specific local emission rates must be extrapolated to regional or global scales, and while scale-specific data may be available, they are much more uncertain than the measured emission rates [104]. As pointed out by Milich [138], "the greatest uncertainty arises in associating measured emission rate with an uncertain extrapolant, even though both the extrapolant and the emission rate may be accurately known. Usually the extrapolant came from data that were obtained for purposes other than global change".

Cultivated wetland areas (ricefields) are generally better characterised and quantified in terms of type of CH_4 source than non-cultivated wetlands but uncertainties still remain. For example, CH_4 emission estimates from Chinese ricefields obtained using several methods suggested emission value of 13.0 ± 3.3 $Tg \cdot year^{-1}$ and a range from 9.7 to 16.2 $Tg \cdot year^{-1}$ [176].

Uncultivated wetlands are often poorly characterised as CH_4 sources and the corresponding area is often difficult to estimate because of:

– the lack of regional data; the work of Barnaud [11] is an example of the difficulties encountered in obtaining geographical quantitative data on natural wetlands in France;

– their large variability in time; for example, in the tropics, variations in precipitation are the major source of seasonal changes and affect sometimes quite dramatically the extent of land inundation [138], which renders extrapolations difficult;

– problems in the legal definitions of wetlands; the national Council for Science and the Environment (USA) has established a web site devoted to 'Wetland Issues' (URL: http://www.cnie.org/nle/crswet.html). Among the twelve reports presented, none refers to CH_4, and the wetland classification used is based mostly on aspects dealing with the conservation of the aquatic environment and wildlife, an approach that is of little use for extrapolating CH_4 emissions.

Despite the uncertainties on the contributions of soils of various cultivated and non-cultivated environments to the CH_4 global budget, it is clear that soils constitute at the global scale a major CH_4 source: production in wetlands is obviously much larger than consumption in uplands. On a short-term basis, the most promising approach to decreasing production by soils is obviously through adequate water management of ricefields. A large range of other approaches has been identified, their potential for adoption will primarily depend on economical aspects.

9. RELATED WEB SITES

Additional information can be found at the following WEB sites:

The Intergovernmental Panel on Climate Change (IPCC): http://www.ipcc-nggip.iges.or.jp/

Publications IPCC: http://www.ipcc.ch/pub/pub.htm

The World Resource Institute: http://www.wri.org/

National Council for Science and the Environment: http://www.cnie.org/

National Library for the Environment: http://www.cnie.org/nle/

United States Environmental Protection Agency: http://www.epa.gov/globalwarming/

MIT Joint Program on the Science and Policy of Global Change: http://salticus-peckhamae.mit.edu/afs/athena.mit.edu/org/g/globalchange/www/

International Rice Research Institute (IRRI): http://www.cgiar.org/irri/

REFERENCES

[1] Adhya T.K., Rath A.K., Gupta P.K., Rao V.R., Das S.N., Parida K.M., Parashar D.C., Sethunathan N., Methane emission from flooded rice fields under irrigated conditions, Biol. Fert. Soils 18 (1994) 245–248.

[2] Adhya T.K., Mishra S.R., Rath A.K., Bharati K., Mohanty S.R., Ramakrishnan B., Rao V.R., Sethunathan N., Methane efflux from rice-based cropping systems under humid tropical conditions of eastern India, Agric. Ecosyst. Environ. 79 (2000) 85–90.

[3] Alberto M.C.R., Arah J.R.M., Neue H.U., Wassmann R., Lantin R.S., Aduna J.B., Bronson K.F., A sampling technique for the determination of dissolved methane in soil solution, Chemosphere-Global Change Sci. 2 (2000) 57–63.

[4] Alperin M.J., Reeburg W.S., Geochemical observations supporting anaerobic methane oxydation, in: Crawford R.L., Hanson R.S. (Eds.), Microbial Growth on C1 Compounds, Am. Soc. for Microbiology, Washington DC, 1985, pp. 282–289.

[5] Ambus P., Christensen S., Spatial and seasonal nitrous-oxide and methane fluxes in Danish forest-ecosystems, grassland-ecosystems, and agroecosystems, J. Environ. Qual. 24 (1995) 993–1001.

[6] Asakawa S., Hayano K., Populations of methanogenic bacteria in paddy field soil under double cropping conditions (Rice-Wheat), Biol. Fert. Soils 20 (1995) 113–117.

[7] Asakawa S., Morii H., Akagawa-Matsushita M., Koga Y., Hayano K., Characterization of *Methanobrevibacter arboriphilicus* SA isolated from a paddy field soil and DNA-DNA hybridization among *M. arboriphilicus* strains, Int. J. Syst. Bact. 43 (1993) 683–686.

[8] Ball B.C., Scott A., Parker J.P., Field N_2O, CO_2 and CH_4 fluxes in relation to tillage, compaction and soil quality in Scotland, Soil Tillage Res. 53 (1999) 29–39.

[9] Banerjee N.K., Mosier A.R., Uppal K.F., Goswami N.N., Use of encapsulated calcium carbide to reduce denitrification losses from urea fertilized flooded rice, Mitteil. Deutsche Bodenkund. Gesellsch. 60 (1990) 245–248.

[10] Banker B.C., Kludze H.K., Alford D.P., Delaune R.D., Lindau C.W., Methane sources and sinks in paddy rice soils - Relationship to emissions, Agric. Ecosyst. Environ. 53 (1995) 243–251.

[11] Barnaud G., Conservation des zones humides: concepts et méthodes appliqués à leur caractérisation, thèse de doctorat, université de Rennes-I (1997) Coll. Patrimoines Naturels, vol. 34, Service du Patrimoine Naturel / IEGB / MNHN, Paris,1998.

[12] Bender M., Conrad R., Kinetics of CH_4 oxidation in oxic soils exposed to ambient air or high CH_4 mixing ratios, FEMS Microbiol. Ecol. 101 (1992) 261–270.

[13] Bender M., Conrad R., Kinetics of methane oxidation in oxic soils, Chemosphere 26 (1993) 687–696.

[14] Bender M., Conrad R., Methane oxidation activity in various soils and fresh-water sediments - occurrence, characteristics, vertical profiles, and distribution on grain-size fractions, J. Geophys. Res. Atmos. 99 (1994) 16531–16540.

[15] Bharati K., Mohanty S.R., Adhya T.K., Banerjee A., Rao V.R., Sethunathan N., Influence of a commercial formulation of tridemorph on methane production and oxidation in a tropical rice soil, Chemosphere 39 (1999) 933–943.

[16] Bharati K., Mohanty S.R., Singh D.P., Rao V.R., Adhya T.K., Influence of incorporation or dual cropping of Azolla on methane emission from a flooded alluvial soil planted to rice in eastern India, Agric. Ecosyst. Environ. 79 (1998) 73–83.

[17] Blake D.R., Rowland F.S., Continuing worldwide increase in tropospheric methane, 1978 to1987, Science 239 (1988) 1129–1131.

[18] Bodelier P.L.E., Frenzel P., Contribution of methanotrophic and nitrifying bacteria to CH_4 and NH_4^+ oxidation in the rhizosphere of rice plants as determined by new methods of discrimination, Appl. Environ. Microbiol. 65 (1999) 1826–1833.

