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Evaluation of Data on the Turnover of NO and N₂O by Oxidative Versus Reductive Microbial Processes in Different Soils

By

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S u m m a r y

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Production of NO and N₂O in soils is mainly caused by microbial ammonium oxidation (nitrification) and nitrate reduction (denitrification). However, the nitrogen oxides are not the end products of these processes. NO and N₂O are also consumed during denitrification. NO is in addition consumed by unspecific oxidation to nitrate catalyzed by heterotrophic bacteria. Production rates of NO, uptake rate constants of NO and release rates of N₂O were measured in various soils from agricultural, meadow, temperate forest, savanna and rain forest sites. The relative contribution of ammonium oxidation to the production of NO and N₂O was determined by the acetylene inhibition technique. The rates of NO and N₂O turnover are strongly affected by soil temperature and moisture. To avoid that these environmental variables mask the controlling effects of other soil characteristics, the turnover rates of NO and N₂O were measured under standardized conditions, i.e. at 25°C and a soil moisture of 60 % WHC. Under these conditions, soils with high N₂O release systematically also exhibited higher NO production rates. The NO uptake rate constants, on the other hand, were not correlated with the NO production rates, both varying over 2 orders of magnitude. However, NO uptake rate constants were systematically larger in those soils which exhibited relatively large rates of NO+N₂O production from denitrification, indicating that denitrification also contributed to NO consumption in the tested soils. Under standardized conditions, the rates of NO production in the various soils were generally higher than the rates of N₂O production, and ammonium oxidation generally contributed more to the production of NO than of N₂O.

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Introduction

The concentrations of NO and N₂O in the atmosphere are only small, amounting to <0.1 and about 310 ppbv, respectively (CONRAD 1996a). Nevertheless, these trace gases exert a strong effect on chemical and physical processes in the atmosphere (CRUTZEN 1979). Soils constitute one of the most important source for these trace gases, contributing about 40 % and 70 % to the annual budgets of atmospheric NO and N₂O, respectively (DAVIDSON 1991, WILLIAMS & al. 1992, DAVIDSON & KINGERLEE 1997, MOSIER 1998). In soils, it is microbial metabolism that basically accounts for the turnover of the gaseous nitrogen oxides (FIRESTONE & DAVIDSON 1989, CONRAD 1996b). However, the involved reactions are complex, and the involved microorganisms are diverse including both bacteria and fungi (CONRAD 2000, KNOWLES 2000). In the field, fluxes can vary over 4 orders of magnitude, depending on the type of environment, the season and the management of the soil site. Therefore, it is a challenge to determine how the emission of NO and N₂O from soils is regulated by environmental variables. Much has been achieved, since the community of IGAC scientists (IGAC = International Global Atmospheric Chemistry) formulated the essential research needs at a Dahlem conference in 1989 (ANDREAE & SCHIMEL 1989). We now know that microbial ammonium oxidation (nitrification) and nitrate reduction (denitrification) are the most important microbial processes involved in NO and N₂O production (DAVIDSON 1991, CONRAD 1996b). We also know that soil temperature, moisture, pH and nutrient content (especially nitrogen compounds) are the most important environmental regulators (KAISER & al. 1996, SKIBA & al. 1997, OTTER & al. 1999, DOBBIE & al. 1999). Therefore, it was possible to construct process-oriented models which proved to predict the actual field data relatively well (e.g.; LI & al. 2000, STANGE & al. 2000). Although the models can rather easily be verified with respect to the final result of the soil-borne processes, i.e. the flux of NO and N₂O between soil and atmosphere, it is more difficult to verify the model-outputs with respect to the actual microbial processes that take place in the soil.

For this purpose, it is necessary to differentiate between NO and N₂O turnover by the different microbial processes. In the following, I will briefly describe the microbial processes involved in the production of nitrogen oxides and summarize experiments in which the turnover of NO and N₂O was studied as a function of ammonium oxidation versus nitrate reduction.

Microbial Processes involved in Turnover of NO and N₂O

The two most important processes involved in NO and N₂O production are nitrification and denitrification (Fig. 1). There are two groups of nitrifiers. The ammonium-oxidizing nitrifiers convert ammonium via hydroxylamine to nitrite using as enzymes the ammonium monooxygenase and the hydroxylamine oxidoreductase, respectively. The nitrite-oxidizing nitrifiers oxidize nitrite to nitrate with

the nitrite oxidoreductase. The denitrifiers reduce nitrate via nitrite, NO and N₂O to N₂ by using the nitrate reductase, nitrite reductase, NO reductase and N₂O reductase as enzymes. Nitrite reductase and N₂O reductase have also been found in ammonium-oxidizing nitrifiers, and thus explain why ammonium-oxidizing nitrifiers can also denitrify nitrite (POTH & FOCHT 1985, REMDE & CONRAD 1990). Basically, the production of N₂O should therefore be the result of the relative activity of two enzymes, the NO reductase and the N₂O reductase, irrespectively in which type of microorganism these enzymes occur. Analogously, NO production should be the result of the relative activity of two enzymes, the nitrite reductase and the NO reductase. Unfortunately, the expression of enzyme activity is regulated in a very complex way and moreover strongly differs among the various microorganisms (ZUMFT 1997). Therefore, it is impossible to a-priori predict how a particular microorganism will behave.

