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Title page

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Sergiy Medinets[a,b,c], Ute Skiba[d], Heinz Rennenberg[c], Klaus Butterbach-Bahl[b,e*]

[a]Regional Centre for Integrated Environmental Monitoring, Odessa National I. I. Mechnikov University (ONU), Mayakovskogo lane 7, 65082 Odessa, Ukraine, s.medinets@gmail.com

[b]Institute for Meteorology and Climate Research (IMK), Karlsruhe Institute of Technology (KIT), Kreuzeckbahnstraße 19, D-82467 Garmisch-Partenkirchen, Germany, klaus.butterbach-bahl@kit.edu

[c]Institute of Forest Sciences, Chair of Tree Physiology, University of Freiburg, Georges-Koehler-Allee 53/54, D-79110 Freiburg, Germany, heinz.rennenberg@ctp.uni-freiburg.de

[d]Centre for Ecology and Hydrology (CEH) Edinburgh, Bush Estate, Penicuik, Midlothian, EH26 0QB, United Kingdom, ums@ceh.ac.uk

[e]International Livestock Research Institute (ILRI), Old Naivasha Road, Nairobi, Kenya

[*]*Corresponding author:*
Klaus Butterbach-Bahl
Institute for Meteorology and Climate Research (IMK), Karlsruhe Institute of Technology (KIT)
Kreuzeckbahnstraße 19, D-82467 Garmisch-Partenkirchen, Germany
tel.: +49 8821 183136
e-mail: klaus.butterbach-bahl@kit.edu

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Sergiy Medinets[a,b,c], Ute Skiba[d], Heinz Rennenberg[c], Klaus Butterbach-Bahl[b,e*]

[a]Regional Centre for Integrated Environmental Monitoring, Odessa National I. I. Mechnikov University (ONU), Mayakovskogo lane 7, 65082 Odessa, Ukraine

[b]Institute for Meteorology and Climate Research (IMK), Karlsruhe Institute of Technology (KIT), Kreuzeckbahnstraße 19, D-82467 Garmisch-Partenkirchen, Germany,

[c]Institute of Forest Sciences, Chair of Tree Physiology, University of Freiburg, Georges-Koehler-Allee 53/54, D-79110 Freiburg, Germany

[d]Centre for Ecology and Hydrology (CEH) Edinburgh, Bush Estate, Penicuik, Midlothian, EH26 0QB, United Kingdom

[e]International Livestock Research Institute (ILRI), Old Naivasha Road, Nairobi, Kenya

Abstract

NO emissions from soils and ecosystems are of outstanding importance for atmospheric chemistry. Here we review the current knowledge on processes involved in the formation and consumption of NO in soils, the importance of NO for the physiological functioning of different organisms, and for inter- and intra-species signalling and competition, e.g. in the rooting zone between microbes and plants. We also show that prokaryotes and eukaryotes are able to produce NO by multiple pathways and that unspecific enzymo-oxidative mechanisms of NO production are likely to occur in soils. Nitric oxide production in soils is not only linked to NO production by nitrifying and denitrifying microorganisms, but also linked to extracellular enzymes from a wide range of microorganisms.

Further investigations are needed to clarify molecular mechanisms of NO production and consumption, its controlling factors, and the significance of NO as a regulator for microbial, animal and plant processes. Such process understanding is required to elucidate the importance of soils as sources (and sinks) for atmospheric NO.

Key words: nitric oxide, nitrification, denitrification, unspecific enzymo-oxidative mechanisms, NOS, SOD, dissimilatory nitrate reduction to ammonium, chemodenitrification, NO signalling, NO consumption, NO production, archaea, protists, invertebrates

Highlights

- Abiotic and biotic pathways of NO transformation are discussed
- Interrelation between NO transformation processes is discussed
- Unspecific enzymo-oxidative mechanisms of NO transformation are proposed
- Physiological NO functions/effects in/for various groups of organisms are shown
- Importance of bacterial NO as signalling substance for others organisms is highlighted

1. Introduction

Nitric oxide (nitrogen monoxide, NO) is a highly reactive constituent of the troposphere (Fowler et al., 2009) and is considered to be the main precursor of ground-level tropospheric ozone in rural areas (Chameides et al., 1994; Laville et al., 2011), impacting human health and plant productivity (Staffelbach et al., 1997; Ludwig et al., 2001). The main sources of NO in the troposphere are fossil fuel combustion, biomass burning, soil emissions and lightning (Delmas et al., 1997). Nevertheless agricultural soils can be the predominant NO source in rural regions, where the contribution of fossil fuel combustion is low (Bouwman et al., 2002; Butterbach-Bahl et al., 2009).

The global soil NO production is estimated at ~8.9 Tg N a^{-1}, of which ~15% is produced in Europe (IPCC, 2007). However, an earlier estimate by Davidson and Kingerlee’s (1997) provided much higher values ranging from 13 to 21 Tg N a^{-1}. Such large divergence between estimates results from insufficient knowledge of the full range of soil microbial processes involved in NO production and consumption and the interactions of these processes with environmental variables.

Biological N transformation processes in soils, namely nitrification and denitrification, are usually considered the dominant sources of soil NO production. However, also abiotic chemical N transformations can be an important source (Ludwig et al., 2001; Butterbach-Bahl et al., 2011, 2013). Linking NO production, consumption and emission to the source and sink processes of nitrification and denitrification *in situ* still remains challenging, as they can occur simultaneously and in the same soil aggregates (Arah, 1997). Moreover, they can be spatially or temporally linked to each other, using products (Garrido et al., 2002) and/or intermediates from one process by the other (Butterbach-Bahl et al., 2013). That is why *in vitro* experiments, applying molecular methods, stable isotopes and inhibitors are important to disentangle processes and mechanisms involved in soil NO production and emission. Simulating field conditions for different soil types from a wide range of climate zones will allow us to crack open the veil of soil NO transformations and reveal potential mechanisms and drivers. Better process understanding is the basis to develop mitigation strategies for reducing soil NO emissions.