[19] Boon P.I., Mitchell A., Methanogenesis in the sediments of an Australian fresh-water wetland - comparison with aerobic decay, and factors controlling methanogenesis, FEMS Microbiol. Ecol. 18 (1995) 175–190.

[20] Boone D.R., Whitman W.B., Rouviere P., Diversity and taxonomy of methanogens, in: Ferry J.G. (Ed.), Methanogenesis, Chapman and Hall Co., New York, 1993, pp. 35–80.

[21] Bosse U., Frenzel P., Activity and distribution of methane-oxidizing bacteria in flooded rice soil microcosms and in rice plants (*Oryza sativa*), Appl. Environ. Microbiol. 63 (1997) 1199–1207.

[22] Bossio D.A., Horwatha W.R., Mutters R.G., van Kessel C., Methane pool and flux dynamics in a ricefield following straw incorporation, Soil Biol. Biochem. 31 (1999) 1313–1322.

[23] Bowman J.P., Jimenez L., Rosario I., Hazen T.C., Sayler G.S., Characterization of the methanotrophic bacterial community present in a trichloroethylene-contaminated subsurface groundwater site, Appl. Environ. Microbiol. 59 (1993) 2380–2387.

[24] Bronson K.F., Mosier A.R., Effect of encapsulated calcium carbide on dinitrogen, nitrous oxide, methane, and carbon dioxide emissions from flooded rice, Biol. Fert. Soils 11 (1991) 116–120.

[25] Bronson K.F., Mosier A.R., Suppression of methane oxidation in aerobic soil by nitrogen fertilizers; nitrification inhibitors; and urease inhibitors, Biol. Fert. Soils 17 (1994) 263–268.
[26] Bronson K.F., Neue H.U., Singh U., Automated chamber measurement of CH_4 and N_2O flux in a flooded rice soil. I. Effect of organic amendments, nitrogen source, and water management, Soil Sci. Soc. Am. 61 (1997) 981–987.
[27] Butterbachbahl K., Papen H., Rennenberg H., Impact of gas transport through rice cultivars on methane emission from rice paddy fields, Plant Cell Environ. 20 (1997) 1175–1183.
[28] Byrnes B.H., Austin E.R., Tays B.K., Methane emissions from flooded rice soils and plants under controlled conditions, Soil Biol. Biochem. 27 (1995) 331–339.
[29] Cai Z.C., Xing G.X., Yan X.Y., Xu H., Tsuruta H., Yagi K., Minami K., Methane and nitrous oxide emissions from rice paddy fields as affected by nitrogen fertilizers and water management, Plant Soil 196 (1997) 7–14.
[30] Castro M.S., Peterjohn W.T., Melillo J.M., Gholz H.L., Lewis D., Effects of nitrogen fertilization on the fluxes of N_2O, CH_4, and CO_2 from soils in a Florida slash pine plantation, Can. J. For. Res. 24 (1994) 9–13.
[31] Castro M.S., Steudler P.A., Melillo J.M., Aber J.D., Bowden R.D., Factors controlling atmospheric methane consumption by temperate forest soils, Global Biogeochem. Cycles 9 (1995) 1–10.
[32] Castro M.S., Steudler P.A., Melillo J.M., Aber J.D., Millham S., Exchange of N_2O and CH_4 between the atmosphere and soils in spruce-fir forests in the Northeastern United-States, Biogeochemistry 18 (1992) 119–135.
[33] Chidthaisong A., Conrad R., Turnover of glucose and acetate coupled to reduction of nitrate, ferric iron and sulfate and to methanogenesis in anoxic ricefield soil, FEMS Microbiol. Ecol. 31 (2000) 73–76.
[34] Cicerone R.J., Oremland R.S., Biogeochemical aspects of atmospheric methane, Global Biogeochem. Cycles 2 (1988) 299–327.
[35] Cicerone R.J., Shetter J.D., Sources of atmospheric methane: measurements in rice paddies and a discussion, J. Geophys. Res. 86 (1981) 7203–7209.
[36] Cicerone R.J., Shetter J.D., Delwiche C.C., Seasonal variation of methane from a California rice paddy, J. Geophys. Res. 88 (1983) 11022–11024.
[37] Conrad R., Control of methane production in terrestrial ecosystems, in: Andreae M.O., Schimel D.S. (Eds.), Exchange of Trace Gases between Terrestrial Ecosystems and the Atmosphere. Dahlem Workshop Reports, Life Sciences Research Report 47, Wiley, New York, 1989, pp. 39–58.
[38] Conrad R., Klose M., How specific is the inhibition by methyl fluoride of acetoclastic methanogenesis in anoxic ricefield soil? FEMS Microbiol. Ecol. 30 (1999) 47–56.
[39] Conrad R., Klose M., Anaerobic conversion of carbon dioxide to methane, acetate and propionate on washed rice roots, FEMS Microbiol. Ecol. 30 (1999) 147–155.
[40] Conrad R., Rothfuss F., Methane oxidation in the soil surface layer of a flooded ricefield and the effect of ammonium, Biol. Fert. Soils 12 (1991) 28–32.
[41] Conrad R., Bak F., Seitz H.B., Thebrath B., Mayer H.P., Schutz H., Hydrogen turnover by psychrotrophic homoacetogenic and mesophilic methanogenic bacteria in anoxic paddy soil and lake sediments, FEMS Microbiol. Ecol. 62 (1989) 285–294.
[42] Conrad R., Lupton F.S., Zeikus J.G., Hydrogen metabolism and sulfate-dependant inhibition of methanogenesis in a eutrophic lake sediment. (Lake Mendota), FEMS Microbiol. Ecol. 45 (1987) 107–115.
[43] Crill P.M., Martikainen P.J., Nykanen H., Silvola J., Temperature and N fertilization effects on methane oxidation in a drained peatland soil, Soil Biol. Biochem. 26 (1994) 1331–1339.
[44] Czepiel P.M., Crill P.M., Harriss R.C., Environmental-factors influencing the variability of methane oxidation in temperate zone soils, J. Geophys. Res. Atmos. 100 (1995) 9359–9364.
[45] Dacey J.W.H., Drake B.G., Klug M.J., Stimulation of methane emission by carbon dioxide enrichment of marsh vegetation, Nature 370 (1994) 47–49.
[46] Dannenberg S., Conrad R., Effect of rice plants on methane production and rhizospheric metabolism in paddy soil, Biogeochemistry 45 (1999) 53–71.
[47] De Datta S.K., Principles and Practices of Rice Production, J. Wiley & Sons, New York, 1981.
[48] Denier van der Gon H.A.C., Neue H.U., Impact of gypsum application on the methane emission from a wetland ricefield, Global Biogeochem. Cycles 8 (1994) 127–134.
[49] Denier van der Gon H.A.C., Neue H.U., Influence of organic matter incorporation on the methane emission from a wetland ricefield, Global Biogeochem. Cycles 9 (1995) 11–22.
[50] Denier van der Gon H.A.C., Neue H.U., Methane emission from a wetland ricefield as affected by salinity, Plant Soil 170 (1995) 307–313.
[51] Denier van der Gon H.A.C., Neue H.U., Oxidation of methane in the rhizosphere of rice plants, Biol. Fert. Soils 22 (1996) 359–366.
[52] Denier van der Gon H.A.C., van Breemen N., Neue H.U., Lantin R.S., Aduna J.B., Alberto M.C.R., Wassmann R., Release of entrapped methane from wetland ricefields upon soil drying, Global Biogeochem. Cycles 10 (1996) 1–9.
[53] Dianoua D., Adachib K., Characterization of methanotrophic bacteria isolated from a subtropical paddy field, FEMS Microbiol. Lett. 173 (1999) 163–173.
[54] Dise N.B., Winter fluxes of methane from Minnesota peatlands, Biogeochemistry 17 (1992) 71–83.
[55] Dlugokencky E.J., Steele L.P., Lang P.M., Masarie K.A., The growth-rate and distribution of atmospheric methane, J. Geophys. Res. Atmos. 9 (1994) 17021–17043.
[56] Dobbie K.E., Smith K.A., Prieme A., Christensen S., Degorska A., Orlanski P., Effect of land-use on the rate of methane uptake by surface soils in Northern Europe, Atmos. Environ. 30 (1996) 1005–1011.