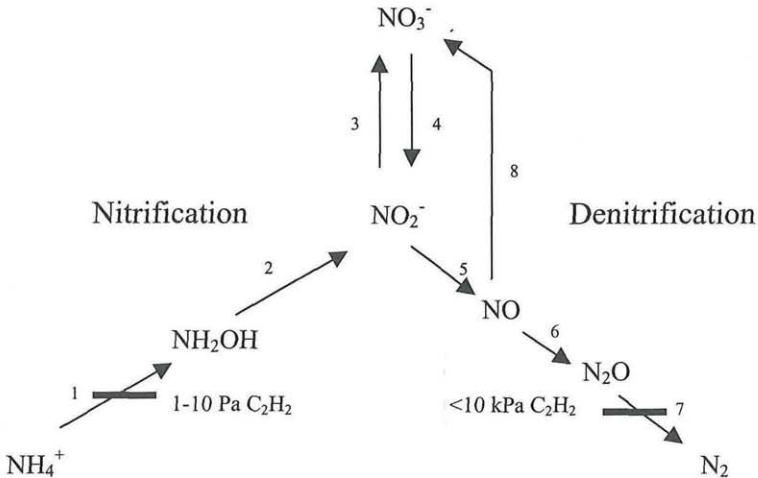


Fig. 1. Scheme of oxidative and reductive nitrogen transformation resulting in the production of NO and N₂O as intermediates. The numbers indicate enzyme reactions, i.e. 1: ammonium monooxygenase; 2: hydroxylamine oxidoreductase; 3: nitrite oxidoreductase; 4: nitrate reductase; 5: nitrite reductase; 6: NO reductase; 7: N₂O reductase; 8: peroxidase. The bars indicate inhibition of the reaction by acetylene (C₂H₂).

Turnover of NO is even more complex than turnover of N₂O, since NO can be consumed by various heterotrophic soil microorganisms which oxidize it to nitrate by the unspecific action of peroxidases (BAUMGÄRTNER & al. 1996, KOSCHORRECK & al. 1996). Hence, NO can be consumed both oxidatively and reductively. It is noteworthy, that the oxidative NO consumption has a much higher

half-saturation constant for NO than the consumption by denitrification (CONRAD 1995, KOSCHORRECK & CONRAD 1997).

In summary, NO and N₂O are both produced and consumed by nitrification and denitrification, but different enzymes and even different microorganisms are involved in the processing of the two trace gases. Therefore, it is interesting to compare the relative production of NO and N₂O in the same soil.

Relative Production of NO and N₂O

We measured both the production of NO and the release of NO (net rate) in various soils sampled from different ecosystems (BOLLMANN & CONRAD 1997a, GÖDDE & CONRAD 2000). The production of NO was determined together with the NO uptake rate constant so that the gross rates of NO production and NO consumption were available. The N₂O release rate was determined as net rate, i.e. the result of N₂O production plus N₂O consumption in the soil (N₂O consumption was in fact negligible under the chosen incubation conditions). The soils were sieved, adjusted to a moisture content of 60 % WHC and incubated at 25°C. For standardization of homogenized soil samples the water content is usually adjusted to a constant percentage of the water holding capacity (WHC) which is determined from the gravimetric water content that saturates the soil sample against gravity. This standardization was done to avoid any effect of soil moisture and temperature which would mask the effects of other controlling variables characteristic for the individual soils. Both, changes in soil temperature and in soil moisture and aeration have a very strong effect on NO production (SLEMR & SEILER 1984, KRÄMER & CONRAD 1991, SAAD & CONRAD 1993, BOLLMANN & CONRAD 1998) which easily may override others. Such masking effects are commonly encountered in the field (SLEMR & SEILER 1991) and in laboratory studies (ROBERTSON 1994). After standardization we found by multivariate statistics that the regulation patterns of 20 different soils could be grouped into three different categories which largely coincided with the land use patterns, i.e. agricultural, meadow and forest soils (GÖDDE & CONRAD 2000).