Endogenous NO is generally considered as a freely diffusible molecule in cells with a significant importance as a signaling substance. Thus, NO acts as a short-lived messenger molecule with numerous molecular targets, playing numerous physiological roles at organelle, intra- and inter-cellular levels in both prokaryotes and eucaryotes (Jacklet, 1997; Gusarov et al., 2008; Johnson et al., 2008; Leitner et al., 2009; Velayutham and Zweier, 2013).

The main purpose of this review is to present recent advances from field and laboratory studies focusing on NO transformation and underlying processes as well as investigating the potential of other processes not yet associated with NO production or consumption, and to highlight the physiological and ecological significance of such processes.

2. Reactivity of NO

NO is a stable free radical with an ionization potential of 9.26 eV and an electron affinity of 0.024 eV (Natalis et al., 1979). Its high reactivity is due to its electronic configuration, i.e. the existence of an unpaired electron residing in a π^* molecular orbital (Wong et al., 1989). Consequentely, NO can be easily oxidized to the nitrosonium ion (NO^+), reduced to the nitroxide ion (NO^-), or converted to nitrogen dioxide (NO_2) by oxygen (O_2) (McCleverty, 2004 and reference therein). NO and its ions share isoelectronic properties with other molecule and ions. For example, NO is isoelectronic with O_2^+, meanwhile NO^- is isoelectronic with O_2 and NO^+ with CO and CN^- (McCleverty, 2004 and reference therein). A very important property of nitric oxide related to its redox-activity in solution is its ability to form nitrosyl as well as multi nitrosyl complexes with transitional metals (e.g., Fe, Mn, Co, Ru) and metal-containing enzymes (e.g., copper-containing nitrite reductase (NIR)) (Ruggiero et al., 1993; Ford and Lorkovic, 2002; Lee et al., 2002 and references therein). It has been shown that the reversible process $NO \leftrightarrow NO^+$ in water is strongly pH-dependent (Lee et al., 1990; Kim and Kochi, 1991) and NO can be produced from nitrite NO_2^- under strongly basic conditions (Stanbury, 1989).

3. Soil processes associated with NO production and consumption

The main microbiological processes of N transformation in soils, such as nitrification, nitrifier and heterotrophic denitrification, as well as abiotic chemodenitrification are classically considered as important pathways of both soil NO production and consumption under different environmental condition (Firestone and Davidson, 1989; Conrad, 1996; Yamulki et al., 1997; Skiba et al., 1997; Zumft, 1997; Gasche and Papen, 1999; Ludwig et al., 2001; Wrage et al., 2001; Garrido et al., 2002; Venterea et al., 2005;

Kesik et al., 2006; Robertson and Groffman, 2007; Skiba, 2008; Kool et al., 2009a, 2009b; Bru et al., 2010; Wu et al., 2010; Baggs, 2011; Ju et al., 2011; Butterbach-Bahl et al., 2011, 2013; Bakken et al., 2012; Luo et al., 2012; Schreiber et al., 2012; Barton et al., 2013; Pilegaard, 2013 and many others). In a recent review Schreiber et al. (2012) provided an overview of microbial and chemical NO and N_2O production processes and innovative experimental approaches, but did not include the role of NO in higher organisms. Another recent review by Pilegaard (2013) focused on soil NO emission and its regulating factors, but did not include process description at the organism level. To fill these gaps we have considered additional processes associated with NO exchange, for example codenitrification (e.g., Shoun et al., 1992; Tanimoto et al., 1992; Spott et al., 2011), dissimilatory nitrate reduction to ammonium (e.g., Bengtsson and Bergwall, 2000; Silver et al., 2001, 2005; Rütting et al., 2008; Templer et al., 2008; Wan et al., 2009; Schmidt et al., 2011), anaerobic ammonium oxidation (e.g., Strous et al., 1996; Humbert et al., 2010; Kartal et al., 2011), nitrite-dependant anaerobic oxidation of methane (e.g., Raghoebarsingetal, 2006; Ettwig et al., 2010; Harron et al., 2013), nitric oxide synthase mediated NO production (e.g., Fritz-Laylin et al., 2009; Messner et al., 2009; Chen et al., 2010; Forstermann and Sessa, 2012) and the theoretically feasible, unspecific enzyme mediated mechanisms of oxidation of soil N described for the first time in this review in detail. We also provide a brief overview of the physiological functions of NO in different groups of organisms living in and on soil (e.g., Jacklet 1997; Gusarov et al., 2008, 2009; Johnson et al., 2008; Fritz-Laylin et al., 2009; Schreiber et al., 2011; Forstermann and Sessa, 2012).

