Effect of water management on soil microbial communities and atmospheric trace gases

R. Conrad, A. Bollmann, H. Yao and R. Roy

Max-Planck-Institut für Terrestrische Mikrobiologie, D-35043 Marburg, Germany

ABSTRACT

Addition of water to the soil (rain, irrigation, flooding) decreases the availability of O_2. For example, nitrifying and denitrifying bacteria respond strongly to changes in soil water and O_2 availability by producing more or less of the atmospheric trace gases NO and N_2O. Consumption of NO also responds to O_2 availability, as it may proceed by reductive or oxidative pathways. Complete depletion of O_2 in the soil (e.g. flooding of rice fields) results in the sequential change of the redox processes until CH_4 is emitted into the atmosphere. Driving forces are the availability of electron donors (organic substrates) and electron acceptors (mainly the content of iron). It is interesting to note that CH_4 production starts almost instantaneously after flooding, then comes to a halt as soon as competing redox processes (iron and sulfate reduction) start, and finally resumes vigorously when ferric iron and sulfate are depleted. Drainage of submerged fields, even short-term, regenerates sulfate and ferric iron and results in long-lasting inhibition of CH_4 production.

Introduction

Atmospheric trace gases, i.e. gases that occur at mixing ratios of <1%, play important roles in the functioning of our environment. For instance NO regulates the oxidizing capacity of our troposphere, CH_4 acts as greenhouse gas, and N_2O results in the destruction of the stratospheric ozone shield (for more information see [14]). Soils contribute significantly to cycling of global trace gases [4]; for instance, soils contribute approximately 70, 60 and 20% to the total source strengths of atmospheric N_2O, CH_4 and NO, respectively. These trace gases are produced by soil microorganisms [4].

Soil microorganisms are in many ways influenced by the physical-chemical conditions in their habitat (e.g. temperature, moisture). Soil moisture is a variable that is to a large extent under the control of humans who irrigate agricultural soils to optimize cropping or submerge soils for cultivation of rice. Hence, water management in agriculture may have a great influence on the structure and function of soil microbial communities. Aerobic microbial respiration rates increase with soil moisture, reach a maximum and then decrease again [8]. The increasing segment of the curve is typically due to the increased diffusivity of substrates in soil solution and the activation of dormant microorganisms by available water. The decreasing segment of the curve is typically due to the decrease of O_2 diffusivity thus limiting respiration until it completely stops when conditions become anoxic. In flooded soils, this condition is rapidly reached when O_2 has been consumed and diffusion of gases is so slow that O_2 typically penetrates only 1-3 mm deep into the soil profile [12].

Microbial Biosystems: New Frontiers
Proceedings of the 8th International Symposium on Microbial Ecology
Bell CR, Brylinsky M, Johnson-Green P (eds)
Atlantic Canada Society for Microbial Ecology, Halifax, Canada, 1999.

In the following we describe the effects of soil moisture on the release of NO and N_2O by nitrifying and denitrifying bacteria. This is a situation that is typical for upland soils which are either irrigated or receive precipitation. We then describe the microbial events, in particular CH_4 production, that are initiated by the complete submergence of soils, a situation that is typical for rice fields.

Control of NO and N_2O release by soil moisture

It is generally accepted that production of NO and N_2O in soils is mainly due to nitrifying and denitrifiying bacteria. Ammonium-oxidizing nitrifiers require ammonium plus oxygen and thus have a similar response to soil moisture as aerobic microbial respiration does; i.e., nitrification increases with soil moisture, reaches a maximum at about 60% water-filled pore space (WFPS), and then decreases again [8]. Denitrifiers, on the other hand, usually require almost anoxic conditions to start reduction of nitrate, nitrite, NO, or N_2O to N_2. Thus, they should become active at soil moisture contents higher than 60% WFPS [8]. However, NO and N_2O are not the end products but intermediates or side products of nitrification and denitrification. Therefore, the rates of NO and N_2O production are not a simple function of the rates of nitrification and denitrification, but also depend on the relative speed with which the intermediates are produced and consumed, i.e. the activities of the enzymes producing and consuming NO and N_2O in the bacteria. This fact has been summarized by the conceptual hole-in-the-pipe model [11] which illustrates nitrification and denitrification as pipes with diameters proportional to their rates and production of NO and N_2O as holes in these pipes which allow a smaller or larger leakage of part of the nitrogen flow. Soil moisture would not only regulate the rates of N flow (i.e. diameter of the pipes) but also the proportions of NO and N_2O relative to the end products (i.e. diameter of the holes). How would the latter respond to changes in soil moisture? A theoretical prediction requires the understanding of how the microbial enzymes producing and consuming NO and N_2O react to changes in soil water content and in the availability of O_2. At the time being such a theoretical prediction is hardly possible, since the enzymatic basis of production and consumption of NO and N_2O in ammonium-oxidizing nitrifiers is not completely understood, and since the patterns of induction and repression of denitrifying enzymes vary with the microbial species [5, 31]. In the case of NO, the situation is even more complicated. The produced NO, once released into the soil, is rapidly consumed by other microorganisms, so that the net release of NO from the soil into the atmosphere is the result of a rapid turnover by simultaneous microbial production and consumption [13, 24]. The consumption of NO can be accomplished by different microbial groups [5], the most important ones being denitrifiers that reduce NO to N_2O under anoxic and O_2-limited conditions and heterotrophic bacteria that oxidize NO to nitrate under oxic conditions [4, 5, 23].