[57] Dong X., Stams A.J.M., Evidence for H_2 and formate formation during syntrophic butyrate and propionate degradation, Anaerobe 2 (1995) 35–39.
[58] Duenas C., Fernandez M.C., Carretero J., Perez M., Liger E., Consumption of methane by soils, Environ. Monit. Assess. 31 (1994) 125–130.
[59] Dunfield P., Knowles R., Kinetics of inhibition of methane oxidation by nitrate, nitrite, and ammonium in a humisol, Appl. Environ. Microbiol. 61 (1995) 3129–3135.
[60] Dunfield P., Knowles R., Dumont R., Moore T.R., Methane production and consumption in temperate and subarctic peat soils - response to temperature and pH, Soil Biol. Biochem. 25 (1993) 321–326.
[61] Escoffier S., Le Mer J., Roger P.A., Enumeration of methanotrophic bacteria in ricefield soils by plating and MPN techniques: a critical approach, Eur. J. Soil Biol. 33 (1997) 41–51.
[62] Escoffier S., Ollivier B., Le Mer J., Garcin J., Roger P.A., Evidence and quantification of thiosulfate-reducers unable to reduce sulfate in ricefield soils, Eur. J. Soil Biol. 34 (1998) 69–74.
[63] Fetzer S., Bak F., Conrad R., Sensitivity of methanogenic bacteria from paddy soil to oxygen and desiccation, FEMS Microbiol. Ecol. 12 (1993) 107–115.
[64] Ford-Robertson J., Robertsona K., Maclaren P., Modelling the effect of land-use practices on greenhouse gas emissions and sinks in New Zealand, Environ. Sci. Pol. 2 (1999) 135–144.
[65] Frenzel P., Bosse U., Janssen P.H., Rice roots and methanogenesis in a paddy soil: ferric iron as an alternative electron acceptor in the rooted soil, Soil Biol. Biochem. 31 (1999) 421–430.
[66] Frenzel P., Rothfuss F., Conrad R., Oxygen profiles and methane turnover in a flooded rice microcosm, Biol. Fert. Soils 14 (1992) 84–89.
[67] Garcia J.L., Patel B.K.C., Ollivier B., Taxonomic, phylogenetic, and ecological diversity of methanogenic Archae, Anaerobe 6 (2000) 205–226.
[68] Garcia J.L., Raimbault M., Jacq V., Rinaudo G., Roger P.A., Activités microbiennes dans les sols de rizière du Sénégal: relations avec les propriétés physico-chimiques et influence de la rhizosphère, Rev. Ecol. Biol. Sol 11 (1974) 169–185.
[69] Gilbert B., Frenzel P., Methanotrophic bacteria in the rhizosphere of rice microcosms and their effect on porewater methane concentration and methane emission, Biol. Fert. Soils 20 (1995) 93–100.
[70] Grant R.F., Simulation of methanotrophy in the mathematical model ecosystem, Soil Biol. Biochem. 31 (1999) 287–297.
[71] Grosskopf R., Janssen P.H., Liesack W., Diversity and structure of the methanogenic community in anoxic rice paddy soil microcosms as examined by cultivation and direct 16S rRNA gene sequence retrieval, Appl. Environ. Microbiol. 64 (1998) 960–969.
[72] Guerra L.C., Bhuiyan S.I., Tuong T.P., Barker R., Producing more rice with less water from irrigated systems, International Rice Research Institute Discussion Papers, Manila, Philippines, 1998.
[73] Hamilton J.D., Kelly C.A., Rudd J.W.M., Hesslein R.H., Roulet N.T., Flux to the atmosphere of CH_4 and CO_2 from wetland ponds on the Hudson-Bay lowlands (Hbls), J. Geophys. Res.-Atmos. 99 (1994) 1495–1510.
[74] Hansen S., Maehlum J.E., Bakken L.R., N_2O and CH_4 fluxes in soil influenced by fertilization and tractor traffic, Soil Biol. Biochem. 25 (1993) 621–630.
[75] Hanson R.S., Hanson T.E., Methanotrophic bacteria, Microbiol. Rev. 60 (1996) 439–471.
[76] Henckel T., Friedrich M., Conrad R., Molecular analyses of the methane-oxidizing microbial community in ricefield soil by targeting the genes of the 16S rRNA, particulate methane monooxygenase, and methanol dehydrogenase, Appl. Environ. Microbiol. 65 (1999) 1980–1990.
[77] Henckel T., Jäckel U., Schnell S., Conrad R., Molecular analyses of novel methanotrophic communities in forest soil that oxidize atmospheric methane, Appl. Environ. Microbiol. 66 (2000) 1801–1808.
[78] Holmes A.J., Roslev P., McDonald I.R., Iversen N., Henriksen K., Murrell J.C., Characterization of methanotrophic bacterial populations in soils showing atmospheric methane uptake, Appl. Environ. Microbiol. 65 (1999) 3312–3318.
[79] Holzapfel-Pschorn A., Seiler W., Methane emission during a cultivation period from an Italian rice paddy, J. Geophys. Res. 91 (1986) 11803–11814.
[80] Holzapfel-Pschorn A., Seiler W., Contribution of CH_4 produced in rice paddies to the global CH_4 budget, Int. J. Biometeorol. 28 (1984) 53–61.
[81] Hosono T., Nouchi I., The dependence of methane transport in rice plants on the root zone temperature, Plant Soil 191 (1997) 233–240.
[82] Huang Y., Sass R.L., Fisher F.M., Methane emission from Texas rice paddy soils - 2 - seasonal contribution of rice biomass production to CH_4 emission, Global Change Biol. 3 (1997) 491–500.
[83] Husin Y.A., Murdiyarso D., Khalil M.A.K., Rasmussen R.A., Shearer M.J., Sabiham S., Sunar A., Adijuwana H., Methane flux from Indonesian wetland rice - The effects of water management and rice variety, Chemosphere 31 (1995) 3153–3180.
[84] Hutsch B.W., Tillage and land use effects on methane oxydation rates and their vertical profiles in soil, Biol. Fert. Soils 27 (1998) 284–292.
[85] Hutsch B.W., Webster C.P., Powlson D.S., Long term effects of nitrogen fertilization on methane oxydation in soil of the broadbalk wheat experiment, Soil Biol. Biochem. 25 (1993) 1307–1315.
[86] Hutsch B.W., Webster C.P., Powlson D.S., Methane oxidation in soil as affected by land use, soil pH and N fertilization, Soil Biol. Biochem. 26 (1994) 1613–1622.
[87] Intergovernmental Panel on Climate Change (IPCC), Climate Change 1994 (Radiative Forcing of Climate Change), Cambridge Univ. Press, Cambridge, UK, 1995.
[88] Intergovernmental Panel on Climate Change (IPCC), Emissions Scenarios, Special Report of the Intergovernmental Panel on Climate Change, Cambridge University Press, UK, 2000available at: http://www.ipcc.ch/pub/pub.htm.