3.1. Abiotic processes

3.1.1. Chemodenitrification

The term chemodenitrification describes the strictly chemical, non-enzymatic conversion of nitrite (NO_2^-) or nitrate (NO_3^-) to gaseous nitrogen species at low pH (below 5). This process normally requires the presence of ammonium (NH_4^+), amines or reduced metals (e.g. Fe^{2+}), as well as high soil organic matter (Clark, 1962; Broadbent and Clark, 1965; Wullstein and Gilmour, 1966; Chalk and Smith, 1983; Zumft, 1997) and soil water contents (Venterea et al., 2005). The most important reaction of chemodenitrification (Equation (1)) is the formation of NO via nitrous acid (HNO_2 (aqueous phase), HONO (gas phase)) decomposition (Van Cleemput and Baert, 1976; Chalk and Smith, 1983; Zumft, 1997; Venterea et al., 2005):

$$3NO_2^- + 3H^+ \leftrightarrow 3HNO_2 \rightarrow 2NO + HNO_3 + H_2O \qquad (1)$$

If reduced metals are available (e.g. Fe^{2+}) the Equation (2) can be presented as:

$$NO_2^- + Fe^{2+} + 2H^+ \rightarrow NO + Fe^{3+} + H_2O \qquad (2)$$

pH is the major controlling factor for chemodenitrification in soils (Chalk and Smith, 1983; Zumft, 1997), while NO_2^- concentrations (Ludwig et al., 2001), temperature (Kesik et al., 2005, 2006) and soil water content (Venterea et al., 2005) have been identified as additional controllers. The chemical decomposition of NO_2^- mainly occurs under acidic soil conditions (pH <4.5), and Yamulki et al. (1997) detected NO emissions from sterile acidic soil. However, also at more neutral pH (5 – 7) ranges, NO may be produced chemically or react with humic substances producing N_2O and CO_2 (Porter,1969; , Stevenson et al., 1970). As for every chemical reaction, reaction rates increase with rising temperature (Kesik et al., 2006) and high rates of soil NO emissions during warm periods from acidic soils were attributed partially to chemodenitrification in agricultural (Cheng et al., 2004) and N-affected temperate forest soils (Kesik et al., 2006; Luo et al., 2012).

Another soil related source of atmospheric NO is the emission of HONO from acidic soils (Su et al., 2011):

$$NO_2^- + H^+ \leftrightarrow HNO_2 \leftrightarrow \overset{\text{(in air)}}{HONO} \leftrightarrow NO + OH^- \qquad (3)$$

Air concentrations of HONO determine the sink and source function of soils. If air HONO concentrations are lower than in the soil aqueous or gaseous phase, a net emission is observed, while otherwise soils function as a sink for atmospheric HONO (Su et al., 2011). For instance, in typical acidic (pH 4-5) tropical forest and boreal soils even small soil NO_2^-

concentrations (ca. 0.001-0.01 μg g^{-1}) can lead to significant HONO emissions into the atmosphere (Su et al., 2011). Therefore, this process seems to be important at least for some natural ecosystems and may be an additional source of atmospheric NO and OH^- (Su et al., 2011).

3.1.2. Chemical consumption

It is widely known that abiotic nitrosation reactions via NO_2- can result in N immobilization or 'chemodenitrification' including the production of NO, N_2O or N_2 (e.g., Bremner and Fúhr, 1966; Stevenson et al., 1970; Williams, 2004). Since both NO_2^- and NO can be considered as nitroso donors and since this reaction is likely to be reversible (Spott et al., 2011 and references there in), it can be assumed that under observed soil NO concentrations of 60-180 ppbv (Dong, Simon and Rennenberg, unpublished data), not only NO_2^- but also NO should be involved in abiotic nitrosation reactions. In particular, the nitrosation reactions of NO_2^- (and thus also of NO) with humic substances (e.g., secondary aliphates, aromates, amides) have been widely reported and proposed to be considered as an abiotic pathway of N incorporation into soil organic matter (SOM) (Bremner and Fúhr, 1966; Smith and Chalk, 1980; van Cleemput and Samater, 1996; Thorn and Mikita, 2000). Azhar et al. (1986a,b) provide evidence that during nitrification the NO_2^- (and likely NO) formed contributes to the nitrosation of organic matter under neutral or weak acidic soil pH conditions. Comparable results for the reaction of NO and organic matter have been reported by Stephenson (1970). In addition, metal-nitrosyl complexes as formed e.g. during denitrification can function as a nitrosyl donor to a variety of N-, O-, S- and C-nucleophilic organic matter constituents (Garber and Hollocher, 1982b). This seems to be a significant process for SOM nitrosation in fertilized soils with high NH_4^+/NH_3 concentrations (Thorn and Mikita, 2000) where NO_2^- accumulates due to the inhibition of *Nitrobacter* spp. - driving the conversion of NO_2^- to NO_3^- in neutral to high pH soils –by increased levels of NH_3.

Chemical reactions of NO in aqueous solution are well documented (e.g. Williams, 2004) and should occur in soils too. According to Williams (2004) NO in aqueous solution (irrespective of the pH) can react with: i) amides to produce N-nitrosamides, ii) alcohols to give alkyl nitrites, iii) hydrogen peroxide to generate peroxynitrous acid, and iv) thiols to form S-nitrosothiols. Moreover, in aerated water NO may react with O_2 to produce NO_2, which can further react with NO to form the nitrosating agent N_2O_3, which then hydrolyzes to NO_2^- (Williams, 2004 and references therein).

The main pathway of consumption of soil emitted NO in surface air and/or inside the canopy is its rapid reaction with O_3 or $R\text{-}OO^*$ (derived from the reaction of mostly biogenic volatile organic carbon (VOC) with OH^*) to form NO_2. Plant leaves can take up NO_2 and further metabolize it. Several studies (Geßler et al., 2000; Butterbach-Bahl et al., 2004; Sparks, 2009) have suggested that soil NO emission and in-canopy conversion to NO_2 results in re-deposition onto plant leaves and uptake as NO_2. Thus, soil NO emissions can be an important process of nutrient dispersal and recycling at ecosystem scale. Also direct diffusive uptake of atmospheric NO by leaves constitutes a canopy sink. However, due to the low solubility of NO in the aqueous solution of the apoplastic space, this process is less important than plant leaf uptake of NO_2 (Hanson and Lindberg, 1991). A second possible pathway of atmospheric consumption of soil NO is the reversible reaction with OH^- to form HONO (Su et al., 2011).