Because of all these complications it is convenient to study the effect of soil moisture on the net release of NO and N_2O from soil and differentiate whether it is due to nitrification or not. This differentiation is easily accomplished by specific inhibition of nitrification, e.g. with low partial pressures (1-10 Pa) of acetylene [15]. Release of NO and N_2O that is not inhibited by acetylene is usually assumed to be due to denitrification. In some soils, however, acetylene-insensitive heterotrophic nitrification may also contribute to NO and N_2O production [17]. Various evidence from field and laboratory studies indicated that NO release is predominant at relatively low soil moisture contents and is mainly due to nitrification, whereas N_2O release is predominant at relatively high soil moisture contents and is mainly due to denitrification (For literature see [2, 5, 7, 28]). This picture has been presented in a model of the relationship between WFPS of soil and relative fluxes of N gases [7] and has been used in a process-oriented model of nitrogen trace gas emissions from soils worldwide [20]. However, a systematic verification of this picture was missing. Recently, Bollmann and Conrad [2] systematically studied the effect of soil moisture on NO and N_2O release by nitrification and denitrification in a loamy silt and a sandy silt agricultural soil and basically confirmed the validity of the above described picture. The results obtained with the loamy silt are summarized in Fig. 1.

The results show that NO was predominantly released by nitrification exhibiting a maximum at intermediate soil moisture contents, while N_2O was mainly released by denitrification especially at higher soil moisture contents. The results also showed that NO release was larger than N_2O release. The relative importance of NO emission compared to

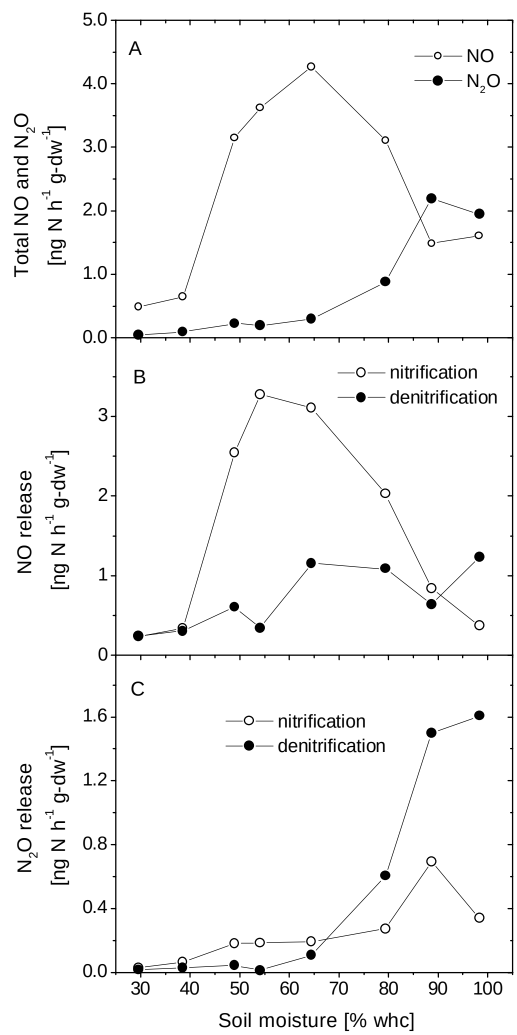

Fig. 1. Influence of soil moisture in terms of water holding capacity (whc) on the release of NO and N_2O due to nitrification and denitrification in a loamy silt soil (data taken from [2]).

N_2O emission has been observed with a large number of different soils [1] and has also been found in field studies [3, 27]. These observations emphasize the importance of NO emission which may play an even greater role than N_2O in the overall nitrogen budget of soils and should not be neglected.

