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REVIEW ARTICLE

Biochemical cycling in the rhizosphere having an impact on global change

L. Philippot · S. Hallin · G. Börjesson ·
E. M. Baggs

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Abstract Changes in chemical properties in soil around plant roots influence many microbial processes, including those having an impact on greenhouse gas emissions. To potentially mitigate these emissions according to the Kyoto protocol, knowledge about how and where these gases are produced and consumed in soils is required. In this review, we focus on the greenhouse gases nitrous oxide and methane, which are produced by nitrifying and denitrifying prokaryotes and methanogenic archaea, respectively. After describing the microbial processes involved in production and consumption of nitrous oxide and methane and how they can be affected in the rhizosphere, we give an overview of nitrous oxide and methane emissions from the rhizosphere and soils and sediments with plants. We also discuss strategies to mitigate emissions from the rhizosphere and consider possibilities for carbon sequestration.

Keywords Nitrifiers · Denitrifiers · Methanogens · Methanotrophs · Greenhouse gas · Rhizosphere

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L. Philippot
INRA,
UMR 1229,
21000 Dijon, France

L. Philippot
University of Burgundy,
UMR 1229,
21000 Dijon, France

S. Hallin · G. Börjesson
Department of Microbiology,
Swedish University of Agricultural Sciences,
Box 7025, 750 07 Uppsala, Sweden

E. M. Baggs
Institute of Biological and Environmental Sciences,
University of Aberdeen,
Cruickshank Building, St Machar Drive,
Aberdeen AB24 3UU, UK

L. Philippot (✉)
Soil and Environmental Microbiology,
UMR 1229, 17 rue Sully,
21065 Dijon Cedex, France
e-mail: Laurent.Philippot@dijon.inra.fr

Introduction

Plants affect local conditions in the rhizosphere soil in many ways that influence microbial activity, abundance and community composition (Lynch 1990; Sørensen 1997). Several of these factors have a direct impact on microbial communities emitting greenhouse gases (GHG), which are of major concern for global change (Molina and Rovira 1964a; Tiedje 1988). The three main terrestrial GHG subject to the Kyoto protocol are carbon dioxide (CO_2), methane (CH_4), and nitrous oxide (N_2O). While CO_2 is produced by all living organisms, N_2O and CH_4 are both produced and reduced by microbial guilds

(Conrad 1996). These gases are of major concern since they have global warming potentials about 298 and 25 times, respectively, that of carbon dioxide over a 100 years period (IPCC 2007). Nitrous oxide is a side product of the aerobic nitrification process and an obligate intermediate in the denitrification pathway (Conrad 1996), and can therefore be emitted by both nitrifiers and denitrifiers. However, only the latter are also a sink of N_2O. Whether soils are a net source or sink of atmospheric N_2O depends on the environmental factors regulating consumption and production, but most soils are a net source (Conrad 1996). Methane is produced by methanogenic archaea in anaerobic soil and consumed by CH_4 oxidizing bacteria in aerobic soil. The main terrestrial CH_4 sources are wetland ecosystems, where both methanogens and methanotrophs are present and active. Methane oxidation occurs in most soils, and upland soils are mostly sinks (LeMer and Roger 2001).

Nitrous oxide production and consumption are regulated by oxygen partial pressure, and nitrification is additionally controlled by the concentration of ammonia and pH, while denitrification is also controlled by availability of carbon and nitrate (Tiedje 1988). Methanogenesis is dependent on strict anaerobic and low Redox conditions as well as on the fermentative production of precursors for the methanogens, whereas CH_4 oxidation is mainly dependent on oxygen and CH_4 availability (LeMer and Roger 2001). All the above mentioned factors are affected by the presence of plant roots. The oxygen partial pressure can be altered in the rhizosphere because of respiration by roots and root-associated microorganisms, root consumption of water, and root penetration into the soil, which decreases soil compaction and creates channels for gas transfer. In contrast, wetland plants can alter the oxygen partial pressure by diffusion of the oxygen through aerenchyma to the roots and the surrounding soil (Armstrong 1971). Plants also release readily available organic compounds in soil solution through rhizodeposition, of which root exudation is the largest component (Nguyen 2003). These root-derived organic compounds are considered as a major driving force for many microbial processes in the rhizosphere (Lynch 1990). Finally concentrations of nitrate and ammonium also fluctuate in the rhizosphere due to root uptake.

With better understanding of the controls on GHG production and reduction in arable soil, it will be possible to develop appropriate management strategies for mitigation. The IPCC (2007) report comprehensively covers options for mitigation of N_2O and CH_4, in addition to CO_2 from agricultural systems. However, few strategies really fully utilize the unique nature of the rhizosphere, and with greater understanding of controls on rhizosphere biogeochemistry, we will be better placed to mitigate GHG emissions at the site of production within the rhizosphere soil, in addition to indirectly through agricultural management. In this review, we describe the microbial processes involved in production and consumption of N_2O and CH_4 and how they can be regulated in the rhizosphere. We then give an overview of GHG emissions from the rhizosphere and cropped soils and discuss strategies to mitigate emissions and possibilities for carbon sequestration.

Microbial processes producing and reducing nitrous oxide and methane in rhizosphere soil

Nitrification

Nitrification is a two-step process, consisting of the conversion of ammonia (NH_3) to nitrite (NO_2^-) and its subsequent conversion to nitrate (NO_3^-). The pioneering work of Winogradsky established that this process is performed by chemolithotrophic bacteria that respire with oxygen and assimilate CO_2. These chemolithotrophic bacteria are classified into two groups, based on their ability to oxidize ammonia to nitrite (ammonia-oxidizing bacteria) or nitrite to nitrate (nitrite-oxidizing bacteria) (Kowalchuk and Stephen 2001). The nitrifying bacteria are phylogenetically affiliated to the β- and γ-Proteobacteria, but recent discoveries have demonstrated Crenarchaea to also be important ammonia oxidizers in soil (Leininger et al. 2006). In addition to chemolithotrophic nitrification, some bacteria and fungi possess the potential for heterotrophic nitrification, oxidizing both organic and inorganic nitrogen compounds, and this process is believed to play a role mainly in forest soils (Killham 1986). However, many of the approaches to study heterotrophic nitrification have been performed in pure culture systems and the significance of heterotrophic nitrification in soils still needs to be determined (DeBoer and Kowalchuk 2001; Stams et al. 1990). During nitrification, the conversion of ammonia to the highly mobile nitrate ion minimizes emissions of ammonia, but provides opportunities for nitrogen losses by leaching or denitrification from soil and the root zone (Giles 2005). The loss of nitrogen from the root zone is an economic drain due to fertilizer loss, but also has environmental implications, such as nitrate pollution of ground water, eutrophication of surface waters and emissions of the greenhouse gas N_2O.