In Fig. 2, the data from BOLLMANN & CONRAD 1997a and GÖDDE & CONRAD 2000 are compiled according to the categories agricultural, meadow, temperate forest, savanna and rain forest soils. The compiled data show that the logarithms of NO production rates are correlated with the logarithms of N₂O release rates ($r^2 = 0.7$; $P < 0.001$) demonstrating that soils with a large N₂O release also exhibit a large NO production. BUTTERBACH-BAHL & al. 1997 observed a similar relationship when measuring the NO and N₂O emission rates from forest soils under field conditions.

The data in Fig. 2 further show that the observed NO production rates were generally higher than the simultaneously observed N₂O release rates, by a factor of 5-50. The latter result can be compared with literature data on emission of NO and N₂O. The published ratios of NO/N₂O emission generally decrease logarithmically with increased water filled porosity (WFPS) demonstrating that low soil moisture

favors NO emission while high soil moisture favors N₂O emission (KELLER & REINERS 1994, VERCHOT & al. 1999). At 60 % WFPS, the ratio of NO/N₂O emission observed by these authors was about 1 and thus, significantly lower than the ratio (>10) that we measured at standardized soil moisture (60 % WHC). BUTTERBACH-BAHL & al. 1997 observed different ratios of NO/N₂O emission depending on the field site; in an acidic spruce forest the ratio was >10, in a limed spruce forest it was about 2, and in a neutral beech forest it was about 0.5.

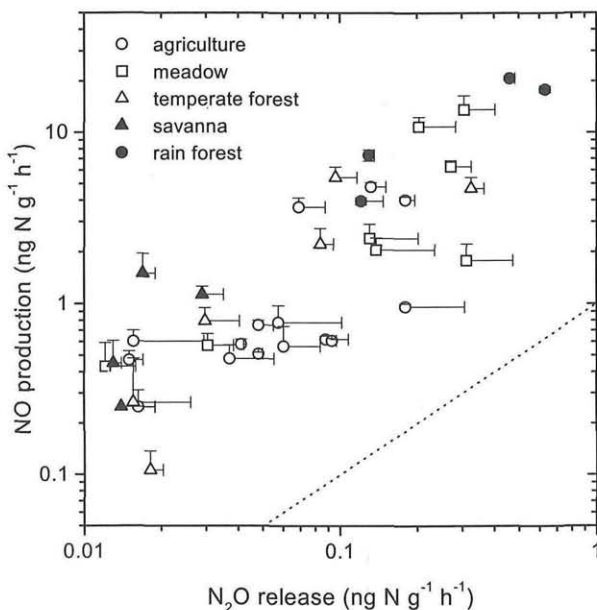


Fig. 2. Correlation of logarithmically transformed NO production and N₂O release rates measured under standardized conditions (25°C; 60 % WHC) in soil samples taken from different sites. The data are taken from BOLLMANN & CONRAD 1997a and from GÖDDE & CONRAD 2000. The error bars indicate standard deviations of replicate measurements ($n=3-12$). The dotted line indicates a 1:1 relationship between NO production and N₂O release. The Pearson correlation coefficient of the data is $r^2 = 0.7$.

The observation of different ratios of NO/N₂O emission at the different soil sites is not necessarily contradictory to the observation of a relatively constant ratio of NO production/ N₂O release in the laboratory, since the latter rates are not significantly influenced by diffusion processes while the field rates are. Both flux measurements and vertical profiles of NO in the soil show that the half life of NO in the soil is only on the order of minutes (RUDOLPH & al. 1996a). The flux of NO is effectively the result of simultaneous production and consumption processes and thus is strongly affected when diffusion in soil changes (REMDE & al. 1993, RUDOLPH & CONRAD 1996). Hence, the effective ratio of NO/N₂O emission may

be expected to be smaller than the ratio of gross NO production versus N₂O release. The latter is apparently relatively constant within a factor of 10 and does not vary systematically among various soils.

Differentiation of NO and N₂O Production Processes by Acetylene Inhibition

A major problem is the differentiation of the individual production and consumption processes of NO and N₂O (CONRAD 2000). One of the most widely used approaches is the specific inhibition of ammonium oxidation by low partial pressures (1-10 Pa) of acetylene which specifically inhibits the ammonium monooxygenase of ammonium-oxidizing bacteria and thus impedes any production of NO and N₂O from ammonium oxidation (HYNES & KNOWLES 1978, BERG & al. 1982, KLEMEDTSSON & al. 1988). Low acetylene partial pressures do not affect the enzymes involved in the turnover of NO and N₂O (numbers 5-8 in Fig.1), but only affect the oxidation of ammonium. As nitrite can no longer be produced from ammonium oxidation, production of NO and N₂O is only driven by the reduction of nitrate. If the soil lacks nitrate, reductive production of NO and N₂O is only possible if nitrate is regenerated from ammonium. Such a coupled nitrification-denitrification may be of particular importance in soils with a high C/N ratio (NIELSEN & al. 1996).