Initiation of CH_4 production after flooding of soil

Thermodynamic theory predicts that after flooding of soil, CH_4 production is initiated at the end of a sequential reduction process which starts with the reduction (depletion) of O_2, followed by that of nitrate, manganese(IV), iron(III) and sulfate. Since CH_4 production from the reduction of CO_2 or methyl groups (e.g. in acetate) is the process which results in the smallest free energy change compared to the other reduction processes, it would be the latest to take place. Indeed, this thermodynamic prediction has largely been verified by observations in flooded soils [18, 19]. However, the question remained by which mechanisms the bacteria would control their activities according to the thermodynamic theory. The most straight forward and widely accepted explanation is the successful competition for substrate by those organisms that can gain the most energy [6, 16]. For example sulfate reducers would successfully compete with methanogens for H_2, since they gain more energy by reducing sulfate ($\Delta G^{o\prime}$ = -38 kJ mol^{-1} H_2) than methanogens would gain by reducing CO_2 ($\Delta G^{o\prime}$ = -34 kJ mol^{-1} H_2). The sulfate reducers would thus decrease the H_2 concentration to a level that no longer allows the methanogens to generate sufficient free energy.

This raised the question whether methanogens in flooded soil would be limited by substrate as long as iron reduction and sulfate reduction take place. This question was addressed in two recent studies which measured CH_4 production together with the concentrations of substrates and products to determine the Gibbs free energy available for methanogenesis [22, 30]. A total of 17 different rice field soils in China, the Philippines and Italy were investigated. The patterns observed were consistent and demonstrated that CH_4 production started right after the flooding of soil at redox potentials (measured with a Pt electrode) that were on the order of +400 mV. Indeed, CH_4 production was thermodynamically possible, since relatively high concentrations of H_2 and acetate were available especially in this early phase of flooding. In more detail, the following events occurred after the soil was flooded:

1. O_2 was depleted and fermentation of organic matter started resulting in the production of H_2 and acetate.
2. The availability of H_2 allowed methanogens to become active even before sulfate and iron reducers did so.
3. As soon as sulfate and iron reducers became active, they competed for H_2 and eventually decreased the H_2 partial pressure so much that CH_4 production stopped.
4. Sulfate and iron reduction continued until sulfate and Fe(III) were depleted.
5. Then, H_2 concentrations increased and CH_4 production resumed.

The reason why methanogens, in particular hydrogenotrophic methanogens [22], became more rapidly activated than iron and sulfate reducers is unknown. Perhaps, the methanogens are more resistant to high redox potentials in soil than the other anaerobic bacteria. Various evidence indicates that methanogens are able to survive in soil when it becomes dry and oxic and are also able to initiate methanogenesis at positive redox potentials [9, 10, 19]. Regardless of the reason, they certainly have an initial advantage which allows an early start of CH_4 production. This early CH_4 production is suppressed later on, when the sulfate and iron reducers compete for H_2. The extent to which this later competition results in suppression of methanogenesis seems to depend on the relative availabilities of electron donors (i.e. H_2) versus electron acceptors (i.e. Fe(III) and sulfate). We were able to distinguish 3 classes of soils for which examples are illustrated in Fig.2. The first class (e.g. soil 8) apparently had a high ratio of electron donors to electron acceptors, since the early CH_4 production was not suppressed even during active sulfate and iron reduction. The Gibbs free energy available to H_2-dependent methanogens was always more negative than –23 kJ mol^{-1} CH_4 which is equivalent to > 1/3 ATP, if we