Nitrification in the rhizosphere of upland soils

Plants affect several factors that influence nitrification. A long-term field trial comparing unfertilized cropped soil and unfertilized bare fallow showed that plants stimulate nitrification (Enwall et al. 2007). This could be due to the increased organic matter that in turn enhances nitrogen turnover in the soil, in combination with increased aeration. Nevertheless, several studies have reported nitrification to be negatively affected in the rhizosphere (Lensi et al. 1992; Molina and Rovira 1964b; Norton and Firestone 1996; Priha et al. 1999; Robinson 1972). As an example, Wheatley et al. (1990) showed that *Pisum sativum*, *Hordeum vulgare*, *Brassica campestris rapifera* and *Lolium perenne* depressed potential nitrification at a certain plant development stage. A recent study demonstrated that this negative rhizosphere effect on gross nitrification rates was variable along the plant root (Herman et al. 2006). Thus, gross nitrification rates in soil near the root tip of *Avena barbata* were the same as those in bulk soil, whereas nitrification was lower in soil near the older root sections. This was due to rapid uptake of NH_4^+ by the older parts of the root, which limited nitrification rates. Not only plants, but also plant species specific effects on nitrification have been reported. During the growing season, nitrification rates were four times greater in *Deschampsia* patches than in *Acomastylis* patches (Steltzer and Bowman 1998), and when comparing potential nitrification in the rhizosphere of *Pisum sativum*, *Hordeum vulgare*, *Brassica campestris rapifera* and *Lolium perenne*, differences up to 10 fold between the plants were shown (Wheatley et al. 1990). Abundance of ammonia oxidizing bacteria, nitrification rates and nitrate concentrations were also significantly lower in the rhizosphere of *Brachiaria humidicola* compared to other pasture species (Ishikawa et al. 2003; Sylvester-Bradley et al. 1988). The observed plant species effects were attributed to large nitrogen inputs by non-symbiotic nitrogen fixation in the rhizosphere of some plants (Brejda et al. 1994) or differential nitrogen uptake or root respiration by the various species. In general, the lower activity of nitrifiers in the rhizosphere can be explained by a decrease in ammonium concentration due to plant uptake or by the heteretrophic microbes being more competitive compared to autotrophic nitrifiers in this carbon rich environment.

Some studies have suggested that the negative effects on nitrification could be due to an inhibition phenomenon, since the existence of plant-derived nitrification inhibitors is well known. However, the hypothesis that the plant itself is capable of releasing inhibitors of nitrification into soil has been at the centre of a controversy for many years because of the absence of direct evidence (Lata et al. 2000; Munro 1966; Rice and Pancholy 1972). The first indirect evidence of an inhibition phenomenon was provided by Moore and Waid (1971), who showed that addition of root washings from different plants reduced the rate of nitrification up to 84% in proportion to the added amount (Moore and Waid 1971). More recently, using transplantation of *Hyparrhenia diplandra* grass originating from high- or low-nitrifying soils, Lata et al. (2004) showed that there was a significant individual plant effect on nitrification. Thus, plants that originated from the low-nitrifying soil decreased nitrification activity in the high-nitrifying soil, and vice-versa.

A direct demonstration of plants decreasing ammonia oxidation activity in soil was obtained by Subbarao et al. (2007), who used a bioluminescence assay based on a recombinant *Nitrosomonas europaea* (Iizumi et al. 1998) to detect ammonia oxidation inhibitors in root exudates of 18 plant species. Inhibition of nitrification varied widely among the different plant species, and the authors concluded that nitrification inhibition was probably a widespread phenomenon in tropical pasture grass (Subbarao et al. 2006, 2007). Inhibition of nitrification has also been observed when cultivating oil seed rape. The tissues of *Brassica* contain many secondary compounds, including glucosinolates, which, upon disruption of tissues, are hydrolyzed to form iso-thiocyanates (ITCs) and other toxic volatile sulphuric compounds (Bending and Lincoln 1999). ITCs can inhibit nitrification by either reducing the abundance of nitrifying bacteria or lowering nitrification rates (Bending and Lincoln 2000). However, the identification of the chemical mediator(s) in root exudates responsible for inhibition of nitrification in the rhizosphere is still missing. Plant control of nitrification could provide an advantage in competition for nitrogen, and since nitrification is the prior step to processes that can reduce the plant available pool of nitrogen, this ability of the plant to inhibit nitrification is a sophisticated way to reduce nitrogen losses through nitrate leaching or denitrification (Fillery 2007). Thus, inhibition of nitrification can induce environmentally significant changes in the ecosystem nitrogen balance (Lata et al. 2004).

Plant effects on nitrification in rice paddies and wetland sediments

Under flooded conditions soils become anoxic almost immediately beneath the soil–water interface. As a result, nitrification is restricted to a millimetre-thick surface layer. However, wetland plants have developed several strategies to transport oxygen to the root-zone, where it can radially diffuse to the rhizosphere (Armstrong 1971; Frenzel et al. 1992, Colmer 2003, Voesnek et al. 2006), thus establishing an aerobic habitat for nitrification (Fig. 1).

Contrasting effects of wetland plants on nitrifiers have been described. When comparing rice-planted and unplanted pots, Chen et al. (1998) could not detect any difference in nitrification rates. On the other hand, a study conducted in irrigated rice fields planted with three different rice cultivars revealed significant differences in both size of the nitrifier community and nitrification rates between the cultivars (Gosh and Kashyap 2003), which were attributed to variation in root porosity among the cultivars. As in upland soils, the effect of plants on nitrification in water saturated systems is most likely dependent on nitrogen concentration, since ammonia oxidizers are competing for nitrogen with plants and heterotrophic bacteria (Verhagen et al. 1994). Thus, Arth and Frenzel (2000) observed that in unfertilized rice paddy, assimilation by the rice roots lowered the available ammonium to a level where nitrification virtually could not occur.

Studies have also been performed to spatially locate root-associated nitrification (Arth and Frenzel 2000; Li et al. 2004). In a fertilized rice paddy, nitrification was detected by multi-channel micro-

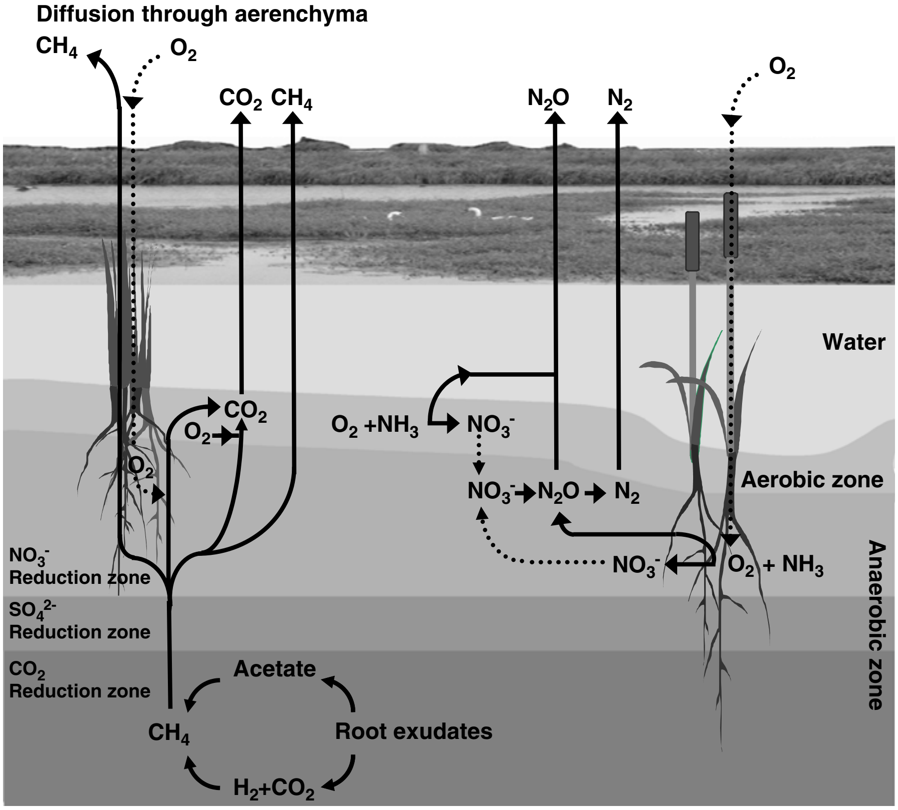

Fig. 1 Production and consumption of N_2O and CH_4 in the rhizosphere of wetland plants