If acetylene is applied at high partial pressures (<10 kPa), it in addition inhibits the N₂O reductase (YOSHINARI & al. 1977), so that N₂O accumulates instead of N₂. This technique has widely been used to estimate denitrification rates in soil (KLEMEDTSSON & al. 1977, PARKIN & al. 1984, HENAULT & GERMON 1995). However, we found that the technique is biased due to scavenging of the denitrification intermediate NO (BOLLMANN & CONRAD 1997a). Acetylene partial pressures >0.1 kPa catalyze in the presence of >20 Pa O₂ the oxidation of NO to NO₂ which subsequently dissolves in the aqueous phase and dismutates to nitrite plus nitrate (BOLLMANN & CONRAD 1997b, MCKENNEY & al. 1997). Thus, part of the nitrogen is recycled from NO to nitrate instead of being reduced to N₂O, resulting in underestimation of the N₂ production by denitrification.

We have used the inhibition method at low acetylene partial pressures to quantify the contribution of ammonium oxidation to the production of NO and N₂O, again under standardized soil conditions (25°C, 60 % WHC). The results, shown in Fig. 3, demonstrate that ammonium oxidation always contributed more to NO production than to N₂O production. In other words, there was a tendency that NO production was more dominated by oxidative processes than N₂O production, independently of the soil site investigated and despite the fact that soil moisture was standardized. It is well known that increase in soil moisture favors NO and N₂O production by reduction processes (i.e. denitrification) versus oxidation processes (i.e. nitrification) (ANDERSON & LEVINE 1987, DAVIDSON 1993, BOLLMANN & CONRAD 1998). In addition, however, there seems to be also a general difference in the production process of NO versus N₂O, in which nitrification produces more

NO than of N_2O . Although this result is consistent with numerous laboratory observations (e.g. ANDERSON & LEVINE 1986, REMDE & CONRAD 1990, ANDERSON & al. 1993), the mechanistic basis is not understood. I speculate that ammonium-oxidizing nitrifiers may be relatively deficient in the NO reductase so that N_2O production by nitrifier-denitrification is much less than NO production. This assumption would also be consistent with the observation that under standardized conditions NO production is generally higher than N_2O production (Fig.2).

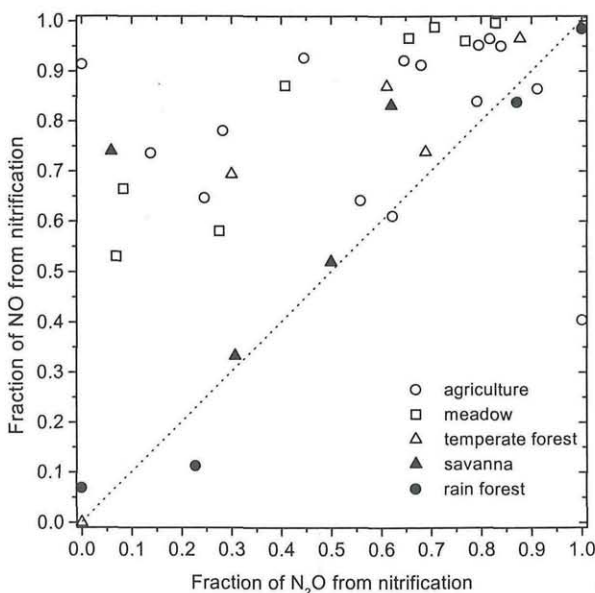


Fig. 3. Correlation of the fractions of NO versus N_2O produced during ammonium oxidation measured under standardized conditions (25°C; 60 % WHC) in soil samples taken from different sites. The data are taken from BOLLMANN & CONRAD 1997a and from GÖDDE & CONRAD 2000. The dotted line indicates a 1:1 relationship.