[89] International Rice Research Institute (IRRI), Rice Production, Methane Emissions, and Global Warming: Links and Effects (2000)http://www.cgiar.org/irri/MethaneEmissions.pdf..

[90] Jarvis S.C., Pain B.F., Greenhouse-gas emissions from intensive livestock systems - their estimation and technologies for reduction, Climatic Change 27 (1994) 27–38.

[91] Jermsawatdipong P., Murase J., Prabuddham P., Hasathon Y., Khomthong N., Naklang K., Watanabe A., Haraguchi H., Kimura M., Methane emission from plots with differences in fertilizer application in Thai paddy field, Soil Sci. Plant Nutr. 40 (1994) 63–71.

[92] Jones H.A., Nedwell D.B., Methane emission and methane oxidation in land-fill cover soil, FEMS Microbiol. Ecol. 102 (1993) 185–195.

[93] Joulian C., Escoffier S., Le Mer J., Neue H.U., Roger P.A., Populations and potential activities of methanogens and methanotrophs in ricefields: relations with soil properties, Eur. J. Soil Biol. 33 (1997) 105–116.

[94] Joulian C., Ollivier B., Neue H.U., Roger P.A., Microbiological aspects of methane emission by a ricefield soil from Camargue (France): 1. Methanogenesis and related microflora, Eur. J. Soil Biol. 32 (1996) 61–70.

[95] Joulian C., Ollivier B., Patel B.K.C., Roger P.A., Phenotypic and phylogenetic characterization of dominant culturable methanogens isolated from ricefield soils, FEMS Microbiol. Ecol. 25 (1998) 135–145.

[96] Jugsujinda A., DeLaune R.D., Lindau C.W., Influence of nitrate on methane production and oxidation in flooded soil, Commun. Soil Sci. Plant Anal. 26 (1995) 2449–2459.

[97] Kajan R., Frenzel P., The effect of chironomid larvae on production, oxidation and fluxes of methane in a flooded rice soil, FEMS Microbiol. Ecol. 28 (1999) 121–129.

[98] Kanno T., Miura Y., Tsuruta H., Minami K., Methane emission from rice paddy fields in all of Japanese prefecture - relationship between emission rates and soil characteristics, water treatment and organic matter application, Nutr. Cycling Agroecosyst. 49 (1997) 147–151.

[99] Keller M., Goreau T.J., Wofsy S.C., Kaplan W.A., McElroy M.B., Production of nitrous oxide and consumption of methane by forest soils, Geophys. Res. Lett. 10 (1983) 1156–1159.

[100] Kelley C.A., Martens C.S., Ussler W., Methane dynamics across a tidally flooded riverbank margin, Limnol. Oceanogr. 40 (1995) 1112–1129.

[101] Kern J.S., Gong Z.T., Zhang G.L., Zhuo H.Z., Luo G.B., Spatial analysis of methane emissions from paddy soils in China and the potential for emissions reduction, Nutr. Cycling Agroecosyst. 49 (1997) 181–195.

[102] Khalil M.A.K., Rasmussen R.A., Global emissions of methane during the last several centuries, Chemosphere 29 (1994) 833–842.

[103] Khalil M.A.K., Rasmussen R.A., Methane emissions from ricefields in China, Environ. Sci. Technol. 25 (1991) 979–981.

[104] Khalil M.A.K., Shearer M.J., Rasmussen R.A., Methane sources in China: historical and current emissions, in: Khalil M.A.K., Shearer M.J. (Eds.), Atmospheric Methane: Sources, Sinks and Role in Global Change. Proceedings of the NATO Advanced Research Workshop, Mount Hood, Oregon, 7–11 October 1991, Chemosphere 26 (1993) 127-142.

[105] Kightley D., Nedwell D.B., Cooper M., Capacity for methane oxidation in landfill cover soils measured in laboratory-scale soil microcosms, Appl. Environ. Microbiol. 61 (1995) 592–601.

[106] Kimura M., Asai K., Watanabe A., Murase J., Kuwatsuka S., Suppression of methane fluxes from flooded paddy soil with rice plants by foliar spray of nitrogen fertilizers, Soil Sci. Plant Nutr. 38 (1992) 735–740.

[107] King G.M., Association of methanotrophs with the roots and rhizomes of aquatic vegetation, Appl. Environ. Microbiol. 60 (1994) 3220–3227.

[108] King G.M., Adamsen A.P.S., Effects of temperature on methane consumption in a forest soil and in pure cultures of the methanotroph *Methylomonas rubra*, Appl. Environ. Microbiol. 59 (1992) 2758–2763.

[109] King G.M., Schnell S., Effect of increasing atmospheric methane concentration on ammonium inhibition of soil methane consumption, Nature 370 (1994) 282–284.

[110] King G.M., Roslev P., Skovgaard H., Distribution and rate of methane oxidation in sediments of the Florida Everglades, Appl. Environ. Microbiol. 56 (1990) 2902–2911.

[111] King J.Y., Reeburgh W.S., Regli S.K., Methane emission and transport by arctic sedges in Alaska: Results of a vegetation removal experiment, J. Geophys. Res. Atmos. 103 (1999) 29083–29092.

[112] Klinger L.F., Zimmerman P.R., Greenberg J.P., Heidt L.E., Guenther A.B., Carbon trace gas fluxes along a successional gradient in the Hudson-Bay lowland, J. Geophys. Res. Atmos. 99 (1994) 1469–1494.

[113] Kludze H.K., Delaune R.D., Gaseous exchange and wetland plant-response to soil redox intensity and capacity, Soil Sci. Soc. Am. J. 59 (1995) 939–945.

[114] Kludze H.K., Delaune R.D., Patrick W.H., Aerenchyma formation and methane and oxygen exchange in rice, Soil Sci. Soc. Am. J. 57 (1993) 386–391.

[115] Krumholz L.R., Hollenback J.L., Roskes S.J., Ringelberg D.B., Methanogenesis and methanotrophy within a Sphagnum peatland, FEMS Microbiol. Ecol. 18 (1995) 215–224.

[116] Kruse C.W., Iversen N., Effect of plant succession, ploughing, and fertilization on the microbiological oxidation of atmospheric methane in a heathland soil, FEMS Microbiol. Ecol. 18 (1995) 121–128.