electrodes at a distance of 0–2 mm from the surface of the rice roots, demonstrating that the effect of rice on nitrification is limited to the root surface (Arth and Frenzel 2000). Accordingly, Briones et al. (2002) showed enrichment of ammonia oxidizing bacteria on rice root surfaces, which suggests that root surface populations of ammonia oxidizing bacteria play a major role in determining nitrification rates in the rice rhizosphere. Stimulation of numbers and activity of nitrifying bacteria has also been described for other oxygen-releasing plants (Bodelier et al. 1996; Engelaar et al. 1995), indicating that nitrification in the rhizosphere of aquatic plants could be a common phenomenon in conditions where nitrogen is not limiting. In constructed wetlands, ammonium removal has been shown to be higher in *Phragmites* sp. stands than in those planted with *Typha* sp. (Gersberg et al. 1986), but it remains unclear whether this is due mainly to higher nitrification rates in the *Phragmites* sp. rhizosphere, or due to a more efficient denitrification in sediments covered with this species. Despite the importance of wetland vegetation for nitrogen removal, studies of plant and plant-species effects on nitrification rates and ecology of nitrifiers are scarce.

Nitrate reduction and denitrification

Dissimilatory nitrate reduction into nitrite can be performed by microorganisms that, in contrast to nitrifiers, belong to most of the prokaryotic families (Philippot 1999). The produced nitrite can be either reduced into ammonia by dissimilatory nitrate reduction to ammonium (DNRA, also termed nitrate ammonification) or into nitric oxide (NO), nitrous oxide (N_2O) or dinitrogen gas (N_2) during denitrification. In both processes, nitrogen oxides are used as terminal electron acceptors instead of oxygen for generation of a transmembrane proton electrochemical potential across the cytoplasmic membrane. Denitrification is the main biological process responsible for returning fixed nitrogen to the atmosphere, thus closing the nitrogen cycle. This reduction of soluble nitrogen to gaseous nitrogen is negative for agriculture, since it can deplete the soil of nitrate, an essential plant nutrient. The denitrification N_2O/N_2 product ratio is variable, and N_2O may even be the dominant end product (Chèneby et al. 1998). However, denitrification also provides a valuable ecosystem service by mediating nitrogen removal from nitrate-polluted waters in sediments and other water saturated soils. The ecology of denitrifiers in agricultural soils has recently been reviewed in detail (Philippot et al. 2007).

Nitrate reduction and denitrification in the rhizosphere of upland soils

Several studies have reported that plants can influence the activity, diversity and abundance of nitrate reducers and denitrifiers. Woldendorp (1962) was the first to show that the living root system stimulated denitrification. This early study was followed by several more quantitative measurements of nitrate reduction or denitrification activities. Rate increases ranging from two to 22 times were observed in rhizosphere soil compared to bulk soil (Bakken 1988; Hojberg et al. 1996; Klemedtsson et al. 1987; Philippot et al. 2006; Smith and Tiedje 1979). The stimulation of denitrification in the rhizosphere is positively correlated with soil nitrate concentration. At low NO_3^- concentrations, denitrification rates can even be lower in the rhizosphere compared to the bulk soil (Qian et al. 1997; Smith and Tiedje 1979). It has also been reported that the rhizosphere effect on denitrification was associated with air-filled pore space (Wollersheim et al. 1987). Thus, denitrification rate increased ten-fold at a low moisture tension, while at medium, or high moisture tension, plants had no, or even a negative, effect on denitrification (Bakken 1988). Accordingly, Prade and Trolldenier (1988) showed that the rhizosphere effect on denitrification was confined to air-filled porosity below 10–12% (*v*/*v*).

The primary driver of rhizosphere microbial community development is the release of plant-derived low molecular weight organic compounds into the soil, and thus denitrification rates are often positively correlated with total C or soluble organic C (Baggs and Blum 2004; Bijay-Singh et al. 1988; Paul and Beauchamp 1989). However, contradictory results have been published concerning the influence of the organic compounds released by roots on denitrification. On one hand, it has been reported that root exudates could not provide metabolizable organic compounds to the denitrification process (Haider et al. 1987), or that root-derived organic compounds were rapidly immobilized or mineralized by microorganisms in the rhizosphere, and thus had little influence on denitrification (McCarty and Bremner 1993). On the other hand, Qian et al. (1997) argued that labile organic compounds from roots influence denitrification losses of nitrogen. In two recent studies, Mounier et al. (2004) and Henry et al. (2008) demonstrated that addition of root exudates or mucilage to soil without plants could stimulate nitrate reduction or denitrification activity with increases in the range of those observed in planted soil. This suggests that the higher denitrification activity in soil surrounding the plant roots is mainly due to rhizodeposition. However, factors regulating denitrification in the rhizosphere are strongly interwoven and the stimulating effect of root-derived organic compounds on denitrification can only be observed under non-limiting concentrations of nitrate and oxygen.

While effects of plants on the activity of the nitrate reducer or denitrifier communities have been widely investigated, there are fewer studies on how plants affect the composition of these functional communities. The distribution of denitrifying isolates from soil with or without maize, differed, and *Agrobacterium*-related denitrifiers were enriched in the planted soil (Chèneby et al. 2004). The nitrate reducer community structure was also significantly different in the maize rhizosphere compared to bulk soil (Chèneby et al. 2003; Philippot et al. 2002). Analysis of the effect of root-derived organic compounds on the structure and density of nitrate reducing and denitrifying communities revealed minor or no changes after addition of mucilage or artificial root exudates, even though nitrate reduction and denitrification activity were strongly stimulated (Henry et al. 2008; Mounier et al. 2004). Therefore, even though root-derived organic compounds can stimulate denitrification activity, it does not seem to be a strong driver of the denitrifier community structure in soil (Philippot et al. 2007).

Effects of plant species have mainly been studied on denitrifier activity rather than denitrifier community structure and are attributed to differences in quality and quantity of organic compound flow from roots. Higher denitrification rates in the rhizosphere of legumes compared to other plants were observed in several studies (Kilian and Werner 1996; Scaglia et al. 1985; Svensson et al. 1991). Significant differences in denitrification activity below grass tufts among three species were also reported by Patra et al. (2006). Some studies have shown plant species to have a significant influence on the composition of the denitrifier community (Bremer et al. 2007; Patra et al. 2006). Nevertheless, comparison of the composition of the nitrate reducer community under *Lolium perenne* and *Trifolium repens* did not reveal any species effect (Deiglmayr et al. 2004). Analysis of the denitrification gene transcripts in the rhizosphere of three plant species revealed that the active denitrifiers differed, even though the denitrifier community structure based on the total gene pool was similar for all plant species investigated (Sharma et al. 2005).