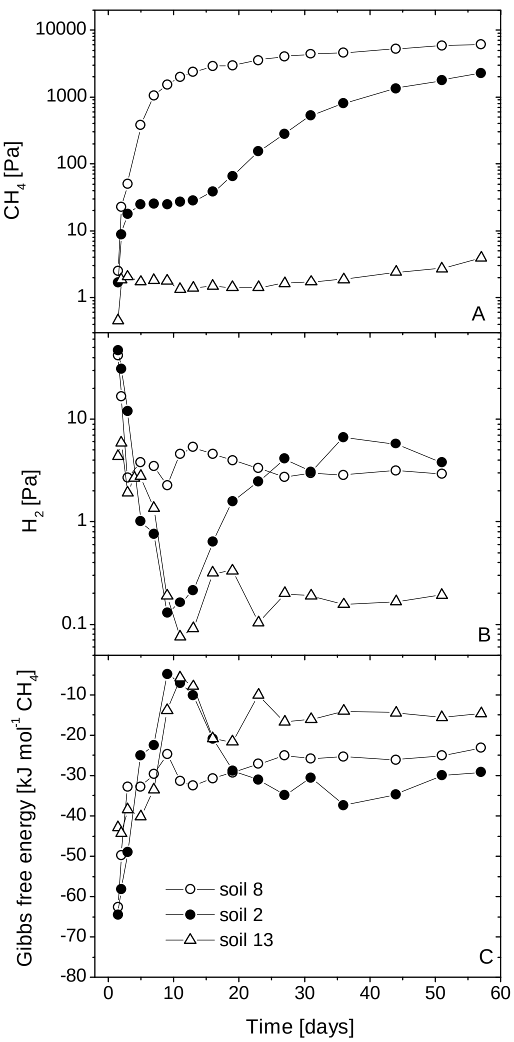

Fig. 2. Temporal change (A) of CH_4 accumulation, (B) of H_2 partial pressures, and (C) of Gibbs free energies of H_2-dependent methanogenesis after flooding of soil. The soils represent three different classes of methanogenic behavior: class 1 (soil 8, Buggallon, The Philippines), class 2 (soil 2, Changchun, China) and class 3 (soil 13, Urdaneta, The Philippines) (data taken from [30]).

assume that methanogenesis is coupled to energy generation. In the second class of soils (e.g. soil 2), however, the early CH_4 production was temporarily suppressed due to competition for H_2 and an increase of the Gibbs free energy to values less negative than –23 kJ mol^{-1}. In the third class (e.g. soil 13), finally, the concentrations of Fe(III) and sulfate were so high, that the suppression of the early CH_4 production lasted for more than 50 days with Gibbs free energies >–23 kJ mol^{-1}. In contrast to H_2, competition for acetate was not relevant, since Gibbs free energies of acetate-dependent methanogenesis were generally <-26 kJ mol^{-1} CH_4 throughout the entire incubation period.

Floodwater management, i.e. intermittent drainage, of rice fields may be a good option to mitigate CH_4 emission into the atmosphere. Indeed, CH_4 emission rates from rice fields were drastically reduced for quite some period after a drainage event [25, 29]. Recent studies showed that the reason for the prolonged suppression of methanogenesis is the regeneration of Fe(III) and sulfate during the drainage by oxidation of reduced iron and sulfur with O_2 [21, 26]. Then, iron and sulfate reducers were again able to successfully compete with methanogens for limiting substrates. Mitigation of CH_4 emission by intermittent drainage thus functions by maintaining high concentrations of Fe(III) and sulfate in the rice field soil. Any other management that achieves these high concentrations would probably have the same mitigation effect: for example, the addition of Fe(III), relying on its continuous regeneration by Fe(II) oxidation in the rice rhizosphere (S.Schnell, presentation at ISME-8).

References

1. Bollmann A, Conrad R (1997) Acetylene blockage technique leads to underestimation of denitrification rates in oxic soils due to scavenging of intermediate nitric oxide. Soil Biol Biochem 29:1067-1077
2. Bollmann A, Conrad R (1998) Influence of O_2 availability on NO and N_2O release by nitrification and denitrification in soils. Global Change Biology 4:387-396
3. Butterbach-Bahl K, Gasche R, Breuer L, Papen H (1997) Fluxes of NO and N_2O from temperate forest soils: impact of forest type, N deposition and of liming on the NO and N_2O emissions. Nutrient Cycling in Agroecosystems 48:79-90
4. Conrad R (1996) Soil microorganisms as controllers of atmospheric trace gases (H_2, CO, CH_4, OCS, N_2O, and NO). Microbiol Rev 60:609-640
5. Conrad R (1996) Metabolism of nitric oxide in soil and soil microorganisms and regulation of flux into the atmosphere. In: Murrell JC, Kelly DP (eds) Microbiology of Atmospheric Trace Gases: Sources, Sinks and Global Change Processes, Springer, Berlin, pp 167-203
6. Cord-Ruwisch R, Seitz HJ, Conrad R (1988) The capacity of hydrogenotrophic anaerobic bacteria to compete for traces of hydrogen depends on the redox potential of the terminal electron acceptor. Arch Microbiol 149:350-357
7. Davidson EA (1991) Fluxes of nitrous oxide and nitric oxide from terrestrial ecosystems. In: Rogers JE, Whitman WB (eds) Microbial Production and Consumption of Greenhouse Gases: Methane, Nitrogen Oxides, and Halomethanes, American Society for Microbiology, Washington, D.C., pp 219-235
8. Davidson EA (1993) Soil water content and the ratio of nitrous oxide to nitric oxide emitted from soil. In: Oremland RS (ed) Biogeochemistry of Global Change, Chapman & Hall, New York, pp 369-386