[117] Kudo Y., Nakajima T., Miyaki T., Oyaizu H., Methanogen flora of paddy soils in Japan, FEMS Microbiol. Ecol. 22 (1997) 39–48.

[118] Kumaraswamy S., Ramakrishnan B., Satpathy S.N., Rath A.K., Misra S., Rao V.R., Sethunathan N., Spatial distribution of methane-oxidizing activity in a flooded rice soil, Plant Soil 191 (1997) 241–248.

[119] Ladha J.K., Tirol-Padre A.C., Punzalan M., Watanabe I., Nitrogen-fixing (C_2H_2 reducing) activity and plant growth characters of 16 wetland rice varieties, Soil Sci. Plant Nutr. 33 (1987) 187–200.

[120] Lauren J.G., Pettygrove G.S., Duxbury J.M., Methane emissions associated with a green manure amendment to flooded rice in California, Biogeochemistry 24 (1994) 53–65.

[121] Lelieveld J., Crutzen P.J., Bruhl C., Climate effects of atmospheric methane, Chemosphere 26 (1993) 739–768.

[122] Le Mer J., Escoffier S., Chessel C., Roger P.A., Microbiological aspects of methane emission by a ricefield soil from Camargue (France): 2. Methanotrophy and related microflora, Eur. J. Soil Biol. 32 (1996) 71–80.

[123] Lessard R., Rochette P., Topp E., Pattey E., Desjardins R.L., Beaumont G., Methane and carbon-dioxide fluxes from poorly drained adjacent cultivated and forest sites, Can. J. Soil Sci. 74 (1994) 139–146.

[124] Levin I., Glatzel-Mattheier H., Marik T., Cuntz M., Schmidt M., Worthy D.E., Verification of German methane emission inventories and their recent changes based on atmospheric observations, J. Geophys. Res. Atmos. 104 (1999) 3447–3456.

[125] Lindau C.W., Methane emissions from Louisiana ricefields amended with nitrogen fertilizers, Soil Biol. Biochem. 26 (1994) 353–359.

[126] Lindau C.W., Bollich P.K., Methane emissions from Louisiana 1st and ratoon crop rice, Soil Sci. 156 (1993) 42–48.

[127] Lindau C.W., Alford D.P., Bollich P.K., Linscombe S.D., Inhibition of methane evolution by calcium sulfate addition to flooded rice, Plant Soil 158 (1994) 299–301.

[128] Lindau C.W., Bollich P.K., Delaune R.D., Effect of rice variety on methane emission from Louisiana rice, Agr. Ecosyst. Environ. 54 (1995) 109–114.

[129] Lindau C.W., Bollich P.K., Delaune R.D., Mosier A.R., Bronson K.F., Methane mitigation in flooded Louisiana ricefields, Biol. Fert. Soils 15 (1993) 174–178.

[130] Lindau C.W., Wickersham P., Delaune R.D., Collins J.W., Bollick P.K., Scott L.M., Lambremont E.N., Methane and nitrous oxide evolution and N-15 and Ra-226 uptake as affected by application of gypsum and phosphogypsum to Louisiana rice, Agr. Ecosyst. Environ. 68 (1998) 165–173.

[131] Lu Y., Wassmann R., Neue H.U., Huang C., Impact of phosphorus supply on root exudation, aerenchyma formation and methane emission of rice plants, Biogeochemistry 47 (1999) 203–218.

[132] Lueders T., Friedrich M., Archaeal population dynamics during sequential reduction processes in ricefield soil, Appl. Environ. Microbiol. 66 (2000) 2732–2742.

[133] Mac Donald I.R., Hall G.H., Pickup R.W., Murrell J.C., Methane oxidation potential and preliminary analysis of methanotrophs in blanket bog peat using molecular ecology techniques, FEMS Microbiol. Ecol. 21 (1996) 197–211.

[134] Mancinelli R.L., The regulation of methane oxidation in soil, Ann. Rev. Microbiol. 49 (1995) 581–605.

[135] Mayer H.P., Conrad R., Factors influencing the population of methanogenic bacteria and the initiation of methane production upon flooding of paddy soil, FEMS Microbiol. Ecol. 73 (1990) 103–112.

[136] Michael J.W., Carbon and hydrogen isotope systematics of bacterial formation and oxidation of methane, Chem. Geol. 161 (1999) 291–314.

[137] Mikkela C., Sundh I., Svensson B.H., Nilsson M., Diurnal variation in methane emission in relation to the water table; soil temperature; climate and vegetation cover in a Swedish acid mire, Biogeochemistry 28 (1995) 93–114.

[138] Milich L., The role of methane in global warming: where might mitigation strategies be focused? Global Environ. Change 9 (1999) 179–201.

[139] Min H., Zhao Y.H., Chen M.C., Zhao Y., Methanogens in paddy rice soil, Nutr. Cycling Agroecosyst. 49 (1997) 163–169.

[140] Minami K., The effect of nitrogen fertilizer use and other practices on methane emission from flooded rice, Fert. Res. 40 (1995) 71–84.

[141] Mishra S., Rath A.K., Adhya T.K., Rao V.R., Sethunathan N., Effect of continuous and alternate water regimes on methane efflux from rice under greenhouse conditions, Biol. Fert. Soils 24 (1997) 399–405.

[142] Mishra S.R., Bharati K., Sethunathan N., Adhya T.K., Effects of heavy metals on methane production in tropical rice soils, Ecotoxicol. Environ. Saf. 44 (1999) 129–136.

[143] Moore T.R., Dalva M., The influence of temperature and water-table position on carbon-dioxide and methane emissions from laboratory columns of peatland soils, J. Soil Sci. 44 (1993) 651–664.

[144] Murase J., Kimura M., Methane production and its fate in paddy fields 7. Electron acceptors responsible for anaerobic methane oxidation, Soil Sci. Plant Nutr. 40 (1994) 647–654.

[145] Nedwell D.B., Methane production and oxydation in soils and sediments, in: Murrell J.C., Kelly D.P. (Eds.), Microbiology of Atmospheric Trace Gases, Springer, 1996, pp. 33–50.

[146] Nesbit S.P., Breitenbeck G.A., A laboratory study of factors influencing methane uptake by soils, Agric. Ecosyst. Environ. 41 (1992) 39–54.

[147] Neue H.U., Fluxes of methane from ricefields and potential for mitigation, Soil Use Manag. 13 (1997) 258–267.

[148] Neue H.U., Roger P.A., Potential of methane emission in major rice ecologies, in: Zepp R.G. (Ed.), Climate Biosphere Interaction: Biogenic Emissions and Environmental Effects of Climate Change, John Wiley and Sons, 1994, pp. 65–93.

[149] Neue H.U., Becker-Heidmann P., Scharpenseel H.W., Organic matter dynamics, soil properties, and cultural practices in ricelands and their relationship to methane production, in: Bouwman A.F. (Ed.), Soils and the Greenhouse Effect, John Wiley & Sons, Chichester, England, 1990, pp. 457–466.

