Control of microbial methane production in wetland rice fields

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Abstract

Methane emission rates are a function of production, transport and oxidation of CH$_4$ in the rice field. Production of CH$_4$ is the prerequisite for any flux. The most important variables that control CH$_4$ production include soil type, rice variety, temperature, soil redox potential, water management and fertilization with organic carbon or nitrogen. The effects of these variables have empirically been assessed on a macroscopic scale. However, the actual mechanisms by which these variables affect the microbial CH$_4$ production on a microscopic scale are little understood. The purpose of the present contribution is to review existing knowledge of microbiological data and microscopic processes that are relevant for the control of CH$_4$ production. These include the flow of carbon and electrons during the anaerobic degradation process, thermodynamic constraints of reactions in-situ and changes in the composition of the microbial community.

Introduction

Wetland rice fields are an important source in the global budget of atmospheric CH$_4$ which has been increasing in abundance and contributes to global warming (Schütz et al., 1991; Shearer and Khalil, 1993; Crutzen, 1995). Since rice fields are managed environments, it is feasible to contemplate possible strategies for mitigation of CH$_4$ emission (Buendia et al., 1997; Yagi et al., 1997; Mosier et al., 1998). For this purpose it is important to know by which factors CH$_4$ emission is controlled. The number of studies measuring CH$_4$ fluxes in rice fields under different conditions, in different regions and at different times of the year have increased dramatically since the first field study in 1981 (Cicerone and Shetter, 1981). These field observations and a number of laboratory studies have been used to describe the general patterns of CH$_4$ emission and to deduce the major variables that affect CH$_4$ emission. This kind of data has resulted in IPCC guidelines for determination of national CH$_4$ inventories (Houghton et al., 1997) and has been used for the development of empirical and semi-empirical models (Cao et al., 1995; Potter, 1997; Huang et al., 1998; Khalil et al., 1998a).

The most important variables that control CH$_4$ emission from rice fields have been described and reviewed (Conrad, 1993; Minami, 1994; Sass and Fisher, 1997; Segers, 1998; Neue and Roger, 2000; Aulakh et al., 2001). These variables include soil type, rice variety, temperature, soil redox potential, water management, fertilization with organic carbon or nitrogen. The effects of these variables have empirically been determined. They affect either one of the principal processes that control CH$_4$ emission, i.e. the production, the transport and the oxidation of CH$_4$ in the rice soil-plant system (Conrad, 1989, 1993; Schütz et al., 1991). However, although production, transport and oxidation of CH$_4$ are obvious processes on a macroscopic scale (e.g. rice fields), they are again the result of a multitude of processes that operate on a microscopic scale (e.g. soil microsites, root surface). It is these microscopic processes that are ultimately controlling the flux of CH$_4$ from rice fields into the atmosphere. Although most of these microscopic processes are too detailed and sophisticated to be included in mechanistic flux models, the understanding of these processes will increase the confidence in the accuracy of the flux models.

The anaerobic microbiology of flooded rice fields
Figure 1. Scheme of the pathway of anaerobic microbial degradation of polysaccharides to methane.

has recently been reviewed in detail by Kimura (2000) and Liesack et al. (2000). The purpose of the present article is to review existing knowledge that explains the effects on CH 4 emission by macroscopic variables (e.g. soil type, water management etc.) on a smaller, microscopic scale. I will focus on processes that are involved in the production of CH 4.

**Methanogenic degradation of organic matter**

Biological CH 4 production is exclusively caused by anaerobic methanogenic microorganisms that are phylogenetically affiliated with the domain *Archaea*, one of the three domains of life (*Bacteria, Archaea, Eucarya*). Methanogenic archaea can only use simple substrates. Thus, methanogens living in freshwater ecosystems produce CH 4 from either acetate or H 2/CO 2 (Conrad, 1989, 1999). Acetate, H 2, and CO 2 are products of the microbial degradation of organic matter (in rice fields mainly polysaccharides) under anoxic conditions. The entire methanogenic degradation process involves the following reactions of which each is catalyzed by a specific physiological group of microorganisms (Figure 1): (1) Hydrolysis of polysaccharides followed by fermentation of sugars to fatty acids (mainly propionate), acetate, H 2, and CO 2; (2) alternatively fermentation to only acetate (homoacetogenesis); (3) syntrophic conversion of fatty acids (e.g. propionate) to acetate, H 2, and CO 2; (4) homoacetogenic conversion of H 2/CO 2 to acetate; (5) methanogenic conversion of H 2/CO 2 to CH 4; and (6) methanogenic disproportionation of acetate to CH 4 and CO 2.