9. Fetzer S, Conrad R (1993) Effect of redox potential on methanogenesis by *Methanosarcina barkeri*. Arch Microbiol 160:108-113
10. Fetzer S, Bak F, Conrad R (1993) Sensitivity of methanogenic bacteria from paddy soil to oxygen and desiccation. FEMS Microbiol Ecol 12:107-115
11. Firestone MK, Davidson EA (1989) Microbiological basis of NO and N_2O production and consumption in soil. In: Andreae MO, Schimel DS (eds) Exchange of Trace Gases between Terrestrial Ecosystems and the Atmosphere. Dahlem Konferenzen, Wiley, Chichester, pp 7-21
12. Frenzel P, Rothfuss F, Conrad R (1992) Oxygen profiles and methane turnover in a flooded rice microcosm. Biol Fertil Soils 14:84-89
13. Galbally IE, Johansson C (1989) A model relating laboratory measurements of rates of nitric oxide production and field measurements of nitric oxide emission from soils. J Geophys Res 94:6473-6480
14. IPCC (1990, 1992, 1994, 1995) Reports of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge.
15. Klemedtsson L, Svensson BH, Rosswall T (1988) A method of selective inhibition to distinguish between nitrification and denitrification as sources of nitrous oxide in soil. Biol Fertil Soils 6:112-119
16. Lovley DR, Goodwin S (1988) Hydrogen concentrations as an indicator of the predominant terminal electron-accepting reactions in aquatic sediments. Geochim Cosmochim Acta 52:2993-3003
17. Papen H, Hellmann B, Papke H, Rennenberg H (1993) Emission of N-oxides from acid irrigated and limed soils of a coniferous forest in Bavaria. In: Oremland RS (ed) Biogeochemistry of Global Change, Chapman & Hall, New York, pp 245-260
18. Patrick Jr. WH, Reddy CN (1978) Chemical changes in rice soils. In: International Rice Research Institute (ed) Soils and Rice, IRRI, Los Banos, Philippines, pp 361-379
19. Peters V, Conrad R (1996) Sequential reduction processes and initiation of CH_4 production upon flooding of oxic upland soils. Soil Biol Biochem 28:371-382
20. Potter CS, Matson PA, Vitousek PM, Davidson EA (1996) Process modeling of controls on nitrogen trace gas emissions from soils worldwide. J Geophys Res 101:1361-1377
21. Ratering S, Conrad R (1998) Effects of short-term drainage and aeration on the production of methane in submerged rice soil. Global Change Biology 4:397-407
22. Roy R, Klüber HD, Conrad R (1997) Early initiation of methane production in anoxic rice soil despite the presence of oxidants. FEMS Microbiol Ecol 24:311-320
23. Rudolph J, Koschorreck M, Conrad R (1996) Oxidative and reductive microbial consumption of nitric oxide in a heathland soil. Soil Biol Biochem 28:1389-1396
24. Rudolph J, Rothfuss F, Conrad R (1996) Flux between soil and atmosphere, vertical concentration profiles in soil, and turnover of nitric oxide. 1. Measurements on a model soil core. J Atmos Chem 23:253-273
25. Sass RL, Fisher FM, Wang YB, Turner FT, Jund MF (1992) Methane emission from rice fields: the effect of floodwater management. Global Biogeochem Cycles 6:249-262
26. Sigren LK, Lewis ST, Fisher FM, Sass RL (1997) Effects of field drainage on soil parameters related to methane production and emission from rice paddies. Global Biogeochem Cycles 11:151-162

27. Veldkamp E, Keller M (1997) Nitrogen oxide emissions from a banana plantation in the humid tropics. J Geophys Res 102:15889-15898
28. Williams EJ, Hutchinson GL, Fehsenfeld FC (1992) NO_x and N_2O emissions from soil. Global Biogeochem Cycles 6:351-388
29. Yagi K, Tsuruta H, Kanda K, Minami K (1996) Effect of water management on methane emission from a Japanese rice paddy field: Automated methane monitoring. Global Biogeochem Cycles 10:255-267
30. Yao H, Conrad R (in press) Thermodynamics of methane production in different rice paddy soils from China, the Philippines, and Italy. Soil Biol Biochem
31. Zumft WG (1997) Cell biology and molecular basis of denitrification. Microb Molec Biol Rev 61:533-616