[150] Neue H.U., Lantin R.S., Wassmann R., Aduna J.B., Alberto M.C.R., Andales M.J.F., Methane emission

from rice soils of the Philippines, in: Minami K., Mosier A., Sass R. (Eds.), CH_4 and NO_2. Global Emission and Controls from Ricefields and Other Agricultural and Industrial Sources, NIAES Series 2, Yokendo, Tokio, 1994, pp. 55–63.

[151] Neue H.U., Wassmann R., Lantin R.S., Alberto M.C.R., Aduna J.B., Javellana A.M., Factors affecting methane emission from ricefields, Atmos. Environ. 30 (1996) 1751–1754.

[152] Nouchi I., Hosono T., Aoki K., Minami K., Seasonal-variation in methane flux from rice paddies associated with methane concentration in soil-water, rice biomass and temperature, and its modeling, Plant Soil 161 (1994) 195–208.

[153] Nugroho S.G., Lumbanraja J., Suprapto H., Sunyoto, Ardjasa W.S., Haraguchi H., Kimura M., Effect of intermittent irrigation on methane emission from an Indonesian paddy field, Soil Sci. Plant Nutr. 40 (1994) 609–615.

[154] Nugroho S.G., Lumbanraja J., Suprapto H., Sunyoto, Ardjasa W.S., Haraguchi H., Kimura M., Methane emission from an Indonesian paddy field subjected to several fertilizer treatments, Soil Sci. Plant Nutr. 40 (1993) 275–281.

[155] Oades J.M., The retention of organic matter in soils, Biogeochemistry 5 (1988) 35–70.

[156] Ojima D.S., Valentine D.W., Mosier A.R., Parton W.J., Schimel D.S., Effect of land use change on methane oxidation in temperate forest and grassland soils, Chemosphere 26 (1993) 675–685.

[157] Olszyk D.M., Centeno H.G.S., Ziska L.H., Kern J.S., Matthews R.B., Global climate change, rice productivity and methane emissions: comparison of simulated and experimental results, Agric. For. Meteorol. 97 (1999) 87–101.

[158] Oremland R.S., Culbertson C.W., Importance of methane-oxidizing bacteria in the methane budget as revealed by the use of a specific inhibitor, Nature 356 (1992) 421–423.

[159] Patrick W.H., Jugsujinda A., Sequential reduction and oxidation of inorganic nitrogen, manganese, and iron in flooded soil, Soil Sci. Soc. Am. J. 56 (1992) 1071–1073.

[160] Potter C.S., Coughlan J.C., Brooks V., Investigations of BOREAS spatial data in support of regional ecosystem modeling, J. Geophys. Res. Atmos. 104 (1999) 27771–27788.

[161] Prieme A., Production and emission of methane in a brackish and a fresh-water wetland, Soil Biol. Biochem. 26 (1994) 7–18.

[162] Pulliam W.M., Carbon-dioxide and methane exports from a southeastern floodplain swamp, Ecol. Monogr. 63 (1993) 29–53.

[163] Raimbault M., Inhibition de la formation de méthane par l'acétylène chez *Methanosarcina barkerii*, Cah. ORSTOM, Sér. Biol. 43 (1981) 45–51.

[164] Rajagopal B.S., Belay N., Daniels L., Isolation and characterization of methanogenic bacteria from rice paddies, FEMS Microbiol. Ecol. 53 (1988) 153–158.

[165] Ramesh R., Purvaja G.R., Parashar D.C., Gupta P.K., Mitra A.P., Anthropogenic forcing on methane efflux from polluted wetlands (Adyar river) of Madras city, India, Ambio 26 (1997) 369–374.

[166] Ratering S., Conrad R., Effects of short-term drainage and aeration on the production of methane in submerged rice soil, Global Change Biol. 4 (1998) 397–407.

[167] Ratha A.K., Swain B., Ramakrishnan B., Panda D., Adhya T.K., Rao V.R., Sethunathan N., Influence of fertilizer management and water regime on methane emission from ricefields, Agr. Ecosyst. Environ. 76 (1999) 99–107.

[168] Ridgwell A.J., Marshall S.J., Gregson K., Consumption of atmospheric methane by soils: A process-based model, Global Biogeochem. Cycles 13 (1999) 59–70.

[169] Rodhe H., A comparison of the contribution of various gases to the greenhouse effect, Science 248 (1990) 1217–1219.

[170] Roger P.A., Biology and management of the floodwater ecosystem in wetland ricefields, International Rice Research Institute, Manila, Philippines, 1996.

[171] Roslev P., King G.M., Aerobic and anaerobic starvation metabolism in methanotrophic bacteria, Appl. Environ. Microbiol. 61 (1995) 1563–1570.

[172] Roslev P., King G.M., Survival and recovery of methanotrophic bacteria starved under oxic and anoxic conditions, Appl. Environ. Microbiol. 60 (1994) 2602–2608.

[173] Rothfuss F., Conrad R., Vertical profiles of CH_4 concentrations; dissolved substrates and processes involved in CH_4 production in a flooded Italian ricefield, Biogeochemistry 18 (1992) 137–152.

[174] Roy R., Conrad R., Effect of methanogenic precursors (acetate, hydrogen, propionate) on the suppression of methane production by nitrate in anoxic ricefield soil, FEMS Microbiol. Ecol. 28 (1999) 49–61.

[175] Rusch H., Rennenberg H., Black alder (*Alnus glutinosa* (L.) Gaertn.) Trees mediate methane and nitrous oxide emission from the soil to the atmosphere, Plant Soil 201 (1998) 1–7.

[176] Sass R.L., Fisher F.M. Jr, Ding A., Huang Y., Exchange of methane from ricefields: National, regional, and global budgets, J. Geophys. Res. Atmos. 104 (1999) 26943–26951.

[177] Sass R.L., Fisher F.M., Harcombe P.A., Turner F.T., Methane production and emission in a Texas ricefield, Global Biogeochem. Cycles 4 (1990) 47–68.

[178] Sass R.L., Fisher F.M., Lewis S.T., Jund M.F., Turner F.T., Methane emissions from ricefields - effect of soil properties, Global Biogeochem. Cycles 8 (1994) 135–140.

[179] Sass R.L., Fisher F.M., Wang Y.B., Turner F.T., Jund M.F., Methane emission from ricefields: The effect of floodwater management, Global Biochem. Cycles 6 (1992) 249–262.

[180] Schink B., Zeikus J.G., Microbial methanol formation: major end product of pectin metabolism, Curr. Microbiol. 4 (1980) 387–389.

[181] Schipper L.A., Reddy K.R., Methane production and emissions from four reclaimed and pristine wetlands of Southeastern United-States, Soil Sci. Soc. Am. J. 58 (1994) 1270–1275.

[182] Schnell S., King G.M., Mechanistic analysis of ammonium inhibition of atmospheric methane consumption in forest soils, Appl. Environ. Microbiol. 60 (1994) 3514–3521.

[183] Schrope M.K., Chanton J.P., Allen L.H., Baker J.T., Effect of CO_2 enrichment and elevated temperature on methane emissions from rice, *Oryza sativa*, Global Change Biol. 5 (1999) 587–599.