Plant effects on nitrate reduction and denitrification in rice paddies and wetland sediments

The release of oxygen by the roots of wetland plants can stimulate nitrification and subsequently denitrification after diffusion of nitrate into the reduced zone of the sediment (Fig. 1). Thus, it is generally agreed that denitrification rates in the rhizosphere of aerenchymatous plants are regulated by the rate of nitrification (Arth et al. 1998; Reedy et al. 1989). Furthermore, aerenchymatous plants could also affect the nitrate reducers and denitrifiers by nitrate uptake and exudation of organic compounds. Arth and Frenzel (2000) showed that while nitrification occurred at a distance of 0–2 mm from the surface around individual rice roots, denitrification occurred at 1.5–5.0 mm. There is a large body of literature estimating denitrification rates from paddy rice (e.g. Arth et al. 1998; Buresh and DeDatta 1990; Xing et al. 2002a; Zhu et al. 2003) and denitrification has been recognized as one of the major ways of nitrogen loss in this agroecosystem, thus contributing to the low nitrogen fertilizer efficiency (Cassman et al. 1993; Reddy and Patrick 1986).

In wetlands, vegetation coverage is an important supplier of organic compounds, fueling denitrification (Kallner-Bastviken et al. 2005). In addition, organic compounds can also indirectly enhance denitrification by increasing aerobic respiration, which lowers oxygen levels in the sediment (Nielsen et al. 1990). Thus, an increase in both size and activity of the nitrate reducers was observed in the *Glyceria maxima* rhizosphere (Nijburg et al. 1997). The composition of the nitrate-reducer community was shown to be driven by the presence of *G. maxima* when nitrate was limiting, but when input levels of nitrate were high, nitrate availability determined the community composition. It is not known whether or not the observed positive effects of wetland plants depend on plant species. Kallner-Bastviken et al. (2003) did not find any difference in potential denitrification activities in intact cores with *Phragmites* sp. or *Typha* sp. shoots, although others have shown that samples from *Typha latifolia* and *Phragmites australis* rhizospheres exhibited significantly different nitrate reduction and denitrification rates (Ruiz-Rueda et al. 2008). These differences were connected to typical *Typha* sp. and *Phragmites* sp. associated denitrifying communities. Not sure what this sentence means Accordingly, in another wetland, the denitrifying community structure differed in sediment with an invasive cattail hybrid *Typha* x *glauca* compared to sediment with the native plant species, *Scirpus* sp. (Angeloni et al. 2006).

Methanogenesis and methane oxidation

Methanogenesis is the microbiological production of CH_4 using small organic compounds as a terminal electron acceptor. Methanogenic organisms belong to the phylum Euryarcheota within the domain Archaea, and produce CH_4 either by converting acetic acid to CH_4 and CO_2, or by converting CO_2 with H_2 to CH_4 (Conrad 2007). These simple substrates are provided by other organisms through fermentation. Other forms of carbon, such as formate or methylated compounds, can also be used by methanogens. Methanogenesis requires strict anaerobiosis and low Redox potential. Thus, CH_4 is produced only after depletion of other electron acceptors; nitrate, sulphate, Mn(IV) and Fe (III) (Conrad 2007), which should occur after the Redox potential has dropped to $Eh \approx -300$ mV (Kludze et al. 1993). However, CH_4 emissions have been observed from irrigated rice fields already at $Eh > 300$ mV (Jiao et al. 2006).

A significant proportion of the CH_4 produced in anaerobic layers is oxidized before it reaches the atmosphere. Therefore, net CH_4 emissions are the results of two opposite processes: CH_4 production by methanogenic archaea and CH_4 oxidation by methanotrophic bacteria. Methane oxidizers use CH_4 as their sole carbon and energy source and have an obligatory aerobic metabolism, thereby depending on access to oxygen. Diffusion rates of methane and oxygen are key factors controlling the activity of methanotrophs. They are divided into two families: the *Methylococcaeae,* belonging to *Gammaproteobacteria,* and the *Methylocystaceae,* belonging to the *Alphaproteobacteria*, also known as type I and type II (Bowman 1999; Hanson and Hanson 1996).

Due to homology between the enzymes catalyzing the first steps in methane oxidation and ammonia oxidation, ammonia oxidizing bacteria may also hold the potential to co-oxidize CH_4. However, several studies have excluded a significant role of ammonia oxidizers in CH_4 oxidation (Bodelier and Frenzel 1999; Klemedtsson et al. 1999). The ecology of both methanogens and methanotrophs has recently been reviewed by Conrad (2007).

Plant effects on methane production and consumption in rice paddies and other soils

Wetland plants regulate the CH_4 budget in several ways (Fig. 1). First, exudation by plant roots provides carbon compound precursors to methanogenic archaea (Aulakh et al. 2001a, b; Frenzel and Bosse 1996; Kankaala and Bergström 2004; van Veen et al. 1989). Pulse labelling of rice plants with $^{13}C–CO_2$ or $^{14}C–CO_2$ showed that plant photosynthates excreted from the roots are converted to CH_4 after being fermented to acetate and H_2, which indicates that plant photosynthates are a major source of CH_4 in the rhizosphere (Dannenberg and Conrad 1999; Minoda and Kimura 1994; Minoda et al. 1996). Watanabe et al. (1999) estimated that the supply of organic compounds from rice plants in the form of exudates and sloughed tissues could represent between 37% and 40% of the carbon sources for CH_4 emission. Stimulation of methanogenesis by exudation has also been shown in the rhizosphere of natural wetland plants (Kludze and DeLaune 1994; Saarnio et al. 2004).

A second effect of wetland plants is the passive transport of CH_4 from the anoxic soil to the atmosphere through the plant aerenchyma. Transport of CH_4 from plant roots to the shoots and release into the atmosphere can represent up to 90% of the total CH_4 flux (Butterbach-Bahl et al. 1997; Cicerone and Shetter 1981; Holtzapfel-Pschorn et al. 1986; Nouchi et al. 1990; Schültz et al. 1989). The aerenchyma of wetland plants is also a conduit pipe for oxygen, allowing oxygen diffusion into the rhizosphere and the adjacent sediment, which can stimulate methane oxidizing bacteria. The transport of oxygen by rice roots was illustrated by the work of Frenzel et al. (1992), who detected oxygen down to the depth of 40 mm in a flooded soil planted with rice, whereas it was confined to a thin surface layer of 3.5 mm in the unplanted soil. Another important consequence of the increased oxygen concentration in the soil is that the Redox potential will change, and reductants such as Fe^{2+}, Mn^{2+} and H_2S will be re-oxidized (Kludze et al. 1993). The increased Redox potential will severely hamper CH_4 production and so lower emissions.

A stimulatory effect of rice plants on CH_4 production has been reported in several studies (Dannenberg and Conrad 1999; Holtzapfel-Pschorn et al. 1986) with decreasing rates with depth and distance from the plant (Sass et al. 1991). Whether the net increase of CH_4 production observed in these studies results from stimulation of methanogenesis, CH_4 plant-mediated transport or an inhibition of CH_4 oxidation is difficult to know. However, in rice fields, variations in CH_4 emission were mostly attributed to variations in methanotrophic activity (Schütz et al. 1989).

