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Effects of vegetation on the emission of methane from submerged paddy soil

A. HOLZAPFEL-PSCHORN, R. CONRAD and W. SEILER
Max-Planck-Institut für Chemie, Saarstr. 23, D-6500 Mainz, FRG

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Summary Methane emission rates from rice-vegetated paddy fields followed a seasonal pattern different to that of weed-covered or unvegetated fields. Presence of rice plants stimulated the emission of CH_4 both in the laboratory and in the field. In unvegetated paddy fields CH_4 was emitted almost exclusively by ebullition. By contrast, in rice-vegetated fields more than 90% of the CH_4 emission was due to plant-mediated transport. Rice plants stimulated methanogenesis in the submerged soil, but also enhanced the CH_4 oxidation rates within the rhizosphere so that only 23% of the produced CH_4 was emitted. Gas bubbles in vegetated paddy soils contained lower CH_4 mixing ratios than in unvegetated fields. Weed plants were also efficient in mediating gas exchnage between submerged soil and atmosphere, but did not stimulate methanogenesis. Weed plants caused a relatively high redox potential in the submerged soil so that 95% of the produced CH_4 was oxidized and did not reach the atmosphere. The emission of CH_4 was stimulated, however, when the cultures were incubated under gas atmospheres containing acetylene or consisting of O_2-free nitrogen.

Introduction

Methane is produced in large quantities in the anoxic soil of submerged paddy fields and is emitted into the atmosphere[3,4,14,19,26,32]. In fact, paddy fields constitute one of the predominant sources in the atmospheric CH_4 cycle[31] and, the intensivation of paddy cultivation may considerably contribute to the observed gradual increase of the atmospheric CH_4 mixing ratio by 1–2% per year[25].

Methane is produced by methanogenic bacteria which are strictly anaerobic and use only a very limited range of substrates. The essential methanogenic substrates are $H_2 + CO_2$ or acetate which are provided by other anaerobic bacteria mineralizing more complex organic substrates[22,23,37,38]. The food chain consisting of fermentative and methanogenic bacteria guarantees that organic matter is mineralized to gaseous products (CH_4, CO_2) even under anerobic conditions. The produced CH_4 is either released into the atmosphere or is oxidized to CO_2 by methanotrophic bacteria as soon as it enters oxic zones of the aquatic environment[13,29].

Compared to other methanogenic eocysystems such as aquatic

sediments, rumen, wetwood, sewage, *etc.* the paddy fields are a unique environment since they include plants growing in an anoxic, CH_4 producing, submerged soil. In this respect, paddy fields resemble the littoral zone of lakes or marshes which are also vegetated. Very little is known about methanogenesis in sediments of the littoral zone of fresh-water lakes[18,39] or in submerged soils of paddy fields[14,19,26,34,36]. Even less is known on the influence of plants on methanogenesis and CH_4 emission in submerged soils[8,17].

Plants may influence the emission of CH_4 from submerged soil into the atmosphere by different processes which are: (1) Plants provide substrates in form of root exudates or root autolysis products[27,28] to the anaerobic food chain and ultimately to methanogenic bacteria and thus, will enhance the production of CH_4. (2) Plants transport CH_4 from the anoxic soil into the atmosphere via the intercellular space and aerenchym systems[24]. (3) Plants generate oxic environments in the anoxic soil by transport of oxygen into the rhizosphere[17] which will stimulate the oxidation of CH_4 and/or inhibit methanogenesis.

Now, we report on field and laboratory studies which were conducted to establish effects of plants on the production, the oxidation and the transport of CH_4 from submerged paddy soil into the atmosphere.