[184] Schütz H., Seiler W., Methane flux measurements: Methods and results, in: Andrae M.O., Schimmel D.S. (Eds.), Exchange of trace gases between terrestrial ecosystems and the atmosphere, John Wiley & Sons, 1989, pp. 209–228.

[185] Schütz H., Holzapfel-Pschorn A., Conrad R., Rennenberg H., Seiler W., A three years continuous record on the influence of daytime, season and fertilizer treatment on methane emission rates from an Italian rice paddy field, J. Geophys. Res. 94 (1989) 16405–16416.

[186] Schütz H., Seiler W., Conrad R., Influence of soil temperature on methane emission from rice paddy field, Biogeochemistry 11 (1990) 77–95.

[187] Seiler W., Conrad R., Contribution of tropical ecosystems to the global budgets of trace gases especially CH_4, H_2, CO, and N_2O, in: Dickinson R.E. (Ed.), The Geophysiology of Amazonia, Vegetation and Climate Interactions, Chapter 9, 1987, pp. 33–162.

[188] Seiler W., Holzapfel-Pschorn A., Conrad R., Scharffe D., Methane emission from rice paddies, J. Atmos. Chem. 1 (1984) 241–268.

[189] Shannon R.D., White J.R., 3-year study of controls on methane emissions from 2 Michigan peatlands, Biogeochemistry 27 (1994) 35–60.

[190] Shao K.S., Li Z., Effect of rice cultivars and fertilizer management on methane emission in a rice paddy in Beijing, Nutr. Cycling Agroecosyst. 49 (1997) 139–146.

[191] Simpsona I.J., Edwards G.C., Thurtella G.W., Variations in methane and nitrous oxide mixing ratios at the southern boundary of a Canadian boreal forest, Atmos. Environ. 33 (1999) 1141–1150.

[192] Singh J.S., Raghubanshi A.S., Reddy V.S., Singh S., Kashyap A.K., Methane flux from irrigated paddy and dryland ricefields, and from seasonally dry tropical forest and savanna soils of India, Soil Biol. Biochem. 30 (1998) 135–139.

[193] Singh S., Kashyap A.K., Singh J.S., Methane flux in relation to growth and phenology of a high yielding rice variety as affected by fertilization, Plant Soil 201 (1998) 157–164.

[194] Singh S., Kumar S., Jain M.C., Methane emission from two Indian soils planted with different rice cultivars, Biol. Fert. Soils 25 (1997) 285–289.

[195] Singh S., Singh J.S., Kashyap A.K., Methane consumption by soils of dryland rice agriculture: influence of varieties and N-fertilization, Chemosphere 38 (1999) 175–189.

[196] Singh S., Singh J.S., Kashyap A.K., Methane flux from irrigated ricefields in relation to crop growth and N-fertilization, Soil Biol. Biochem. 31 (1999) 1219–1228.

[197] Sitaula B.K., Bakken L.R., Nitrous oxide release from spruce forest soil-relationships with nitrification; methane uptake; temperature; moisture and fertilization, Soil Biol. Biochem. 25 (1993) 1415–1421.

[198] Sitaula B.K., Bakken L.R., Abrahamsen G., CH_4 uptake by temperate forest soil - effect of N input and soil acidification, Soil Biol. Biochem. 27 (1995) 871–880.

[199] Sitaula B.K., Hansen S., Sitaula J.I.B., Bakken L.R., Methane oxidation potentials and fluxes in agricultural soil: Effects of fertilization and soil compaction, Biogeochemistry 48 (2000) 323–339.

[200] Sorrell B.K., Boon P.I., Convective gas-flow in *Eleocharis sphacelata*; methane transport and release from wetlands, Aquat. Bot. 47 (1994) 197–212.

[201] Sorrell B.K., Boon P.I., Biogeochemistry of billabong sediments. II. Seasonal variations in methane production, Freshw. Biol. 27 (1992) 435–445.

[202] Steudler P.A., Bowden R.D., Melillo J.M., Aber J.D., Influence of nitrogen fertilization on methane uptake in temperate forest soil, Nature 341 (1989) 314–316.

[203] Steudler P.A., Jones R.D., Castro M.S., Melillo J.M., Lewis D.L., Microbial controls of methane oxydation in temperate forest and agricultural soils, in: Murrell J.C., Kelly D.P. (Eds.), Microbiology of Atmospheric Trace Gases, Springer, 1996, pp. 69–84.

[204] Sundh I., Mikkela C., Nilsson M., Svenson H., Potential aerobic methane oxydation in a sphagnum-dominated peatland - controlling factors and relation to methane emission, Soil Biol. Biochem. 27 (1995) 829–837.

[205] Takai Y., The mechanism of methane fermentation in flooded paddy soil, Soil Sci. Plant Nutr. 16 (1970) 238–244.

[206] Takeda K., Characteristics of a nitrogen-fixing methanotroph, *Methylocystis* T-1, Antonie Leeuwenhoek Int. J. G. 54 (1988) 521–523.

[207] Thiele J.H., Zeikus J.G., Control of interspecies electron flow during anaerobic digestion: significance of formate transfer versus hydrogen transfer during syntrophic methanogenesis in flocs, Appl. Environ. Microbiol. 54 (1988) 20–29.

[208] Thompson A.M., Hogan K.B., Hoffman J.S., Methane Reductions - Implications for global warming and atmospheric chemical change, Atmos. Environ. 26 (1992) 2665–2668.

[209] Topp E., Effects of selected agrochemicals on methane oxidation by an organic agricultural soil, Can. J. Soil Sci. 73 (1993) 287–291.

[210] Topp E., Hanson R.S., Metabolism of radiatively important trace gases by methane-oxidizing bacteria, in: Rogers J.E., Whitman W.B. (Eds.), Microbial Production and Consumption of Green House Gases: Methane, Nitrogen Oxydes and Halomethanes, American Society for Microbiology, Washington DC, 1991, pp. 71–90.

[211] Topp E., Pattey E., Soils as sources and sinks for atmospheric methane, Can. J. Soil Sci. 77 (1997) 167–178.

[212] Torn M.S., Chapin F.S., Environmental and biotic controls over methane flux from Arctic tundra, Chemosphere 26 (1993) 357–368.

[213] Trolldenier G., Methanogenesis during rice growth as related to the water regime between crop seasons, Biol. Fert. Soils 19 (1995) 84–86.

[214] Tyler S.C., The global methane budget, in: Rogers J.E., Whitman W.B. (Eds.), Microbial Production and Consumption of Green House Gases: Methane, Nitrogen Oxydes and Halomethanes, American Society for Microbiology, Washington DC, 1991, pp. 7–38.

[215] Tyler S.C., Bilek R.S., Sass R.L., Fisher F.M., Methane oxidation and pathways of production in a Texas paddy field deduced from measurements of flux, delta-C-13, and delta-D of CH_4, Global Biogeochem. Cycles 11 (1997) 323–348.

[216] Van Bodegon P.M., Stams A.J.M., Effects of alternative electron acceptors and temperature on methanogenesis in rice paddy soils, Chemosphere 39 (1999) 167–182.

[217] Van den Pol-van Dasselaar A., Oenemaa O., Methane production and carbon mineralisation of size and density fractions of peat soils, Soil Biol. Biochem. 31 (1999) 877–886.