Under balanced conditions, the polysaccharides are anaerobically degraded to 50% CO 2 and 50% CH 4, the latter originating by >66% from acetate and <33% from H 2/CO 2 (Conrad, 1999). However, balanced conditions, when all the individual degradation operate in quasi steady state, are only established when the soil stays anoxic for several weeks. Quasi steady state conditions are also characterized by constant and low concentrations of the methanogenic substrates H 2 (<2 Pa) and acetate (<100 µM). Concentrations of H 2 and acetate are much higher in the beginning of anoxia (Table 1). At this time, processes are not yet balanced, and fermentation reactions produce acetate faster than it can be consumed by the methanogens (Chidthaisong et al., 1999). In the end, however, quasi steady state is reached during which CH 4 and CO 2 are produced at equal rates. Deviation from this degradation pattern indicates an imbalance in the electron budget which, for example, can occur when the oxidation status of soil organic matter changes during decomposition (Yao and Conrad, 2000a).

**Initiation of CH 4 production upon flooding of rice fields**

Textbooks describe methanogenic archaea to be killed by exposure to O 2 and to be highly sensitive to redox potentials of E h > −200 mV. This characteristic seems to be consistent with the observation that CH 4 production in rice fields is inversely correlated to the E h of soil (Wang et al., 1993; Yagi et al., 1996). However, this concept is not completely correct.

Many methanogens, those isolated from soil in particular, are neither very sensitive to high redox potentials nor to exposure to O 2 (Fetzer et al., 1993; Fetzer and Conrad, 1993). Some methanogenic species were even found to live specifically in oxic habitats (Leadbetter and Breznak, 1996) and apparently are even able to consume O 2 if supplied at low concentrations (Brune, pers. comm.). Indeed, methanogens in rice field soil easily survive desiccation after drain-
Table 1. Microbial processes determining the different phases of CH4 production after flooding of soil

<table>
<thead>
<tr>
<th>Phase</th>
<th>Processes</th>
<th>Duration (d)</th>
</tr>
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<tbody>
<tr>
<td>0</td>
<td>General lag phase</td>
<td>&lt;1</td>
</tr>
<tr>
<td>1</td>
<td>Fermentation produces H2 and acetate</td>
<td>&lt;10</td>
</tr>
<tr>
<td></td>
<td>Iron reducers and sulfate reducers are still inactive</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Production of CH4 is limited by the methanogens themselves</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Iron reducers and sulfate reducers become active</td>
<td>&lt;30</td>
</tr>
<tr>
<td></td>
<td>They deplete H2</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Production of CH4 is suppressed by the deficiency of H2</td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>Iron(III) and sulfate are depleted</td>
<td>&lt;30</td>
</tr>
<tr>
<td></td>
<td>Iron reducers and sulfate reducers become inactive</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Concentration of H2 increases again (acetate still high)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Production of CH4 is thus possible at a relatively a high rate</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>Fermentation is getting limited by hydrolysis of biopolymers</td>
<td>&lt;100</td>
</tr>
<tr>
<td></td>
<td>Acetate and H2 reach relatively low but constant values</td>
<td></td>
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<tr>
<td></td>
<td>Rates of CH4 production decrease to relative constant value (steady state)</td>
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Methanogens in rice field soil are inhibited, though not killed, by exposure to O2. However, they are apparently not inhibited by positive Eh provided that the substrate H2 is available at a concentration that is sufficient for exergonic CH4 production (Roy et al., 1997; Yao and Conrad, 1999). Studies of numerous rice field soils from China, the Philippines and Italy demonstrated that CH4 production is initiated immediately after inundation at still positive Eh values. This early initiation was found in virtually all soils tested and was permitted due to active H2 production by fermenting bacteria (Table 1). Production of CH4 continued as long as the Gibbs free energy of the CH4-producing reaction was more exergonic than about −25 kJ mol⁻¹ CH4 (Yao and Conrad, 1999). This amount of energy corresponds to the minimum energy quantum that bacteria theoretically can use (Schink, 1997). The availability of H2 and thus the magnitude of the Gibbs free energy depends on whether other H2-utilizing microorganisms become active. Bacteria that utilize H2 by reducing ferric iron or sulfate are able to deplete H2 to concentration levels that are no longer permissible for exergonic CH4 production (Table 1).