Methods

Field studies

Field studies were carried out in 1984 in rice paddies of the Italian Rice Research Institute in Vercelli, located in the valley of River Po (45°20′ N; 8°25′ W). The soils of the paddy fields consist of sandy loam containing 60% sand, 25% silt, 12% clay, 2.5% organic matter, 0.15% total nitrogen, pH of 6.0. The determinations were made in March before flooding. The fields were dry fallow during the winter, ploughed in the beginning of April, flooded on May 3, and planted with pregerminated seeds on May 5. The fields were either planted with rice (variety Roma, type japonica), with different species of weeds (*Echinogloa crus-galli, Cyperus iria, Alisma plantago, Scirpus mucronatus*) or were kept in a vegetation-free state. CH_4 emission rates under field conditions were determined by a static box tecnhique as described in detail[32] (Holzapfel-Pschorn and Seiler, submitted).

Gas bubbles present in the submerged soil of the paddy field were collected by placing a water-filled funnel over the soil surface and stirring the submerged soil to force ebullition. The trapped gas bubbles were retrieved with an air-tight syringe through a septum fixed at the upper part of the funnel and analyzed immediately after sampling. Gas bubbles being released from the submerged soil under undisturbed conditions were trapped by installing the funnel for several hours until sufficient gas had accumulated.

Laboratory studies

Glass beakers (volume = 800 ml) were filled with 600 g (dry weight) of air dried, sieved (3 mm mesh) paddy soil collected from the fields of the Italian Rice Research Institute in Vercelli. The soil depth within the beaker was approx. 10 cm and was covered by approx. 5 cm

of distilled water. Rice seeds (variety Roma, type japonica) were obtained from the Italian Rice Research Institute in Vercelli. After germination on filter paper soaked with water for 2–4 days, 10 seeds were planted into the soil of each beaker. Subsequently, the cultures were incubated in a water bath kept at 25°C and illuminated with incandescent light (Osram power star, light bulb, 400 W) at a radiation density of approx. 200 W m^{-2}. The light regime was kept at a cycle of 13–14 h light and 10–11 h darkness. After two weeks of incubation the tillers of the rice had reached a length of 15 cm. Weed cultures were prepared by incubating submerged soil in the light so that the weed seeds present in the air-dried soil samples could develop. In rice cultures the developing weed plants were removed. Unvegetated cultures were prepared in the same way, but were incubated in darkness.

For measurement of CH_4 emission rates the cultures in the glass beakers were placed in a big glass incubation vessel, gassed for 10 min with ambient air or N_2 and pressurized to 1.1 bar. Gas samples (10 ml) were taken repeatedly from the incubation vessel by gas tight syringes and analyzed for CH_4 in a gas chromatograph. Emission rates were determined from the temporal increase of the CH_4 mixing ratio and the volume and presure of the gas space of the incubation vessel. In vegetated soils, a total incubation time of 30 min was sufficient to allow the detection of a CH_4 emission rate of 0.2 $\mu g\ h^{-1}$ which is equivalent to 0.03 mg $h^{-1}\ m^{-2}$ of soil surface area. Unvegetated soils had to be incubated for up to 1 week because of irregular emission of CH_4-containing gas bubbles.

Rates of methanogenesis were measured in serum bottles (V = 120 ml) into which cores of submerged soil (length = 10 cm, ϕ = 1 cm) were transferred. Cores were taken from the laboratory cultures by pressing a glass tube with an open valve at the upper end into the sediment. After the glass tube was filled the valve was closed and the core retrieved and pressed with N_2 into the serum bottle which was flushed with N_2. The bottles were stoppered, evacuated and refilled 6 times with N_2, pressurized with N_2 to a final pressure of 1.4 bar and incubated at 25°C. The temporal increase of the CH_4 mixing ratio in the headspace of the bottles was measured by taking gas samples (1 ml) which were analyzed by gas chromatography. After a short lag phase of 1–4 hours, CH_4 mixing ratios increased linearly with time for at least one day. The rate of methanogenesis was determined from the rate of increase of the CH_4 mixing ratio in the serum bottles, the volume and pressure of the headspace and the dry weight of the soil core in the serum bottle. The dry weight of the sediment was determined gravimetrically at the end of the incubation by drying at 108°C for 24 hours. The sediment typically contained 0.5 g water per gram (d.w.) soil. The lower detection limit for rates of methanogenesis was approx. 0.5 ng $CH_4\ h^{-1}\ g^{-1}$ d.w. soil or 0.5 $\mu g\ h^{-1}$ for the total rate of CH_4 production in the laboratory cultures.