In contrast to CH_4 production, which shows pronounced variation during the year, the composition of the methanogenic community in rice fields seems to be rather stable (Krüger et al. 2005). The methanogenic community structure was also very similar between rice root and soil samples, with a relatively lower abundance of *Methanosaetacae* on the roots as the only observed difference. Recently, Lu and Conrad (2005) demonstrated that rice cluster I methanogens, an uncultured lineage forming a distinct clade within the phylogenetic radation of *Methanosarcinales* and *Methanomicrobiales*, were the key players in CH_4 production from plant-derived organic compounds in rice microcosms. In addition to rice cluster I, *Methanosarcinae*, *Methanosaetaceae*, and *Methanosarcinaceae*, were shown to be present on rice roots (Chin et al. 2004).

The alteration of CH_4 oxidation rates by plants have been observed in several studies showing higher potential rates in the root compartments than in root-free compartments of rice microcosms (Bodelier and Frenzel 1999; Gilbert and Frenzel 1998). However, the extent to which root-associated methane oxidation varies among plant taxa and among wetland ecosystems is unknown (King 1996). Similarly to CH_4 production, temporal variation of CH_4 oxidation was observed in rice paddies. Thus, Eller and Frenzel (2001) found that in situ CH_4 oxidation was important only during the vegetative growth phase of the plants and then later became negligible. In contrast, Bosse and Frenzel (1998) observed that CH_4 oxidation occurred during the whole growth period of rice. The fact that methanotrophs are able to profit from the oxygen release from the rice plants is reflected not only by increase of their potential activities, but also by their increase in numbers in the rhizosphere. Thus, MPN counts of methanotrophs were 15 times higher in the root compartment compared to in the non-root compartment (Bodelier and Frenzel 1999). A similar increase was reported by Gilbert and Frenzel (1998), who observed one order of magnitude higher numbers of methane-oxidizing bacteria in the rhizosphere than in the bulk soil. Methanotrophs are also found in surface-sterilised roots and basal culms, which indicates their ability to colonise the interior of roots and culms (Bosse and Frenzel 1997). Investigation of the methanotroph community structure in rice paddies revealed the presence of both the *Methylococcaceae* and *Methylocystaceae* families in soil and root compartments over the whole season (Eller and Frenzel 2001). A recent study demonstrated that *Methylococcaceae* and *Methylocystaceae* populations in the rhizospheric soil and on the rice roots changed differently over time with respect to activity and population size, and that *Methylococcaceae* methanotrophs played a particularly important role in the rice field ecosystem (Shrestha et al. 2008).

Emissions of greenhouse gases from the rhizosphere

Nitrous oxide emissions from rhizosphere soil

Evidence from different cropping systems

Emissions of N_2O are typically greater in the presence of growing plants, particularly legumes, than from bare soil (e.g. Kilian and Werner 1996; Klemedtsson et al. 1987). Emission factors vary from 0.1% to 7% of nitrogen applied in different agricultural systems (Skiba and Smith 2000), reflecting differences in vegetation type, crop management and climate. Measured emissions can vary significantly with crop type, for example ranging from 0.2 to 0.7 kg N_2O–N 100 kg^{-1} N applied for small grain cereals, 0.3–5.8 kg N_2O–N 100 kg^{-1} N applied from cut grassland (Dobbie et al. 1999), and 3.9–8.7 kg N_2O–N ha^{-1} $year^{-1}$ from maize fields (Sehy et al. 2003). In legume fields, emissions range from 0.34 to 4.6 kg N_2O–N ha^{-1} $year^{-1}$ (Eichner 1990), including natural emissions, those associated with cultivation, and those derived from nitrogen fixed by the legume. Yang and Cai (2006) demonstrated the effect of soybean growth on N_2O emission to vary with plant growth stage, primarily being controlled by available nitrogen and mineralization during the early growth stage, but in later growth by quantity of root exudates, itself being closely related to plant photosynthesis.

There are several reports of low N_2O emissions from rice paddy fields were low (Buresh and Austin 1988; Lindau et al. 1990; Smith et al. 1982), with less than 0.1% of the applied nitrogen emitted as N_2O in temperate and tropical rice fields when soils are flooded (Freney 1997). However, it has since been found that N_2O is mainly emitted during the non-flooding periods (Xing 1998). For example, the annual N_2O emission from a rice-flooding fallow system, which received 300 kg N fertilizer, and a rice–wheat cropping system receiving 680 kg N fertilizer were 1.4 and 4.3 kg N_2O–N ha^{-1} $year^{-1}$, respectively (Xing et al. 2002b). Similar emission rates (1.3 and 3.6 kg N_2O–N ha^{-1} $year^{-1}$) were reported in other nitrogen fertilized rice cropping systems with crop rotations including fallow or green manure (Xiong et al. 2002).

Despite the plethora of data on emissions from different cropping systems, few attempts have been made to attribute N_2O emission to rhizosphere soil per se, where, for example comparisons are made within and between crop rows. These have demonstrated a strong influence of plant roots, with decreasing emissions measured with distance away from the root (Smith and Tiedje 1979). We also lack long-term studies encompassing several cropping seasons or crop rotations, so that any gradual loss of residual fertilizer- or residue nitrogen remains unquantified, despite it being recognized that in a variable climate, several years' data is required to obtain a robust estimate of emissions (Dobbie et al. 1999).

Primary drivers of nitrous oxide production in the rhizosphere and their effects on the N_2O-to-N_2 ratio

Nitrogen application, oxygen partial pressure, carbon availability and pH are considered the primary determinants of rates of ammonia oxidation and denitrification in the rhizosphere. Nitrogen fertilizer application results in short-term increased N_2O emissions (Bouwman 1996; Mosier 1994) that last between several days and up to a few weeks (VanCleemput et al. 1994). This increase in N_2O emissions can be exacerbated by a raised denitrifier N_2O-to-N_2 product ratio following nitrogen fertilizer application since nitrate is preferred over N_2O as an electron acceptor for denitrifiers at concentrations of >10 μg g^{-1} (Baggs et al. 2003; Blackmer and Bremner 1978). Inubishi et al. (1996) found that denitrifier N_2O production rapidly responded to nitrate application, whereas there was a lag in the response of nitrifiers, even when a large quantity of ammonium was added to soils. In contrast, Baggs et al. (2003) observed that nitrification was the predominant N_2O producing process over denitrification in the rhizosphere of *Lolium perenne* during the first seven days after application of NH_4NO_3. In conditions where nitrification and denitrification are limited by ammonium and nitrate, respectively, roots compete with the microorganisms for nitrogen and may lower emissions. This means that sometimes greater emissions are reported for fallow than for cropped systems (Duxbury et al. 1982).

The anaerobic volume of soil is a key factor affecting both nitrification and denitrification. Tillage has an important role to play in altering the aeration status of soil through modifying the soil structure, with typically higher N_2O emission from no-till soils compared to tilled soils (Baggs et al. 2003, 2006; Linn and Doran 1984). In terms of potential for denitrification, this is exacerbated by the often higher soil organic matter availability in the upper topsoil of no-till soils (Nieder et al. 1989). Denitrification is the predominant N_2O producing process above 70–80% water-filled pore space (WFPS; Davidson 1991), or at oxygen partial pressures below 0.5% (Parkin and Tiedje 1984), with ammonia oxidation demonstrated to be predominant at lower WFPS (Bateman and Baggs 2005). The N_2O-to-N_2 ratio falls approaching 100% WFPS, but the nitrous oxide reductase is thought to lag behind the nitrate reductase in time following anoxic conditions (Letey et al. 1980).