In the troposphere, NO can react with hydroperoxy radicals (HO_2^*) (Hertel et al., 2011) and organic peroxy radicals (RO_2^*) (Finlayson-Pitts and Pitts, 1986; Primblecombe, 1996) to produce NO_2. In sunlight (hv = 200-420 nm) NO_2 photo-dissociates to form NO and the very short-lived $O(^3P)$ radical, which in most cases combines with O_2 to form O_3; during night-time NO_2 can react with O_3 to form the NO_3^* radical and O_2 (Primblecombe, 1996, Hertel et al., 2011). After aldehydes are photo-dissociated or react with OH^-, an alkyl radical is formed and can be converted to a peroxy acetyl radical, which can react with NO_2 to form peroxy acetyl nitrate (PAN) (Primblecombe, 1996, Fowler et al., 2009). Alternatively, NO_2 can react with OH^- to form HNO_3 at an average rate of ca. 5% per hour (Primblecombe, 1996).

3.2. Biotic processes

3.2.1. Nitrification

Nitrification is the biological oxidation of ammonium (NH_4^+) via hydroxylamine (NH_2OH) to nitrite (NO_2^-) and further on to nitrate (NO_3^-) (Equation (4)) (Wrage et al., 2001; Butterbach-Bahl et al., 2011, 2013). It is one of the most important processes of ecosystem N-cycling, both in agricultural and natural soils (Ludwig et al., 2001).

$$\begin{array}{l} NH_4^+ \rightarrow NH_2OH \rightarrow NO_2^- \rightarrow NO_3^- \qquad (4) \\ \quad\quad \downarrow \\ \quad\quad\quad NO \end{array}$$

Nitrification can be performed by heterotrophic and autotrophic nitrifiers. Autotrophic nitrifiers use the oxidation of NH_4^+ or NO_2^- as an energy source for CO_2 fixation, while heterotrophic nitrifiers use N-containing organic substances as energy and C source (Prosser, 1989; Wrage et al., 2001; Arp et al., 2002; Conrad, 2002; Costa et al., 2006; Butterbach-Bahl et al., 2011). Heterothrophic nitrifiers (e.g. *Arthrobacter*) can oxidize both NH_4^+ and organic N with similar intermediates, but use different enzymes for the transformation of these substrates (Wrage et al., 2001; Conrad, 2002). Ammonium oxidizing bacteria (AOB) are very specific organisms, e.g. *Nitrosomonas*, *Nitrosospira*, *Nitrosococcus* spp., that oxidize NH_4^+ to NH_2OH catalysed by ammonia monooxygenase (AMO) and NH_2OH to NO_2^- catalysed by hydroxylamine oxidoreductase (HAO). Ammonium can also be oxidized by autotrophic ammonium oxidizing archaea (AOA), belonging to the phylum *Thaumarchaeota* (Könneke et al., 2005; Brochier-Armanet et al., 2008; Tourna et al., 2008; Martens-Habbena et al., 2009; Spang et al., 2010). AOA may even dominate NH_4^+ oxidation in soils (Leininger et al., 2006; Prosser and Nicol, 2008, 2012). Nitrite-oxidizing bacteria (NOB), e.g. *Nitrobacter, Nitrospira, Nitrococcus, Nitrospina* spp., perform further oxidation of NO_2^- to NO_3^-, catalysed by nitrite oxidoreductase (NXR).

Whilst heterotrophic nitrifying bacteria can use ammonia as well as organic N forms as substrate (Papen et al., 1989), fungal nitrification seems to exclusively rely on organic pathways (Robertson and Groffman, 2007):

$$R\text{-}NH_2 \rightarrow R\text{-}NHOH \rightarrow R\text{-}NO \rightarrow R\text{-}NO_2^- \rightarrow NO_3^- \qquad (5)$$

Typically this process involves oxidation of amines or amides, is not coupled to ATP production and, therefore, is not involved in heterotrophic energy production (Robertson and Groffman, 2007). Heterotrophic nitrifiers have been shown to produce NO from organic N and inorganic substrates (e.g. Papen et al., 1989).

Altogether, a large number of heterotrophic bacteria (e.g. *Paracoccus, Alcaligenes*, *Thiosphaera*, *Pseudomonas* spp., described by Kuenen and Robertson (1994), Moir et al. (1996), Daum et al. (1998), Nishio et al. (1998)) and fungi (e.g. *Ascomycota* and *Basidiomycota* (Shoun et al., 1992, 2012; Prendergast-Miller et al., 2011), and *Glomeromycota* groups (Cousins et al., 2003; Porras-Alfaro et al., 2011; Bates et al., 2012)) can nitrify.