Gas analysis

CH_4 was analysed in a gas chromatograph (GC-mini, Shimadzu) equipped with a flame-ionization detector. The gas samples were injected through a sampling loop and separated on a molecular sieve column (13 × 60/80 mesh, 100 cm length) at 70°C. The lower detection limit was approx. 3 ppbv CH_4.

Results

Emission of CH_4 from submerged paddy soil was studied under field conditions during an entire growing season by using an automated semi-continuously working static box system. The seasonal change of the daily mean CH_4 emission rates from the flooding of the fields on May 3 till Sept. 13, 1985 is illustrated in Fig. 1 for a rice paddy field, a field planted with weeds (mono- and dicotyls) and a field which was kept unplanted. The total amount of methane emitted during the whole vegetation period was 36.3, 18.4 and 20.1 g m^{-2} for the rice paddy, the weed and the unplanted field, respectively, indicating that the presence

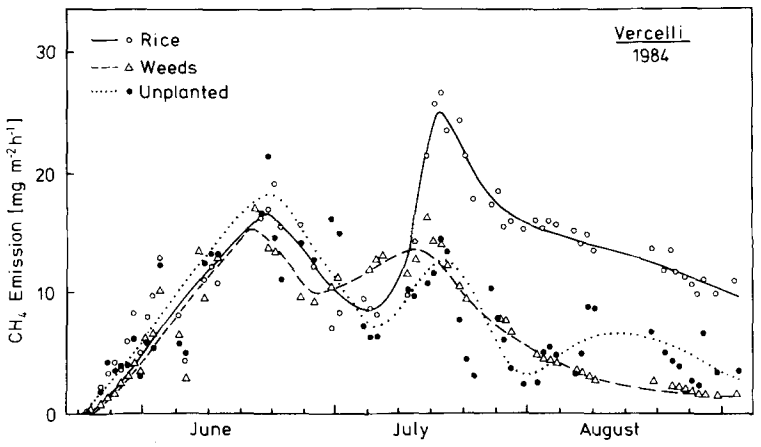

Fig. 1. Seasonal change of CH_4 emission rates from paddy fields. The fields were flooded on May 3, and planted on May 5, 1984. The first CH_4 emission was recorded on May 22. The data points are daily mean values of 8 individual determinations by automated flux measurements in 3 hour rhythm.

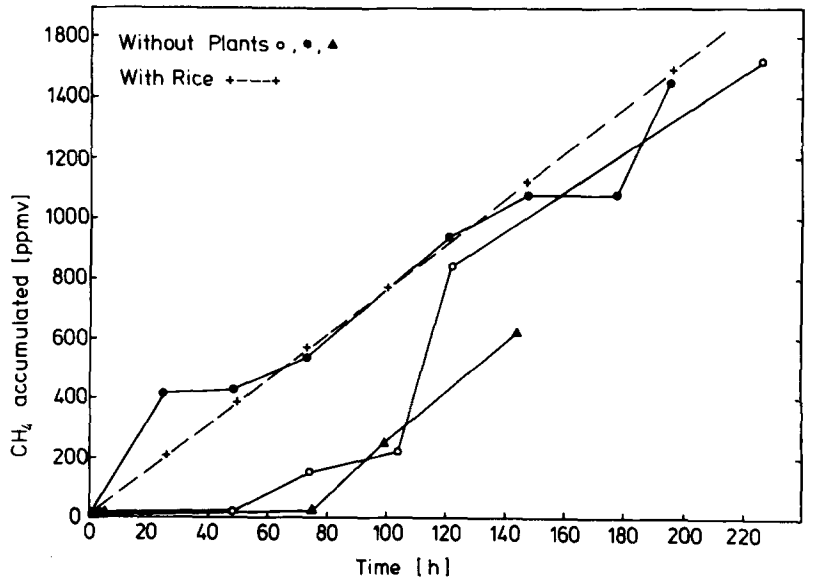

Fig. 2. Temporal release of CH_4 from laboratory cultures of vegetated and unvegetated paddy soil.

of rice plants, but not of weed plants, had a stimulatory effect on the CH_4 emission.