The role of organic carbon in the regulation of N_2O-to N_2 ratios is still poorly understood and the importance of root-derived organic compounds flow in the rhizosphere is unknown against that of soil organic matter. Haller and Stolp (1985) provided evidence for rhizosphere stimulation of denitrification, with *Pseudomonas aeruginosa* producing 1.8 ml N_2O–

N day^{-1}, which was equivalent to consumption of 72 mg glucose-C day^{-1} from root exudation. Emissions of N_2O have also been reported to be raised, by a factor of 10 or more, following cutting or damage of plants (Beck and Christensen 1987). This is most likely in response to organic compounds released from the roots stimulating denitrification. Recently, an effect of root exudate composition on the denitrifier N_2O-to-N_2 ratio was reported by Henry et al. (2008), where, N_2O-to-N_2 ratios of 0.3 and 1 were observed in microcosms amended with artificial root exudates containing 80% and 40% of sugar, respectively. Increased belowground organic compounds allocation by *Lolium perenne* swards under elevated partial pressure of carbon dioxide has also been demonstrated to stimulate denitrifier N_2O production (Baggs and Blum 2004; Baggs et al. 2003).

Another key factor that can affect N_2O production in soil is pH, but plant-mediated pH effects on N_2O production during nitrification and denitrification have yet to be directly determined. Activity of ammonia oxidizing bacteria may be expected to be reduced at low pH, due to a decline in NH_3 availability. However, the pH effect on N_2O emissions by nitrification is not clear and both greater (Martikainen and DeBoer 1993) and less (Goodroad and Keeney 1984) nitrifier-N_2O production has been reported at soil pH 4 than at pH 6. Production of N_2O by denitrification can also be influenced by decreased pH in the rhizosphere. The nitrous oxide reductase is known to be sensitive to low pH (Firestone et al. 1980) and Thomsen et al. (1994) showed that reduction of N_2O to N_2 was inhibited at low pH values in *Paracoccus*. Accordingly, several studies reported that decreasing soil pH increases N_2O production by denitrification (Nägele and Conrad 1990; Šimek and Cooper 2002).

Where is nitrous oxide produced in the rhizosphere?

Most of the above studies have measured net emissions from cropped soil, but it is unknown spatially where this N_2O is produced in the rhizosphere. However, it is generally accepted that denitrifier activity decreases with distance from roots (Smith and Tiedje 1979). The different drivers of nitrification and denitrification support the idea that these processes are spatially distinct within the rhizosphere, with denitrification being more dependent on root-derived organic compounds and lowered oxygen availability, but nitrification sensitive to pH effects, and competition with plants for available ammonium (Fig. 2). Spatial location of N_2O production may also diverge over time in conjunction with altered root exudation or root respiration during plant growth and development. The significance and location of any ‘hotspots and hot moments’ have yet to be verified, and we currently still rely on theoretical models (Arah and Smith 1989; Smith 1980). Poor characterization at the micro scale raises the question of whether the key process drivers, for denitrification and nitrification are the same, and of the same ranked significance, with differing scale? Only if this is so, can known responses at the plot scale be used to understand interactions within the rhizo-

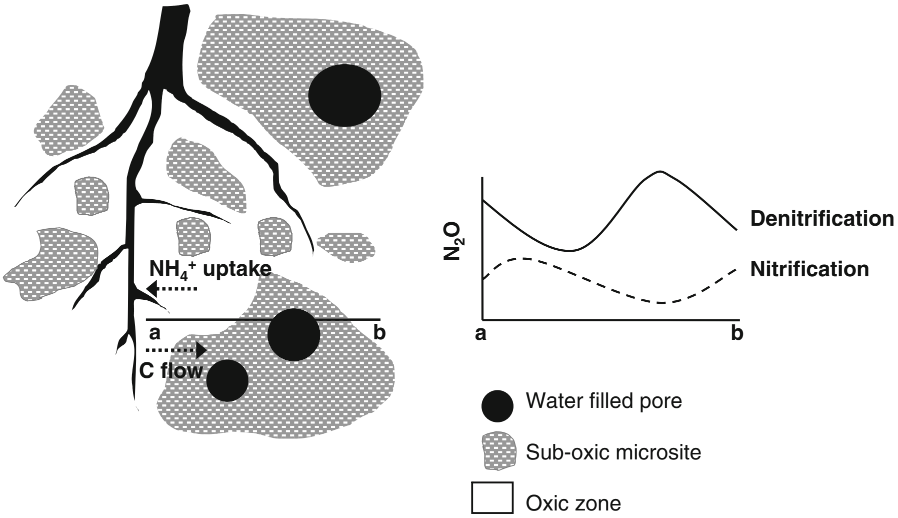

Fig. 2 Conceptual representation of the spatial arrangement of microsites in the rhizosphere, and hypothesized N_2O production by nitrification and denitrification with distance from a plant root as influenced by carbon, oxygen and [NH_4^+] gradients. N_2O production is based on putative nitrification and denitrification rates

sphere. However, at the plot or field level soil hydrology and frequency and duration of rainfall events often become the primary drivers of denitrifier-N_2O production (Dobbie and Smith 2006; Sextone et al. 1985).

Methane emissions from rhizosphere soil

Rice paddies are one of the most important sources of atmospheric CH_4, with a global emission ranging from 30 to 50 Tg CH_4 year^{-1}, which account for about 10% to 20% of the global CH_4 budget. Rice photosynthates can comprise up to more than 50% of total CH_4 emissions (Watanabe et al. 1999) and transport of CH_4 up to 90%. There is an impressive literature on CH_4 emissions from rice paddies. A seasonal pattern of CH_4 emissions is commonly reported with two or three maxima observed in irrigated rice fields during the cropping season. A diurnal pattern is also observed with maximum rates in the afternoon (Schültz et al. 1989). Mean CH_4 emission rates observed in rice fields during the growing season in China, India or the Philippines ranged from 0.02 to 1.3 g CH_4 m^{-2} day^{-1}, depending mainly on the irrigation and fertilization regimes (Jing et al. 2002; Gosh et al. 2003; Wassmann et al. 1999). As examples of the great variability of CH_4 emissions, rates ranging from 0.0035 to 0.180 g CH_4 m^{-2} day^{-1} were reported from flooded rice paddies in California (Cicerone and Shetter 1981).

Methane emissions from cultivated or natural wetlands are usually lower than 0.2 g CH_4 m^{-2} h^{-1} (Le Mer and Roger 2001). In wetlands, aquatic plants generally transport ten times the amount of CH_4 relative to non-vegetated areas (Chanton 2005) and this differ between plant species (Ding et al. 2005). CH_4 transport through the aerenchyma are estimated to account for 50% to 90% of total emissions (Cicerone and Shetter 1981). However, ebullition is thought to account for 18–50% of total CH_4 emissions from Swedish wetlands (Christensen et al. 2003).