The extent and duration for which CH4 production is suppressed mainly depends on the ratio of available organic matter to reducible ferric iron (Yao et al., 1999; Watanabe and Kimura, 1999). In many rice field soils, this ratio is so low, that after an initial production phase, methanogenesis stops until most of the ferric iron is reduced. Then, methane production starts again, and it is this second and persistent phase of CH4 production which coincides with a low Eh. At constant temperature, this phase sooner or later turns into steady state with relatively constant CH4 production rates (Yao et al., 1999). However, since many soils exist which have a high ratio of organic matter to ferric iron (or sulfate), CH4 production often starts right from the beginning of inundation (Yao and Conrad, 1999).

**Stimulation of CH4 production by rice straw**

Addition of organic matter such as rice straw to the soil stimulates the production of CH4 and enhances CH4 emission from rice fields (Schütz et al., 1989; Yagi and Minami, 1990; Sass et al., 1991; Denier van der Gon and Neue, 1995; Chidthaisong et al., 1996; Rath et al., 1999). Rice straw consists of cellulose (32–37%), hemicellulose (29–37%), lignin (5–15%) and contains inorganic components such as silica (Tsutsuki and Ponnamperuma, 1987; Watanabe et al., 1993). Rice straw is rapidly colonized by bacteria (Kimura and Tun, 1999) which mainly consist of clostridia belonging to the taxonomic clostridial
clusters I, III and XIVa (Weber et al., 2001). These clostridial clusters are known to consist of hydrolytic and fermenting bacteria, and thus explain the rapid accumulation of a large variety of fatty acids upon addition of straw to rice soil (Glissmann and Conrad, 2000). Aromatic compounds also accumulate (Tsutsuki and Ponnamperuma, 1987). However, the accumulation of these fermentation products is only transient, and after a few weeks, when the easily degradable straw polysaccharides are exhausted, the fermentation pattern in straw-amended soil is virtually the same as in unamended soil, with acetate and propionate being the only important fermentation products (Glissmann and Conrad, 2000). One may speculate that much of the degradable soil organic matter is nothing else than tiny straw particles that have been left over from previous years, thus explaining why the degradation of more recent rice straw is qualitatively not different from that of soil organic matter. This conclusion is supported by the observation that the bacterial community colonizing rice straw is only moderately different from that present in unamended soil (Weber et al., 2001; Chin et al., 1999a; Hengstmann et al., 1999). In the end, rice straw is becoming an integral part of soil organic matter and, with a mean half life about 2 years, is becoming increasingly recalcitrant to further degradation (Neue and Scharpenseel, 1987).

Nevertheless, CH$_4$ production keeps being enhanced after a single addition of straw over periods of weeks and months, only gradually decreasing with time. Methane production seems to be limited by the hydrolysis of polysaccharides which itself is limited by the accessibility of the polymers rather than by the activity of the hydrolytic enzymes (Glissmann and Conrad, 2000). Hence, the entire degradation process to CH$_4$ seems to be in steady state, but at a quantitatively higher level than in unamended soil. This concept is in agreement with the observation that although the density of microbial colonization of straw increases with time (Kimura and Tun, 1999), the diversity and activity of the bacterial colonizers does not (Weber et al., 2001).

**Syntrophic propionate degradation**

Next to acetate propionate is usually the most important fermentation product in rice field soil, the production being stimulated by addition of rice straw (Krylova et al., 1997). Many of the fermenting bacteria that are abundant in rice soil seem to produce propionate as a fermentation product (Chin et al., 1999a). Propionate can only be degraded in syntrophy with H$_2$-consuming methanogens because of thermodynamic constraints (Krylova and Conrad, 1998). Even in the presence of H$_2$-consuming methanogens, the Gibbs free energy available to propionate-degrading syntrophs (catalyzing: Propionate $\rightarrow$ Acetate+CO$_2$+3 H$_2$) is usually not more exergonic than about $-10$ kJ mol$^{-1}$ propionate in microbial culture (Scholten and Conrad, 2000) and is on the average only about $-7$ kJ mol$^{-1}$ propionate in various rice field soils (Yao and Conrad, 2001). Hence, the syntrophic propionate degraders are tightly constrained by thermodynamics. Nevertheless, they can provide nearly all the H$_2$ that is required to drive CH$_4$ production from CO$_2$ reduction which is up to a third of total CH$_4$ production (Krylova et al., 1997). Besides rice straw, propionate metabolism is also enhanced on rice roots. There, accumulation of H$_2$ plus acetate from fermenting bacteria can result in propionate synthesis by the reversal of the syntrophic degradation reaction (Conrad and Klose, 1999, 2000).