The effect of rice or weed plants on CH_4 emission was further studied by laboratory experiments. When the submerged soil was vegetated,

CH_4 was emitted in a stepwise manner (Fig. 2) During short test periods of 30 min methane was usually not emitted at all. This difference is explained by the different methane transport from the submerged soil into the atmosphere; *i.e.*, ebullition of CH_4 from unvegetated soil and CH_4 transport through the aerenchym and intercellular gas space systems of the plants in vegetated soil.

The importance of the plant transport system was demonstrated in field experiments by cutting the plant stems below the water surface, which reduced the CH_4 emission from fields covered with rice, weed, or reed to 6–40% of the original value (Table 1). However, laboratory experiments with darkening of rice plants for up to 3 days did not result in a significant change of the emission rates (Table 2).

Table 3 shows that the rates of methanogenesis were significantly higher in submerged soil vegetated with rice plants than in unvegetated submerged soil. The vegetation of weeds, on the other hand, did not stimulate the methanogenesis in the submerged soil.

Table 3 also shows that only 5–35% of the produced CH_4 was actually emitted into the atmosphere either by bubble or plant-mediated transport. The rest of the produced CH_4 was apparently oxidized before it could reach the atmosphere. The fraction of CH_4 that was emitted into the atmosphere showed minimum values in weed-vegetated soils. In the weed cultures the percentage of the oxidized CH_4 was especially large. It is of interest that the redox potential measured in the weed-vegetated soil was more positive (-29 ± 74 mV) than in the rice-vegetated soil (-213 ± 35 mV).

Table 4 shows that ebullition rates measured under field conditions were much lower in vegetated than in unvegetated fields because of plant-mediated transport of CH_4. Gas bubbles within unvegetated soils showed significantly higher CH_4 mixing ratio than in soils with rice plants. In addition, the CH_4 mixing ratios of gas bubbles emitted from the submerged soils were significantly lower than those measured in bubbles taken directly from the submerged soil. This observation is again indicative for active oxidation of CH_4 in the oxidized surface layer of the submerged soil or the oxidized zones within the rhizosphere.

CH_4 emission from rice or weed cultures was stimulated by adding 5% of acetylene to the air atmosphere (Table 5). Incubation for 1 day under a O_2-free nitrogen atmosphere resulted in even larger increase of CH_4 emission. The effect of different incubation atmospheres on CH_4 emission was even more pronounced in soils vegetated with weeds (Table 5).

The CH_4 production in submerged soil results in the formation of

Table 1. Inhibition of CH_4 emission by cutting the stems of the plants below the water surface

Plant	CH_4 emission rates (mg m^{-2} h^{-1}) before cutting	after cutting	Inhibition
Rice[a)]	11.8 ± 5.6	0.7 ± 0.7	94
Weeds[a)]	8.3 ± 1.4	1.3 ± 1.0	84
Reed[b)]	1.0 ± 0.1	0.4 ± 0.1	60

a) The experiments were carried out in 3 replicates under field conditions in an Italian rice paddy. The weed plants consisted of different, mainly monocotyl, species, *e.g. Eclinogloa crus-galli, Cyperus iria, Scirpus mucronatus, Alisma plantago.*

b) The experiments were carried out under field conditions in a swamp vegetated with *Typha latifolia* which was situated close to the paddy fields.

Table 2. Influence of darkening on CH_4 emission from rice cultures[a)]

Incubation time (days)	CH_4 emission rate ($\mu g\ h^{-1}$)	
	Permanent light	Permanent darkness
0	64 ± 6	
1	71 ± 7	78 ± 8
3	74 ± 1	67 ± 14

a) Mean values from 3 replicates incubated at 25°C.