In soil solution with sufficient oxygen supply, nitrification is controlled predominantly by the availability of NH_4^+ (Robertson, 1989; Ludwig et al., 2001) or easy decomposable organic N (e.g. amines and amides), if fungal nitrification prevails (Conrad, 2002). Many studies support the idea that in a wide range of soils nitrification is the dominating process for soil NO production as an intermediate in the oxidation of NH_2OH to NO_2^- (Hooper and Terry, 1979; Firestone and Davidson, 1989; Bollmann et al., 1999; Dunfield and Knowles, 1999; Gasche and Papen, 1999; Godde and Conrad, 2000; Venterea and Rolston, 2000; Ludwig et al., 2001; Garrido et al., 2002; Cheng et al., 2004; Wan et al., 2009; Wu et al., 2010; Ju et al., 2011; Mei et al., 2011; Cui et al., 2012; Luo et al., 2012 and others). Rates of nitric oxide formation during nitrification were estimated as 0.1-10% of gross NH_4^+ oxidation (Ludwig et al., 2001 and reference therein), but Garrido et al. (2002) reported a tighter range of 0.6-2.5%. It is also well known that some, but not all, AOB and AOA in both natural and agricultural soils are very sensitive to high substrate concentrations and that nitrification can be inhibited by substrate concentrations in the range of 1.0–5.0 mM NH_4^+ or NH_3 (Anthonisen et al., 1976; Stark and Firestone, 1996; Shi and Norton, 2000; Carrera et al., 2004; Koper et al., 2010; Norton and Stark, 2011). AOB, less sensitive to NH_3 compared to AOA (Prosser and Nicol, 2012), prefer to colonize areas with high soil NH_4^+ or NH_3 concentrations (Hayden et al., 2010; Ollivier et al., 2011).

As for all biological processes, temperature is an important parameter determining the rate of nitrification (Machefert et al., 2002; Robertson and Groffman, 2007) with specific optima depending on the microbial community active in different environments (Singh et al., 1993; Stark, 1996; Stark and Firestone, 1996; Norton and Stark, 2011). In general temperature optima for AOB of temperate climate zone soils are around 22-30 ˚C (Koops et al., 1991; Singh et al., 1993; Stark, 1996; Stark and Firestone, 1996; Norton and Stark, 2011), however, for tropical soils optima can be close to 35 ˚C (Myers, 1975). In spite of these high temperature optima, reasonable rates of nitrifier activity were reported also at low soil temperatures, such as 2–10 ˚C (Cookson et al., 2002; Avrahami et al., 2003; Avrahami and Conrad, 2005), and were even observed in frozen soil together with detectable NO emission rates (Freppaz et al., 2007). The temperature effect on nitrification has been described by many process models. For example, Stark (1996) tested 5 different models and argued that the best fit model, the generalized Poisson density function (Parton et al., 1987), successfully describes the temperature response of nitrification activity over a temperature range of 5-50 ˚C. But he also stated that the Arrhenius equation (Laudelout, 1978) can still be used, providing adequate simulation over a more narrow temperature range of 5-28 ˚C (Fig. 1).

INSERT Fig. 1 HERE

The increase in NO emission rates in response to temperature is site specific (Saad and Conrad, 1993; Martin et al., 1998; Gasche and Papen, 1999; Ludwig et al., 2001; Schindlbacher et al., 2004; Kitzler et al., 2006; Laville et al., 2009; Yao et al., 2010). However, over the temperature range 0 to 35 ˚C the average NO response shows a Q_{10} of ≈ 2-4 (Williams and Fehsenfeld, 1991; Martin et al., 1998; Gasche and Papen, 1999; Yu et al., 2008, 2010; Laville et al., 2009; Yao et al., 2010).

Optimum conditions for nitrification are normally met at a water filled pore space (WFPS) of 30-60% (Firestone and Davidson, 1989; Bouwman., 1998; Davidson et al., 2000). Following the conceptual Hole-In-the-Pipe

(HIP) model of Firestone and Davidson (1989), soil moisture content seems to be the most general and robust driver for determining the proportions of soil N gases emitted from different ecosystems, with NO dominating soil N gas emissions at WFPS <30-60%, and N_2O and N_2 dominating soil N gas emissions at WFPS >60-65%.

A soil with near neutral pH of 6.5-7.0 (Killham, 1990; Machefert et al., 2002) generally appears to favor nitrification by AOB and also mesophilic archaea (Jung et al., 2014; Stieglmeier et al., 2014a). The pH optimum is much lower (ca. 4.5) for acidophilic AOA (Nicol et al., 2008; Lehtovirta-Morley et al., 2011). Nitrification rates were found to be strongly ($p < 0.05$) correlated with NO production during incubation experiments for a range of acidic, neutral and alkaline soils (Garrido et al., 2002; Cheng et al., 2004). Highest nitrification rates as well as NO emissions were observed for neutral to alkaline soils (Cheng et al., 2004). For example, nitrification is thought to be the main process for NO production in cropland on calcareous soils (Wan et al., 2009; Ju et al., 2011; Mei et al., 2011; Cui et al., 2012) and in acid forest soils receiving high rates of atmospheric N (Gasche and Papen, 1999; Wu et al., 2010; Luo et al., 2012). In other studies (Nagele and Conrad, 1990; Yamulki et al., 1997; Ste-Marie and Pare, 1999) increasing pH stimulated nitrification rates and N_2O and NO release under aerobic conditions. Prevailing NO production was also shown in aerobic soils by Garrido et al. (2002). In aerobic and anaerobic incubation experiments with five soil types plus or minus the addition of 10 Pa of the nitrification inhibitor acetylene (C_2H_2) to the headspace the authors showed that NO was likely to be produced exclusively from nitrification. Zhu et al. (2013)

suggested that at high O_2 concentration (21%) nitrification seems to be the main responsible process for NO formation from NH_3.