**Control of CH$_4$ production by water management**

Drainage of rice fields results in decrease of CH$_4$ emission rates. This immediate reaction is plausible, since O$_2$ can better penetrate into non-flooded soil and thus suppress CH$_4$ production. However, suppression of CH$_4$ production usually persists for quite some time even when fields are flooded again (Yagi et al., 1996). Even short-term drainage is sufficient for rather long-term suppression of CH$_4$ emission. The reason for this behavior was found in the regeneration of oxidants during the short drainage and aeration period (Sigren et al., 1997; Ratering and Conrad, 1998). The penetration of O$_2$ into the soil allows the oxidation of reduced sulfur to sulfate and of ferrous iron to ferric iron. Sulfate and Fe(III) allow the operation of sulfate-reducing and iron-reducing bacteria, respectively. These bacteria utilize acetate and H$_2$, the two most important methanogenic substrates, more efficiently than the methanogens. As a consequence, concentrations of H$_2$ and acetate decrease to values that are no longer thermodynamically permissive for CH$_4$ production, and CH$_4$ production stops (Sigren et al., 1997; Ratering and Conrad, 1998). The same effect is observed when sulfate or ferric iron are added to methanogenic soil (Achtman et al., 1995; Chidthaisong and
Conrad, 2000). Sulfate, for example, may be added by application of ammonium sulfate fertilizers. Normally, however, iron is the quantitatively more important oxidant in rice field soils, usually accounting for >50% of the organic carbon that is oxidized to CO₂ during the season (Yao et al., 1999). Therefore, any regeneration of ferric iron during drainage may result in a dramatic reduction of total CH₄ production.

Recent studies in Italian rice fields showed that relatively high concentrations of ferric iron (and to a minor extent also of sulfate) in soil resulted in acetate conversion to CO₂ rather than to CH₄. In parallel, acetate concentrations decreased and so did CH₄ production rates (Krüger et al., 2001). The residual CH₄ production was then largely due to CO₂ reduction, which in turn influenced the ¹³C-isotopic composition of the produced CH₄ (Krüger et al., 2002). Hence, drainage not only affects the quantity but also the quality of CH₄ production.

**Control of CH₄ production by temperature**

Temperature affects the rates of all microbiological reactions similarly as chemical reactions. Temperature dependence can in principle be described by the Arrhenius equation, ideally by assuming a constant apparent activation energy or a constant Q₁₀. This is trivial. However, temperature effects are more complex. Immediately after flooding, the reduction of ferric iron and sulfate is enhanced by increasing temperature so that steady state CH₄ production is reached earlier (VanHulzen et al., 1999; Yao and Conrad, 2000b). Thus, the beginning of CH₄ production critically depends on temperature.

At steady state, temperature not only affects the rate of CH₄ production, but also significantly affects the pathway of carbon flow (Chin and Conrad, 1995; Fey and Conrad, 2000). The pathway changes since some microbial processes are more sensitive to temperature than others. At low temperature, for example, the formation of acetate is favored relative to the formation of propionate and thus, CH₄ is increasingly produced from acetate rather than from H₂/CO₂ (Figure 2). At intermediate temperature, on the other hand, H₂/CO₂ contributes about 33% to total CH₄ production, as theoretically expected for methanogenic degradation of polysaccharides (Conrad, 1999). Rice soil apparently contains thermophilic microorganisms which allow, albeit after adaptation, CH₄ production at temperatures as high as 50 °C. At this high temperature, CH₄ is exclusively produced from H₂/CO₂, while acetate is no longer consumed and accumulates (Fey et al., 2001). The temperature-dependent shift in the methanogenic pathway greatly affects the stable isotopic signature of the produced CH₄, as the fractionation of carbon and hydrogen isotopes depends on the biochemical mechanism of CH₄ formation (Krzycki et al., 1987; Burke, 1993; Gelwicks et al., 1994; Botz et al., 1996; Summons et al., 1998; Whiticar, 1999). Indeed, the δ¹³C of CO₂, CH₄ and acetate in rice field soil was found to depend on temperature (Fey and Conrad, in prep.).