Table 3. Methanogenesis and CH_4 emission by laboratory cultures of rice and weed plants in submerged soil

Culture	CH_4 production[a)] ($\mu g\ h^{-1}$)	CH_4 emission[b)]	Percentage emitted
Rice	220 ± 33	51 ± 4	23
Weed	55 ± 46	3 ± 2	5
no plants	96 ± 49	34 ± 9[c)]	35

a) Experiments carried out in 3 replicates after 60–100 days of cultivation.
b) Emission measured during 30 min of incubation.
c) Emission measured during 1 week of incubation.

Table 4. CH_4 mixing ratios in gas bubbles and CH_4 ebullition rates from unvegetated and vegetated rice paddy fields[a)]

Field	CH_4 mixing ratio (%)		Ebullition rate (mg CH_4 m^{-2} h^{-1})
	Bubbles within submerged paddy soil	Ebullition gas	
unvegetated	35.1 ± 7.3	13.5 ± 12.0	14.4 ± 19.9
vegetated with rice	16.0 ± 6.3	2.3 ± 3.8	1.7 ± 2.2

a) Mean value (± standard deviation) rate from 6–15 individual samples taken on 14–16 July 1984.

Table 5. Influence of the incubation atmosphere on CH_4 emission from rice or weed cultures

Atmosphere	CH_4 emission rate ($\mu g\ h^{-1}$)	
	Weeds	Rice
Air	1	78
Air + 5% C_2H_2	4	106
N_2 [a)]	25	267

[a)] Preincubated for 1 day under N_2

Table 6. CH_4 emission by rice cultures which had been evacuated to remove gas bubbles from the submerged soil

Time after evacuation (h)	CH_4 emission rate (% of unevacuated control)
2	37
4.5	45
24	81

gas bubbles which remain in the soil until their buoyancy is sufficient for ebullition. In vegetated soil the vertical transport of gas bubbles may in addition be reduced by the dense root mat, so that CH_4-containing gas bubbles will accumulate from which CH_4 gradually diffuses into the roots. Removal of the gas bubbles by brief evacuation to a pressure of 0.1 bar resulted in a immediate reduction of the CH_4 emission rate which only gradually recovered to 80% of its original value after 24 h (Table 6). This observation may be interpreted by the necessity of CH_4 bubble reservoirs in the rhizosphere for maximum CH_4 emission via plant-mediated transport.

Discussion

The CH_4 emission rates from rice paddy fields showed a seasonal pattern which was different for vegetated and unvegetated plots. During the first 7 weeks after flooding the emission rates observed in the unvegetated field plots as well as in the field plots vegetated with rice or weed plants followed the same temporal pattern with a significant maximum in the end of June. Rice and weed plants were still very small during this period and obviously did not influence the magnitude of the CH_4 fluxes. It is suggested that this phase is mainly due to methanogenesis based on mineralization of soil organic matter, *e.g.* straw, left in the soil from the previous growing season. By contrast, the CH_4 emission rates measured afterwards were significantly different in rice paddy fields and in unplanted fields. Whereas the rice

fields showed a pronounced second maximum of CH_2 emission at the end of the tillering stage, the CH_4 emission rates remained at low levels in the unvegetated fields. We therefore believe, that the second maximum of CH_4 emission was related to processes induced by the presence of rice plants. This conclusion is supported by laboratory experiments which showed stimulation of rates of methanogenesis in submerged soil when rice plants were present.

A likely explanation of the observed enhanced CH_4 emission rates in vegetated rice paddies is the release of root exudates or root autolysis products which may serve as additional substrates for the methanogenic food chain and thus may enhance the CH_4 production rates. As darkening of rice plants had no effect on CH_2 emission, the general physiological conditions of the plant seems to be more important for stimulation of methanogenesis than the momentary rate of photosynthesis. This explanation, however, is rather speculative, since our knowledge on the factors influencing the quality and quantity of root exudates is insufficient[11,12]. With respect to methanogenesis it would be important to know which species of exudates are decomposed to methane precursors especially to acetate which seems to be the predominant substrate for methanogenic bacteria in submgerged paddy soils[34].