3.2.1.1. AOB vs. AOA: distribution and contribution to nitrification

In terrestrial ecosystems where the total soil N concentration is greater than 0.7%, nitrification is a highly significant and important process (Ollivier et al., 2011). Based on data of alpine glacier forefields in Austria (Nicol et al., 2005; Deiglmayr et al., 2006; Kandeler et al., 2006; Hämmerli et al., 2007) and Switzerland (Duc et al., 2009; Lazzaro et al., 2009; Brankatschk et al., 2011) it was summarized by Ollivier et al. (2011) that nitrification activity was predominantly driven by AOA, despite of its lower abundance compared to AOB. Apparently, archaea were more active compared to bacteria under extreme conditions, such as ammonium-poor environments (Di et al., 2009), low pH (Nicol et al., 2008; Lehtovirta-Morley et al., 2011) and temperature stress (Schleper et al., 2005; Valentine, 2007). A surprisingly large abundance of AOA was also demonstrated by Su et al. (2010) in soils from moderate climatic zones (arable land (Cambisol), Southern Germany), where AOB were exhausted by freeze-thaw cycles, whilst archaeal communities thrived. Thus, AOA may be important players for ammonia oxidation processes, and may contribute substantially to NO production during freeze-thaw events.

So far there is only little evidence that AOA are involved in soil NO production or that AOA do express the HAO enzyme. For example, Vajrala et al. (2013) demonstrated by a combined physiological and stable isotope tracer analyses that NH_2OH is an intermediate product of NH_3 oxidation to NO_2^- in the archeon *Nitrosopumilus maritimus*. The authors proposed that an archeal AMO homolog is responsible for NH_2OH formation, while the oxidation of NH_2OH to NO_2^- is likely performed by an archaea unique enzyme system. This enzyme system may be connected to soluble periplasmic multicopper oxidases (MCO) and membrane-anchored copper-binding proteins described by Walker et al. (2010). The latter authors also found *nirK* genes in archaea, though its role remained unclarified (Walker et al., 2010 and references therein; Jung et al., 2014; Park et al., 2014). Thus, in analogy to AOB, NO production by AOA may be linked to NH_2OH oxidation to NO_2^- or AOA produced NH_2OH may be used as substrate by other microorganisms to produce NO. Another NO production pathway for AOA may be the formation of nitroxyl hydride (HNO) during NH_3 oxidation (Schleper and Nicol, 2010; Walker et al., 2010), with HNO being converted to NO by copper-complexes/copper-containing proteins (Hughes, 1999). A significant importance of NO in the AOA energy metabolism, earlier postulated by Walker et al. (2010) and Schleper and Nicol (2010), has been recently confirmed experimentally (Yan et al., 2012; Shen et al., 2013). Apparently, AOA can form N_2O by direct oxidation of NH_3 rather than from NH_2OH (Vajrala et al., 2013), while Stieglmeier et al. (2014b) described N_2O formation as a hybrid of NO_2^- reduction and NH_3 oxidation.

3.2.2. Denitrification

Denitrification is the stepwise reduction of nitrate to nitrite, nitric oxide, nitrous oxide and dinitrogen gas (Equation (6)), catalyzed by the enzymes nitrate reductase (membrane-bound (NAR) or periplasmic (NAP)), nitrite reductase (NIR), nitric oxide reductase (NOR), and nitrous oxide reductase (N_2OR) (Payne, 1973, 1981; Knowles, 1982; Stouthamer, 1988; Revsbech and Sørensen, 1990; Zumft, 1992, 1997).

$$NO_3^- \rightarrow NO_2^- \rightarrow NO \rightarrow N_2O \rightarrow N_2 \qquad (6)$$

The absence of NO emission during denitrification may be explained by the “diffusion limitation” hypothesis (Firestone and Davidson, 1989; Skiba et al., 1997). This hypothesis suggests that at low O_2 concentrations, i.e. conditions which favour denitrification such as waterlogging, the NO produced is unlikely to escape from the soil to the atmosphere due to limited gas diffusion. Thus, the NO is trapped and is available as denitrification substrate for further reduction to N_2O and/or N_2. This has recently been experimentally confirmed in river sediments using ^{15}NO stable isotops (Schreiber et al., 2014). However, under such conditions plant NO production and emission may be an important source of atmospheric NO (see below sections 3.2.9 and 3.2.10).

Controlling factors for denitrification are soil moisture content, soil temperature, $N\text{-}NO_3^-$ and easily decomposable C availability, soil properties affecting soil aeration and microbial activity (e.g. texture and organic matter content), and agricultural management (Stouthamer, 1988; Revsbech and Sørensen, 1990; Zumft, 1997; Bouwman et al., 2002; Skiba, 2008; Rees et al., 2013). High rates of denitrification tend to be observed in N fertilized soils and highly irrigated loam soils when mineral N as well as C is not limiting (Barton et al., 1999; Groffman et al., 2009). Based on numerous published studies with agricultural (grassland and cropland) and forest soils, Barton et al. (1999) concluded that denitrification rates tended to be higher in agricultural soils (mean rate 13 kg N ha^{-1} a^{-1}) than in natural forest soils (e.g. mean rate 1.9 kg N ha^{-1} a^{-1}). However, these estimates are mainly based on the acetylene blockage technique with results being highly questionable if used under aerobic conditions (Bollmann and Conrad, 1997; Butterbach-Bahl et al., 2013).