Fifteen percent of the net carbon fixed by wetlands may be released to the atmosphere as CH_4 (Brix et al. 2001). Thus, most of the CH_4 flux in a northern Minnesota peatland was derived from recently fixed carbon in living vegetation, and not much from decomposition of old peat (Chanton et al. 1995). In peat-forming wetlands, bryophytes (liverworts, hornworts and mosses) are more sensitive to water table position than vascular plants, and may therefore be used as predictors of CH_4 emission (Joabsson et al. 1999). Nilsson and Bohlin (1993) found that both CH_4 and CO_2 concentrations in Swedish mires were positively correlated with *Sphagnum* remains and negatively correlated with *Carex* remains in peat. This difference was attributed to less easily degradable carbon in *Carex* compared to *Sphagnum*. Importance of vegetation type was confirmed in a large national inventory of Swedish mires comprising 3,157 measured chamber flux rates, where it was estimated that sedge mires accounted for 96% of the CH_4 emitted from natural wetlands in Sweden (Nilsson et al. 2001). Vegetation composition was also found to be an important factor controlling CH_4 emission from an ombrotrophic peatland, with greater CH_4 emissions observed from *Eriophorum* sp. areas than from *Sphagnum* areas (Frenzel and Rudolph 1998). Accordingly, CH_4 emissions of about 72 mg CH_4 m^{-2} day^{-1} were observed in areas containing both *E. vaginatum* L. and *Sphagnum*, which was more than six times higher than areas without *E. vaginatum* (Greenup et al. 2000). Similar results were reported by Minkkinen and Laine (2006), who observed the highest emissions of 29 mg CH_4 m^{-2} day^{-1} from *E. vaginatum* L., with a decreasing trend to *Sphagna* (10.0 mg CH_4 m^{-2} day^{-1}) and forest moss (2.6 mg CH_4 m^{-2} day^{-1}). An effect of plant cover was also reported in freshwater marshes in China with higher CH_4 fluxes during the summer season of 168 to 744 mg CH_4 m^{-2} day^{-1} in the rhizosphere of a *Carex* marsh than in the *Deyeuxia angustifolia* marsh (Ding et al. 2004).

Potential feedback controls of greenhouse gas production in the rhizosphere

Carbon sequestration in the rhizosphere

Carbon sequestration in soil is described as a promising way for reducing the increasing atmospheric carbon dioxide concentration (3.2 Pg C y^{-1}) and carbon storage in agricultural soils is mentioned under Article 3.4 of the Kyoto Protocol. The terrestrial carbon reservoir is 1,500~1,600 Pg of organic-C in the first meter depth (Eswaran et al. 1995), which is more than twice that in the vegetation or the atmospheric pools (Lal 2004). Terrestrial carbon sequestration is controlled by the balance of carbon inputs from primary production and subsequent storage in soil, and outputs through degradation of organic compounds, for which both plants and microbes are accountable. Carbon input from plants mainly includes transfer of the carbon stored in dead plant biomass into the soil by decomposition, and accumulation of soil organic matter due to the humification process after plant death is well documented. The humification rate varies depending on climatic conditions, and plant biochemical composition. Perennial and early successional systems increase storage of soil carbon (Robertson et al. 2000), but in agricultural soils, carbon losses exceed the gains. Conversion of natural ecosystems to agricultural land resulted in the loss of 30% to 75% of their antecedent soil organic carbon pool, which is estimated at 50 to 100 Pg of C (0.8 Pg per year) (Jarecki and Lal 2003; McLauchlan et al. 2006; Schlesinger 1984). The rhizosphere could hypothetically make a significant contribution to carbon input, since about 17% of the plant-fixed carbon is transferred to the rhizosphere soil through root exudates, which corresponds to up to 50% of the plant biomass (Nguyen 2003). However, only a few studies on soil carbon input from rhizodeposits exist and hitherto, it has been shown that most of the root exudates are oxidized to carbon dioxide within a few hours (Jones and Hodge 1999; Kuzyakov and Demin 1998; Verburg et al. 1998), and less than 5% of the carbon transferred to the rhizosphere through root exudates is incorporated into soil organic matter (Kumar et al. 2006; Nguyen 2003). Another source of C input in the rhizosphere is Mycorrhiza which act as a plant C-sink. Thus, a recent study suggested that turnover of mycorrhizal external mycelium may be of importance for the transfer of root derived C to soil organic matter (Godbold et al. 2006). On the other hand, the rhizosphere can also be source of carbon dioxide through the decay of soil organic matter, which can be stimulated by plant-derived carbon and is referred to as the ‘rhizosphere priming effect’ (Kuzyakov and Demin 1998). However, the supply of labile carbon, such as soluble sugars, amino acids, root mucilage or rhizosphere extract, induces no or little affect on decomposition of soil organic matter, compared to more recalcitrant plant derived carbon, such as ryegrass, cellulose or wheat straw (Fontaine et al. 2007; Mary et al. 1992, 1993).

Whilst the rhizosphere may have a potential contribution to carbon sequestration, the amount of carbon stored in soil mainly depends on land-management practices, edaphic factors and climate. There is a large body of literature on management strategies to increase the net carbon storage in agricultural soils (Post et al. 2004). Such practices include reduced tillage, increasing residue inputs, crop rotation with cover crops, green manures, or perennial crops. Most of the increases in soil carbon associated with these practices result from reversing processes by which traditional management has depleted the soil carbon stocks that accumulated under native perennial vegetation (Cole et al. 1997). Thus, assuming a recovery of 50% of carbon losses in agricultural soils, the global potential for C sequestration over the next 50–100 years would be approximately 25–50 Pg C. In Europe, estimates of the carbon sequestration capacity of agricultural soils are up to 16–23 Tg C year^{-1} (Freibauer et al. 2004; Smith et al. 1998).

Opportunities for mitigation of nitrous oxide emissions in the rhizosphere

Most pertinent to mitigation of rhizosphere N_2O emissions in arable soil are synchronization of nitrogen application to crop demand, precision farming strategies with use of slow- or controlled-release fertilizers (McTaggart and Tsuruta 2003), application of nitrification inhibitors such as dicyandiamide (Di et al. 2007; Hoogendorn et al. 2008) and drainage and aeration of soil (Monteny et al. 2006). It has been estimated that a better synchronization of nitrogen application to crop demand and more closely integrating animal waste and crop residue application with crop production, could decrease N_2O emissions by about 0.38 Tg N_2O–N (Cole et al. 1997). Controlled-release fertilizer, nitrification inhibitors and water management could further lower these emissions by about 0.3 Tg N_2O–N, resulting in a total potential reduction of 0.7 (0.36 to 1.1) Tg N_2O–N, representing 9% to 26% of current emissions from agricultural soil (Cole et al. 1997). Another option to mitigate N_2O emissions in arable soil is no-tillage farming (Li et al. 2005), but its benefits may only be realized in the long-term (Six et al. 2004). One emerging and potentially promising option that did not appear in the IPCC report is the combined application of lime and zeolite. This has recently been demonstrated to lower N_2O emission and increase reduction to dinitrogen in urea amended soil (Zaman et al. 2007), and its potential to be used in the rhizosphere warrants further investigation. A more speculative mitigation possibility is in manipulating exudated carbon compounds and their flow into the rhizosphere, through plant breeding. However, we still do not know if there is any active selection for organic compounds within the denitrifier community, and any carbon preference, and the impact of this on the selection of denitrifiers that have a nitrous oxide reductase or the impact on the regulation of the nitrous oxide reductase itself. Until these relationships are verified, it may be preferable to manage agro-ecosystems to encourage temporary nitrogen immobilization with re-mineralization in the spring in timing with crop demand.