Rice plants also stimulate the transport of CH_4 into the atmosphere. The strong inhibition of CH_4 emission by cutting rice plants below the water surface indicates that the plant's gas space system constitutes the predominant transport mechanism for CH_4 from submerged soil into the atmosphere. This observation confirms earlier field studies[32]. Some of the gas bubbles in the vegetated soil seem to be in contact with the root system thus facilitating the continuous flux of CH_4 via the plant's gas space system into the atmosphere. This transport process apparently is independent from the physiological conditions of the plant, since cutting the plants above the water level as well as darkening or increase of CO_2 in the atmosphere do not significantly effect the CH_4 emission rates[32].

Swamp plants develop aerenchym and intercellular gas space systems in order to supply the roots with oxygen[35]. On the other hand, the gas space system also enables the transport of CO_2 between roots and leaves[15,16] and the diffusional exchange of other gas species between submerged soil and atmosphere, such as ethylene or acetylene[21,24], nitrous oxide[24], mercury compounds[20] and methane[7,8,24]. Gas transport in rice occurs by molecular diffusion[2]. Since the plant's gas space system allows the transport of oxygen into the roots, the rhizosphere may provide oxic sites for the oxidation of CH_4 by methanotrophs[17]

in addition to the oxic surface layer of the submerged paddy soil[8]. Evidence for the stimulation of the CH_4 oxidation in rice-vegetated submerged soil was provided by the observation that (1) Gas bubbles in vegetated soil contained less CH_4 than in unvegetated soil; (2) the percentage of produced CH_4 which was not emitted into the atmosphere was larger in vegeated than in unvegetated soil; (3) acetylene, an inhibitor of methanotrophic bacteria[9] stimulated the emission of CH_4.

It is reasonable to expect that other aquatic plants effect CH_4 production, oxidation and emission in a similar way as rice plants. Our field studies showed however, that significantly less CH_4 was emitted from weed fields than from rice fields. Similar to rice plants, weed plants mediate the transport of CH_4 into the atmosphere and of O_2 into the rhizosphere. However, this transport may occur by different mechanisms like molecular diffusion, transpiratin or pressurized ventilation[2,5,6,30]. The efficiency of O_2 transport into the submerged soil will be due to the particular transport mechanism and/or to the extent to which the roots penetrate the soil. A better efficiency of O_2 transport into the rhizosphere may explain why weed plants stimulated CH_4 oxidation to a greater extent than the rice plants.

In contrast to rice, weeds did not stimulate the rates of methanogenesis in laboratory cultures of submerged soil. The lack of stimulation by the weed plants may have been due to lacking root exudations, but more likely it is due to inhibition of methanogenesis by O_2 transport into the rhizosphere. The latter assumption is supported by the relatively high redox potentials observed in weed-vegetated soil and by the relatively strong stimulation of CH_4 emission after incubation of weed cultures under a N_2 atmosphere.

Our results conclusively demonstrate that rice paddies, swamps and other ecosystems of vegetated submerged soils exhibit complex interactions between plants, soil and atmosphere. Plants may influence the rates of methanogenesis by root exudates or by transport of oxygen into the rhizosphere, may affect the rates of CH_4 oxidation in the rhizosphere and in addition accomplish the transport of the CH_4 from the soil into the atmosphere. Because of this complexity estimates of the global CH_4 emission rates from anoxic ecosystems (1) on basis of laboratory measurements of methanogenesis in submerged soil samples[10,19] (2) on basis of estimates of the productivity of various ecosystems[33] or (3) on basis of temperature correlations of CH_2 ebullition rates[1] may result in unreliable figures.

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