[218] Vandernat F.J.W.A., Middelburg J.J., Vanmeteren D., Wielemakers A., Diel methane emission patterns from *Scirpus lacustris* and *Phragmites australis*, Biogeochemistry 41 (1998) 1–22.

[219] Van Hulzena J.B., Segersa R., van Bodegoma P.M., Leffelaar P.A., Temperature effects on soil methane production: an explanation for observed variability, Soil Biol. Biochem. 31 (1999) 1919–1929.

[220] Vavilin V.A., Lokshinaa L.Y., Rytova S.V., Kotsyurbenkob O.R., Nozhevnikovab A.N., Description of two-step kinetics in methane formation during psychrophilic H_2/CO_2 and mesophilic glucose conversions, Biores. Technol. 71 (2000) 195–209.

[221] Wagnera D.M., Pfeiffera E., Mand E., Bockb E., Methane production in aerated marshland and model soils: effects of microflora and soil texture, Soil Biol. Biochem. 31 (1999) 999–1006.

[222] Wang B., Neue H.U., Samonte H.P., Effects of cultivars difference (IR72, IR65598 and Dular) on methane emission, Agric. Ecosyst. Environ. 62 (1997) 31–40.

[223] Wang B., Neue H.U., Samonte H.P., Factors controlling diel patterns of methane emission pattern via rice plants, Nutr. Cycling Agroecosyst. 53 (1999) 229–235.

[224] Wang F.L., Bettany J.R., Methane emission from a usually well-drained prairie soil after snowmelt and precipitation, Can. J. Soil Sci. 75 (1995) 239–241.

[225] Wang Z.P., Delaune R.D., Lindau C.W., Patrick W.H., Methane production from anaerobic soil amended with rice straw and nitrogen fertilizers, Fert. Res. 33 (1992) 115–121.

[226] Wang Z.P., Delaune R.D., Masscheleyn P.H., Patrick W.H., Soil redox and pH effects on methane production in a flooded rice soil, Soil Sci. Soc. Am. J. 57 (1993) 382–385.

[227] Wang Z.P., Lindau C.W., Delaune R.D., Patrick W.H., Methane emission and entrapment in flooded rice soils as affected by soil properties, Biol. Fert. Soils 16 (1993) 163–168.

[228] Wassmann R., Neue H.U., Alberto M.C.R., Lantin R.S., Bueno C., Llenaresas D., Arah J.R.M., Papen H., Seiler W., Rennenberg H., Fluxes and pools of methane in wetland rice soils with varying organic inputs, Environ. Monit. Assess. 42 (1996) 163–173.

[229] Wassmann R., Neue H.U., Lantin R.S., Aduna J.B., Alberto M.C.R., Andales M.J., Tan M.J., Vandergon H.A.C.D., Hoffmann H., Papen H., Rennenberg H., Seiler W., Temporal patterns of methane emissions from wetland ricefields treated by different modes of N-application, J. Geophys. Res. Atmos. 99 (1994) 16457–16462.

[230] Wassmann R., Papen H., Rennenberg H., Methane emission from rice paddies and possible mitigation strategies, Chemosphere 26 (1993) 201–217.

[231] Watanabe A., Kajiwara M., Tashiro T., Kimura M., Influence of rice cultivar on methane emission from paddy fields, Plant Soil 176 (1995) 51–56.

[232] Watanabe I., Hashimoto T., Shimoyama A., Methane-oxidizing activities and methanotrophic populations associated with wetland rice plants, Biol. Fert. Soils 24 (1997) 261–265.

[233] Weier K.L., N_2O and CH_4 emission and CH_4 consumption in a sugarcane soil after variation in nitrogen and water application, Soil Biol. Biochem. 31 (1999) 1931–1941.

[234] West A.E., Schmidt S.K., Acetate stimulates atmospheric CH_4 oxidation by an alpine tundra soil, Soil Biol. Biochem. 31 (1999) 1649–1655.

[235] West A.E., Brooks P.D., Fisk M.C., Smith L.K., Holland E.A., Jaeger C.H. III, Babcock S., Lai R.S., Schmidt S.K., Landscape patterns of CH_4 fluxes in an alpine tundra ecosystem, Biogeochemistry 45 (1999) 243–264.

[236] Whalen S.C., Reeburgh W.S., Effect of nitrogen fertilization on atmospheric methane oxidation in boreal forest soils, Chemosphere-Global Change Sci. 2 (2000) 151–155.

[237] Whalen S.C., Reeburgh W.S., Barber V.A., Oxidation of methane in boreal forest soils - a comparison of 7 measures, Biogeochemistry 16 (1992) 181–211.

[238] Whalen S.C., Reeburgh W.S., Sandbeck K.A., Rapid methane oxidation in a landfill cover soil, Appl. Environ. Microbiol. 56 (1990) 3405–3411.

[239] Whiting G.J., Chanton J.P., Primary production control of methane emission from wetlands, Nature 364 (1993) 794–795.

[240] Whiting G.J., Chanton J.P., Plant-dependent CH_4 emission in subarctic Canadian fen, Global Biogeochem. Cycles 6 (1992) 225–231.

[241] Willison T.W., Webster C.P., Goulding K.W.T., Powlson D.S., Methane oxidation in temperate soils - effects of land- use and the chemical form of nitrogen-fertilizer, Chemosphere (1995) 539–546.

[242] Woese C.R., Magrum L.J., Fox G.E., Archaebacteria, J. Mol. Evol. 11 (1978) 245–252.

[243] Wu X., Vulgarisation d'une technique d'irrigation des rizières économe en eau, Proceedings of the 17th Congress of the International Commission for Irrigation and Drainage, Granada, Spain, Water for Agriculture in the Next Millenium, 1999.

[244] Yagi K., Minami K., Effects of organic matter application on methane emission from Japanese paddy fields, in: Bouwman A.F. (Ed.), Soil and the Greenhouse Effects, John Wiley, 1990, pp. 467–473.
[245] Yagi K., Chairoj P., Tsuruta H., Cholitkul W., Minami K., Methane emission from rice paddy fields in the central plain of Thailand, Soil Sci. Plant Nutr. 40 (1994) 29–37.
[246] Yagi K., Tsuruta H., Minami K., Possible options for mitigating methane emission from rice cultivation, Nutr. Cycling Agroecosyst. 49 (1997) 213–220.
[247] Yao H., Conrad R., Thermodynamics of methane production in different rice paddy soils from China, the Philippines and Italy, Soil Biol. Biochem. 31 (1999) 463–473.
[248] Yao H., Conrad R., Wassmann R., Neue H.U., Effect of soil characteristics on sequential reduction and methane production in sixteen rice paddy soils from China, the Philippines, and Italy, Biogeochemistry 47 (1999) 269–295.
[249] Yavitt J.B., Fahey T.J., Simmons J.A., Methane and carbon-dioxide dynamics in a northern hardwood ecosystem, Soil Sci. Soc. Am. J. 59 (1995) 796–804.
[250] Zaiss U., Winter P., Kaltwasser H., Microbial methane oxidation in the river Saar, Z. Allgem. Mikrobiol. 22 (1982) 139–148.