Temperature also affects the growth of microbial populations and consequently may result in a nonlinear response of CH₄ production to temperature (Schütz et al., 1990). Indeed, the community of methanogens in Italian rice field soil was found to be different at low (15 °C) than at high (30 °C) temperature (Chin et al., 1999b). *Methanosaeta* species in rice soil seem to be able to adapt to a larger temperature range than *Methanosarcina* species which seem to prefer higher temperatures (Chin et al., 1999b; Wu
et al., 2001). The two groups of methanogens have also different kinetic characteristics ($K_m$, threshold) with respect to acetate utilization, and *Methanosaeta* species are able to exploit lower acetate concentrations than *Methanosarcina* species (Jetten et al., 1990). The ratio of *Methanosaeta/Methanosarcina* indeed was found to dynamically change with temperature and acetate concentration in rice soil slurries (Chin et al., 1999b; Lueders and Friedrich, 1999; Fey and Conrad, 2000). Such changes in the methanogenic community were found to affect the pathway and rate of CH$_4$ production, and in addition also the resistance and resilience towards stress situations, e.g. caused by aeration, water management or temperature change (Wu and Conrad, 2001; Wu et al., 2002).

**Role of rice plants for the production of CH$_4$**

Rice plants have different effects on CH$_4$ production. The extent of these effects strongly depends on the type of rice cultivar. For example, Fe(III) is permanently regenerated from Fe(II) in the rhizosphere of the plants. Rice plants not only allow the diffusion of CH$_4$ from the soil into the atmosphere (Holzapfel et al., 1985; Schütz et al., 1991; Nouchi and Mariko, 1993), but also allow the diffusion of O$_2$ from the atmosphere through their aerenchyma system into the roots. From there O$_2$ partially leaks into the soil (Armstrong, 1979; Frenzel et al., 1992; Revsbech et al., 1999) and thus allows various oxidation processes in the rhizosphere, e.g. of CH$_4$ to CO$_2$ (Bosse and Frenzel, 1997; Gilbert and Frenzel, 1998), ammonium to nitrate (Reddy et al., 1989; Arth et al., 1998), sulfide to sulfate (Wind and Conrad, 1997), and Fe(II) to Fe(III) (Begg et al., 1994). The regeneration of Fe(III) in the rhizosphere results in partial suppression of CH$_4$ production within the upper soil layers where most of the rice roots are found (Frenzel et al., 1999; Ratering and Schnell, 2000).

Rice cultivars with increased ventilation capacity were claimed to emit more CH$_4$ over the season (Butterbach-Bahl et al., 1997; Watanabe and Kimura, 1998). This effect was discussed to be caused by a more efficient CH$_4$ oxidation in the rhizosphere when CH$_4$ is less rapidly ventilated (Watanabe and Kimura, 1998). It is unclear, whether decreased ventilation would also impede the regeneration of oxidants, Fe(III) in particular, and thus release the suppression of CH$_4$ production.

A further effect of rice plants is the supply of additional organic matter to the soil microbial community. The organic matter is derived from rhizodeposition, i.e. root exudation, sloughed-off cells and decay of roots. The CO$_2$ that is photosynthetically assimilated by the rice plants is partially excreted from the roots, fermented to acetate and H$_2$, and finally converted into CH$_4$ (Dannenberg and Conrad, 1999). About a third of total CH$_4$ emission is derived from photosynthetically assimilated CO$_2$ (Watanabe et al., 1999), thus emphasizing the importance of rice plants for CH$_4$ production. Rice cultivars with more root exudation also tend to emit more CH$_4$ (Wang et al., 1997; Watanabe and Kimura, 1998).

Most of the CH$_4$ produced from root exudation is probably generated by the soil microflora in some distance to the roots. However, the root surface itself is also colonized by methanogenic archaea. The composition of the root methanogenic flora is different from the soil methanogenic flora (Großkopf et al., 1998a, b; Lehmann-Richter et al., 1999). The root surface is also colonized by fermenting bacteria which are able to produce H$_2$, acetate, propionate and butyrate at high rates (Conrad and Klose, 1999, 2000; Rosenkrantz et al., 1999). More than 50% of CH$_4$ produced on the roots is derived from H$_2$/CO$_2$, the remainder from acetate (Lehmann-Richter et al., 1999; Conrad et al., 2000). However, much of the acetate is also produced homoactogenically, so that the conversion of H$_2$ plus CO$_2$ to acetate is followed by acetoclastic methanogenesis (Figure 3). Obviously, the methanogenic pathway on roots is different from that in soil and thus, may affect the $\delta^{13}$CH$_4$ of the produced CH$_4$ (Conrad et al., 2000). However, it is unclear how much the root-produced CH$_4$ is in comparison to the soil-produced CH$_4$.