Soil moisture content and soil temperature are key drivers of denitrification and their alterations can commonly explain up to 95% of the variation of the N_2O emission (Butterbach-Bahl et al., 2013). In addition, freeze-thaw events can trigger pulses of soil N_2O emissions and can contribute significantly to the annual N_2O emission rate in regions experiencing several weeks of subzero winter temperatures (Mørkved et al., 2006; Sharma et al., 2006; Wagner-Riddle et al., 2008; Kim et al., 2012; Luo et al., 2012). Freeze-thaw induced N_2O emissions are due to a complex mix of soil physical and microbial processes that require anaerobic conditions and a surplus of easily degradable substrates (De Bruijn et al., 2009). Little is known if freeze-thaw periods also significantly stimulate soil NO emissions. The multi-year data set on soil NO emissions from an acid forest soil in the South of Germany reported by Gasche and Papen (1999) and Luo et al. (2012) does not indicate that freeze-thaw periods trigger high NO emissions, though at the same site high pulse emissions of N_2O were observed in approximately 1 out of 3 years (Luo et al., 2012). However, it has been recently confirmed that NO emissions during the cold seasons (16 of October – 15 of April periods) contribute ca. 29% to the annual NO budget based on 16 years of measurement data in a forest stand (Höglwald) in South Germany (Medinets et al., unpublished data). The microbial processes involved have not been identified; however, we assume that denitrification plays an important role, since high denitrifier activity has been demonstrated during freeze-thaw events (Mørkved et al., 2006; Sharma et al., 2006; Wagner-Riddle et al., 2008; Kim et al., 2012; Luo et al., 2012). There is a need for more continuous NO flux measurements during cold periods and winter/spring transition periods, in order to improve our estimates of annual flux rates.

Soil pH is another important factor determining denitrification rates. Bakken et al. (2012) showed that the ratio of $N_2O/(N_2+N_2O)$ is negatively correlated with soil pH over the pH range 5-8, which is typical for agricultural soils. The authors concluded that low pH interfers with the synthesis of the N_2O reductase enzyme, most likely by affecting the enzyme assembly in the periplasm. Thus, liming can be an efficient way to reduce N_2O (Bakken et al., 2012) and also NO emissions (Gasche and Papen (1999). Comparing limed and non-limed areas in the Höglwald Forest, Gasche and Papen (1999) concluded that an increase in NO consumption rather than a decrease in NO production was driving the decrease in soil surface NO emissions.

3.2.2.1. Heterothrophic (classical) denitrification

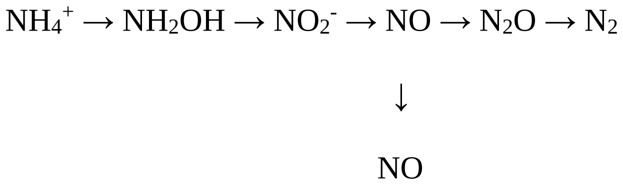
Most denitrifiers are facultative aerobes (including bacteria (e.g. *Alcaligenes faecalis, Pseudomonas stutzeri, Paracoccus denitrificans*), fungi (e.g. *Fusarium oxysporum, Cylindrocarpon tonkinense*) and archaea (e.g. *Methanosaeta concilii, Pyrobaculum aerophilum*)), but in case of O_2 depletion they can switch to anaerobic respiration using NO_3^- as electron acceptor (Payne, 1981; Knowles, 1982; Stouthamer, 1988; Revsbech and Sørensen, 1990; Zumft, 1992, 1997; Kobayashi et al., 1996; Park et al., 1997; Cabello et al., 2004; Hayatsu et al., 2008; Shoun et al., 2012). Although large denitrification rates are linked to low O_2 concentrations, aerobic denitrification has been demonstrated for some bacteria (Lloyd, 1993). For example, Bateman and Baggs (2005) used isotopic tracer to identify aerobic denitrification in dry soil (20% WFPS).

It is well known that NO and N_2O can be produced in soils simultaneously, and the emission ratio of N-NO/N-N_2O is conventionally used to assess the dominance of microbial production pathways for NO and N_2O. At a ratio >1 nitrification is supposed to be the main process, while at a ratio <1 denitrification is generally assumed to dominate N trace gas production (Davidson, 1991; FAO and IFA, 2001; Parton et al., 2001; Garrido et al., 2002; Akiyama and Tsuruta, 2003; Cheng et al., 2004; Nakajima et al., 2005; del Prado et al., 2006). Contradictory to this suggestion, Wang et al. (2011) observed during gas-flow-soil-core incubation experiments of soils enriched with NO_3^- and excess glucose (ratio of C:N = 6) and maintained under anaerobic condition that denitrification was the main process of NO production even though the N-

NO/N-N_2O ratio was above 1. Similarly in a previous laboratory study (Anderson and Levine, 1986), the emission ratio of N-NO/N-N_2O was 3 for a pure denitrifier culture of *A. faecalis* under micro-aerobic conditions. These results suggest that at high soil NO_3^- concentrations and micro-aerobic or anaerobic conditions, NO production is exclusively associated with denitrification (Ludwig et al., 2001; Russow et al., 2009; Wang et al., 2011). Bergaust et al. (2012) observed that NOR-deficient strains of denitrifying bacteria could grow by denitrification under conditions that allow NO to escape and/or be consumed by other organisms, thus avoiding NO toxicity. These findings indicate that the role of denitrification as source of atmospheric NO should be revisited.