Opportunities for mitigation of CH_4 in the rhizosphere

Mitigation of CH_4 emission can be achieved by lowering methanogenesis and/or CH_4 transport to the atmosphere, or by stimulating methanotrophy. In upland soils, such as forest and agricultural soils, no or little CH_4 is produced, instead atmospheric CH_4 can be oxidized. Forest soils tend to be good sinks for methane, because the trees help to keep the water table well below the surface, which allows for methanotrophy. Thus, well drained non-agricultural soils contribute 5% to 10% of the global CH_4 sink (Cicerone and Oremland 1988; Crutzen 1991). However, the low concentration of CH_4 in upland soils, is likely to be the limiting factor for CH_4 oxidation. Increasing the CH_4 sink can be done through selection of tree species, since forest composition affects CH_4 uptake rates (Menyailo and Hungate 2003). Conversion of natural ecosystems to agricultural land usually lowers CH_4 oxidation, but mitigation of CH_4 emissions can be achieved by limiting cultural practices affecting CH_4 and O_2 availability. For example, soil compaction by tractors may reduce CH_4 oxidation by 50% (Hansen et al. 1993), and drainage can also be crucial in determining the size of the soil methane sink.

Mitigation of methane production in peatland ecosystems

Plant species differ in properties that constrain microbial respiration as well as properties that promote CH_4 oxidation, and this plant associated CH_4 oxidation has been reported from a wide range of wetland species (Sorrell et al. 2002). Further examples include CH_4 oxidation associated with roots and rhizomes of *Sparganium eurycarpum*, where 1% to 58% (mean 27%) of the total CH_4 flux was oxidized (King 1996). In the rhizosphere of *Carex lasiocarpa* and *C. meyeriana*, CH_4 oxidation lowered potential CH_4 emissions by 3.2–35.9% and 4.3–38.5%, respectively (Ding et al. 2004). Similarly, Popp et al. (2000), found that rhizospheric CH_4 oxidation in a *Carex*-dominated fen in Canada lowered net CH_4 emissions by around 20%. Lower CH_4 oxidation was observed in *Carex*-dominated wetlands compared to other types of sedge vegetation (*Eriophorum* and *Juncus*) in southern Sweden (Ström et al. 2005). In agreement, it was shown that CH_4 oxidation was not associated with *Eriophorum* (Frenzel and Rudolph 1998).

The importance of plant cover in influencing net CH_4 emissions is also related to their capacity to transport CH_4 through their aerenchyma. Transport is linked to root porosity (intercellular gas spaces and aerenchyma), which differ substantially among plants (Colmer 2003) but also within genus (e.g. 5% to 30% in *Rumex*, Laan et al. 1989) or between cultivars (Huang et al. 1994). Thus, the choice of plant species in, for example, constructed wetlands could be a way to contribute to CH_4 mitigation. Plant cover can also have implications for the management of peatlands as sources or sinks for CH_4. In addition, lowering of CH_4 emissions could be accomplished through drainage, independent of any ecological or financial considerations. On the other hand, drainage of peat increases the emissions of CO_2 and N_2O. Thus it has been shown that drainage for forestry stimulates N_2O emission on fertile and fertilized sites and that agricultural use of peatland induces considerable and long-lasting emissions of CO_2 and N_2O (Alm et al. 2007).

Mitigation of methane production in rice paddies

The complexity of the role of the rice plant for regulating CH_4 production has been well investigated and reviewed (Aulakh et al. 2001b; Conrad 2002; Frenzel 2000; Wassmann and Aulakh 2000). Up to 90% of the CH_4 emitted in rice paddies is released through rice transport (Cicerone and Shetter 1981; Conrad 2007), while between 19% and 90% of the

CH_4 produced is oxidized (Bosse and Frenzel 1997; Conrad 1996; Gilbert and Frenzel 1995; Holtzapfel-Pschorn et al. 1985), with up to 75% of the CH_4 oxidation taking place in the rhizosphere (Frenzel 2000). Accordingly, strategies to lower net CH_4 emission from rice fields include reduction of CH_4 production, increasing CH_4 oxidation, and lowering CH_4 transport through the plant. Among the CH_4 emission mitigation strategies that do not compromise rice productivity, introduction of drainage periods during the crop cycle appears to be the most efficient (Neue 1993). Thus, it has been estimated that intermittent drainage periods in one third of the poorly drained rice fields in China could reduce 10% the agricultural CH_4 emissions (9.9 Tg, Kern et al. 1997). However, a major drawback of this strategy is that it consumes two to three times more water than continuous flooding and can increase the N_2O emissions (Hou et al. 2000). Another strategy to lower emissions may be oriented toward rice cultivar selection and use of rice cultivar characterized by a low root exudation and porosity to limit production and transport of CH_4. There are 90,000 known rice cultivars with large variations in genotype and phenotype that can affect CH_4 production, rhizospheric CH_4 oxidation and plant-mediated CH_4 transport efficiency. Accordingly, several studies reported large differences in CH_4 emissions between cultivars that can reach up to 500% (Jia et al. 2002; LeMer and Roger 2001; Wassmann and Aulakh 2000). Mitigation of CH_4 emissions in rice paddies also includes amendment with compost residues instead of uncomposted material (Conrad 2007; LeMer and Roger 2001) and direct seeding instead of transplanting.

Concluding remarks

Emissions of CH_4 and N_2O from soils and how they are affected by the presence of plants have now been investigated for several decades and most studies have shown a strong influence of plant roots. The soil oxygen partial pressure is a major factor regulating nitrification, denitrification, methanogenesis and methanotrophy, which is clearly reflected in studies reported in this review indicating that the rhizosphere effect on these underpinning processes controlling greenhouse gas emissions vary widely from upland to wetlands soils. Thus, in uplands soils, inhibition of nitrification by plants is commonly reported whereas denitrification is most often stimulated in the rhizosphere. Also in upland soils, methanotrophy largely dominates over methanogenesis. By contrast, nitrification in wetlands is stimulated next to the roots where radial oxygen losses occurred. Wetland plants also stimulate methanogenesis through root exudation and can facilitate CH_4 transportation to the atmosphere in their tissues. The development of molecular approaches allowed significant progress in the knowledge of the ecology of the microbial guilds involved in greenhouse gas emissions and now we know that the size and/or the diversity of the nitrifier, denitrifier, methanogen and methanotroph communities are also influenced by the presence of plant roots. However, it remains unclear whether these changes in microbial communities in the rhizosphere affect greenhouse gas emissions. Because the rhizosphere effect is complex and results from the action of several strongly interwoven factors such as organic carbon and oxygen availability, further research is required in order to reconcile apparently conflicting results. In addition, prediction of a general rhizosphere effect is difficult since there is evidence that it is both plant species and soil-type dependent. Thus, our incomplete knowledge of the complex rhizosphere effect on microbial guilds controlling greenhouse gas emissions is still limiting the development of plant-based strategies to mitigate emissions of both CH_4 and N_2O.

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