**Effect of fertilization and options for mitigation of CH$_4$ production**

The acetate-utilizing methanogens that colonize the root surface are sensitive to phosphate (Conrad et al., 2000). This may explain why addition of phosphate fertilizer results in decreased CH$_4$ emission (Lu et al., 1999). However, phosphate fertilization also decreases the total amount of root exudation by decreasing the root/shoot ratio (Lu et al., 1999). Nevertheless, phosphate deficiency possibly stimulates CH$_4$ production and consequently, application of sufficient phosphate
would mitigate CH$_4$ emission from rice fields. In addition, crop yields would be maximized.

Production of CH$_4$ is inhibited by nitrate for the same reason as it is inhibited by sulfate or ferric iron, i.e. nitrate reducers utilize acetate and H$_2$ more efficiently than methanogens (Achtnich et al., 1995; Klüber and Conrad, 1998a; Chidthaisong and Conrad, 2000). In addition, CH$_4$ production is inhibited by nitrite, NO and N$_2$O that accumulate transiently during the reduction of nitrate and are toxic for methanogens (Klüber and Conrad, 1998b). Nitrate is not a customary nitrogen fertilizer in rice agriculture. Instead, ammonium or urea fertilizers are applied. However, nitrate is rapidly produced from these fertilizers in the rhizosphere (Reddy et al., 1998; Arth et al., 1998) and thus may contribute to suppression of CH$_4$ production in rooted soil. Hence, nitrogen fertilization contributes to the mitigation of CH$_4$ emission without compromising crop yields.

In addition, nitrogen fertilization stimulates the CH$_4$-oxidizing bacteria in the rhizosphere so that CH$_4$ emission can be further reduced (Bodelier et al., 2000a, b). Of course, nitrogen fertilizers must not be applied in too high quantities to avoid the eventual emission of the greenhouse gas N$_2$O which would be a trade-off to the mitigated CH$_4$. However, N$_2$O emission from flooded rice fields is usually low and only becomes significant during drainage periods (Bronson et al., 1997; Hua et al., 1997; Cai et al., 1997; Khalil et al., 1998b; Suratno et al., 1998). Nitrogen fertilization can also enhance the emission of NH$_3$ which, however, may largely be avoided by deep placement of the fertilizer (DeDatta, 1995; Gaudin and Dupuy, 1999).

A further mitigation option is fertilization with iron. Increased soil iron contents seem to guarantee that the rhizosphere always keeps sufficient ferric iron contents to suppress CH$_4$ formation (Watanabe and Kimura, 1999; Jäckel and Schnell, 2000). Field experiments with iron fertilization also resulted in decreased CH$_4$ emissions without compromising crop yields (Jäckel and Schnell, in prep.).

Conclusions

A large diversity of microorganisms is to some extent involved in the production of CH$_4$. This diversity is not only large with respect to the various functional groups of microorganisms (fermenting bacteria, iron reducers, methanogens etc.) but is also large with respect to the different populations being active within one particular functional group, e.g. the methanogens.
which are dominated by different species at different temperatures, or when comparing soil and roots. The different population structures obviously affect the pathway and/or rate of CH₄ formation. However, CH₄ production is not only affected by the direct methane producers themselves, but also by other microbial populations that influence the availability of methanogenic substrates. It is the interaction between the various microorganisms which eventually determines the rate of CH₄ production over time. A good example for these interactions is the following. Upon flooding of soil, different phases of CH₄ production can be observed. Usually, CH₄ production starts after an extended lag phase, then CH₄ production rates accelerate and finally, rates decrease again and become more or less constant. Yao et al. (1999) called these three phases ‘reduction phase’, ‘methanogenic phase’ and ‘steady state phase’. Table 1 illustrates these different phases in the light of the principal microbial processes that interact and ultimately limit CH₄ production. The phases 0–3 are analogous to the reduction phase, phases 3 and 4 to the methanogenic and steady state phases, respectively. The understanding of the ultimate causes of CH₄ production events on a microbial and microscopic process level will help to formulate process models with better confidence.

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