Consumption of NO

The release of NO from soil is the result of simultaneously operating production and consumption processes. Emission rates of NO from soil can consequently be predicted when the rates of NO production and the rate constants of NO uptake are known (REMDE & al. 1993, RUDOLPH & al. 1996a, OTTER & al. 1999). Sensitivity analysis shows that the NO flux may depend even stronger on the NO consumption rate constant than on the NO production rate (REMDE & al. 1993). A compilation of NO production rates and NO uptake rate constants that were simultaneously measured in various soils demonstrates that the two parameters vary over

(68) >2 orders of magnitude without any clear correlation to each other (Fig. 4). Such a correlation is not to be expected since the processes involved in NO production and consumption are not necessarily the same. Whereas NO is produced during both nitrification and denitrification, NO is consumed by either denitrification or unspecific oxidation to nitrate (Fig.1). The two NO uptake processes can be differentiated by isotopic labeling (RUDOLPH & al. 1996b), but such a procedure is cumbersome for routine tests. A compilation of data from various soils, which have been assayed under standardized conditions (25°C, 60 % WHC), indicates that the logarithms of the NO uptake rate constants increase ($r^2 = 0.29$; $P < 0.001$) with the logarithms of the production rates of NO + N₂O from denitrification (Fig.5). This observation shows that soils with a relatively large rate of nitrogen oxide production from denitrification also exhibit a relatively large uptake rate constant for NO, and thus may suggest that NO consumption is at least partially caused by denitrifying bacteria. Almost 30 % of the variability of the data would be explained by this assumption. The importance of denitrification for reductive NO consumption even under oxic soil conditions has already been pointed out by REMDE & CONRAD 1991 and SCHÄFER & CONRAD 1993. Other studies (KOSCHORRECK & CONRAD 1997, DUNFIELD & KNOWLES 1999, GÖDDE & CONRAD 2000), on the other hand, concluded that NO consumption is largely due to oxidative processes.

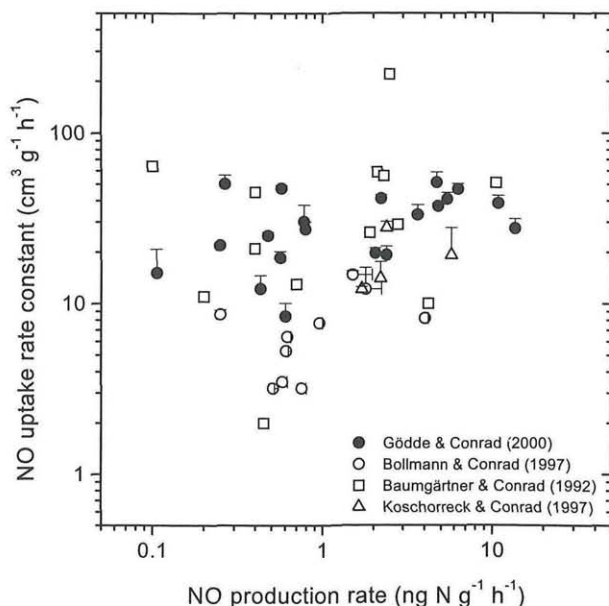


Fig. 4. Correlation of logarithmically transformed NO uptake rate constants and NO production rates measured in soil samples taken from different sites. The error bars indicate standard deviations of replicate measurements (n=3-12).

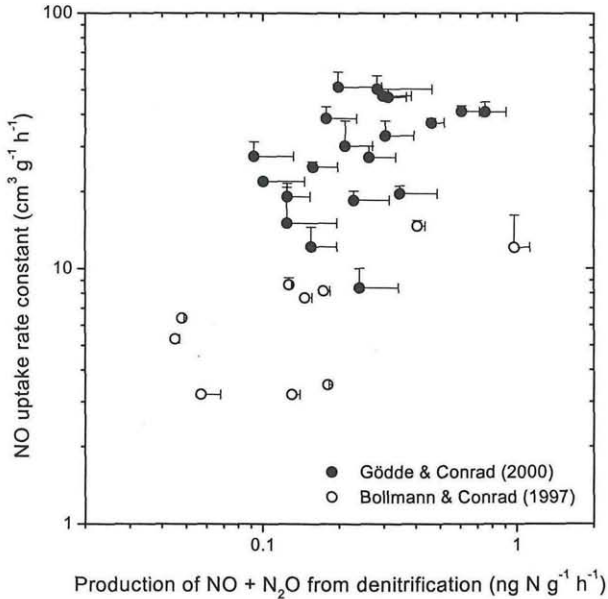


Fig. 5. Correlation of logarithmically transformed NO uptake rate constants and the rates of NO+N₂O production measured in soil samples taken from different sites. The error bars indicate standard deviations of replicate measurements (n=3-12). The Pearson correlation coefficient is $r^2 = 0.29$.

Conclusion

The data measured on various soils under standardized conditions (25°C, 60 % WHC) confirm the concepts (1) that NO production is quantitatively as important as N₂O production, (2) that ammonium oxidation contributes more to the production of NO than of N₂O, (3) that NO consumption is as important a process as NO production, and (4) that denitrification contributes to NO consumption.

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