3.2.2.2. Nitrifier denitrification

Nitrifier denitrification (Equation (7)) is a process in which NO_2^- is reduced to gaseous NO, N_2O and N_2 by AOB with NH_4^+ as an electron donor under O_2 limitation (Poth and Focht, 1985; Poth, 1986; Wrage et al., 2001). Basically the same enzymes (NIR, NOR, N_2OR) involved in the stepwise denitrification reduction cascade from nitrate to nitrous oxide or di-nitrogen are also activated during nitrifier denitrification. Ammonia oxidizing bacteria are responsible for this process and were found to denitrify under a wide range of environmental conditions from arctic to tropical climatic zones (Kool et al., 2009a, 2009b, 2010; Szukics et al., 2010; Baggs, 2011; Banerjee et al., 2011; Toyoda et al., 2011; Wertz et al., 2012; Vanitchung et al., 2013). This process is important to avoid accumulation of toxic levels of NO_2^- (Stein and Arp, 1998; Beaumont et al., 2004, 2005; Baggs, 2011).



$$\begin{tikzcd}[column sep=small] NH_4^+ \arrow[r] & NH_2OH \arrow[r] & NO_2^- \arrow[r] & NO \arrow[r] \arrow[d] & N_2O \arrow[r] & N_2 \\ & & & NO & & \end{tikzcd} \qquad (7)$$

Nitrifier denitrification is a significant source of NO emitted from soils. NO is an intermediate of NO_2^- reduction by nitrifiers (Remde and Conrad, 1990; Wrage et al., 2001) with N_2O production being often the final step of nitrifier denitrification (Poth and Focht, 1985). However, further reduction to N_2 may also be possible (Poth, 1986), although a NOR homolog has so far not been identified in AOB. WFPS (Garrido et al., 2002) and pH (Nagele and Conrad, 1990; Yamulki et al., 1997; Ste-Marie and Pare, 1999; Cheng et al., 2004) can affect NO and N_2O emission rates under aerobic conditions. Soil core incubation experiments using a range of agricultural soil types collected in France showed that under aerobic condition around 0.6-2.5% of the NH_4^+ applied was emitted as N-NO, while 0.06-1% was emitted as N-N_2O (Garrido et al., 2002). Recently, Zhu et al. (2013) during laboratory experiments on loam, sandy loam and clay loam soils (sampled in California, USA) found under controlled condition (temperature, O_2 concentration, N-application) that at O_2 >0% (0.5-21%) most of the released NO (72-97%) was produced by the NH_3 oxidation pathways (nitrifier denitrification, nitrification-coupled denitrification and nitrification). Moreover NO production increased while the O_2 concentration declined. This demonstrates that nitrifier denitrification and/or partially coupled nitrification-denitrification processes (Wrage et al., 2001; Zhu et al., 2013) could have been responsible for the observed NO emission. Nitrifier denitrification may contribute significantly to losses of NH_4^+ as NO and N_2O emission from soils (Zumft, 1997; Zhu et al., 2013), however, a contribution of nitrification (at least up to the formation of NO_2^- or directly via NH_2OH aerobically) cannot be excluded (Zhu et al., 2013).

3.2.3. The contribution of nitrification and denitrification to NO production

Both, the nitrifier and denitrifier microbial communities can play significant roles in NO production in the soil of terrestrial ecosystems under a wide range of oxygen concentrations. This was recently confirmed by Russow et al. (2009), who demonstrated significant increases of NO emission rates with declining O_2 partial pressure during soil laboratory incubation experiments. They carried out three separate experiments using the tracers $^{15}N\text{-}NH_4^+$, $^{15}N\text{-}NO_3^-$ or $^{15}N\text{-}NO_2^-$ in a soil reactor with a continuously well-mixed headspace (Russow et al., 2009) under a range of O_2 concentrations (Table 1).

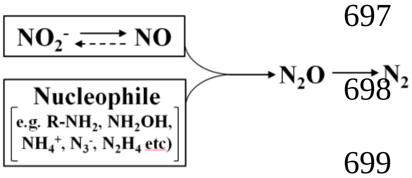
INSERT Table 1 HERE

The results clearly showed that NO_2^- was the main precursor of NO under any oxygen condition, but that the source of NO_2^- was different. Under aerobic conditions (O_2 = 20 vol. %) NO_2^- formed by nitrification from ammonium contributed 70% of the emitted NO and 10% of the emitted NO came from NO_2^- which was formed from the reduction of nitrate by denitrification (Table 1). However, it is likely that in the described experiment nitrifier denitrification contributed to the aerobic NO production. In contrast, under anaerobic condition 87% of the emitted NO was generated by denitrification of nitrate. However, the emission rate under anaerobic (denitrification prevailing) condition was ca. 4-fold higher than under aerobic (nitrification prevailing) conditions (Table 1). Russow et al. (2009) also reported that the fate of NO_2^- freshly added to the soil was different from endogenous NO_2^-, i.e. NO_2^- generated by nitrification and denitrification in the soil. Apparently, exogenous or freshly added NO_2^- undergoes rapid microbial as well as chemical decomposition (Van Cleemput and Baert, 1976; Van Cleemput and Samater, 1996; Venterea and Rolston, 2000; Islam et al., 2008).

Russow et al. (2009) demonstrated very clearly that NO was the exclusive precursor of N_2O under anaerobic condition, i.e. NO produced by denitrification was also consumed by denitrification. This confirms the “diffusion limitation” hypothesis (Firestone and Davidson, 1989; Skiba et al., 1997), which assumes that diffusion limitation in soils with a WFPS >>60% increases the likeliness that NO produced under anaerobic condition *in situ* is further reduced to N_2O (and N_2) by the denitrifying microbial community.

3.2.4. Codenitrification

Codenitrification is a metabolic process, co-occurring during conventional denitrification, where NO_2^- or NO is reduced by other nucleophilic N compounds (e.g., amines ($R\text{-}NH_2$), NH_2OH, NH_4^+, azide (N_3^-), hydrazine (N_2H_4) and salicylhydroxamic acid) to form N_2O and/or N_2 (Shoun et al., 1992; Tanimoto et al., 1992; Spott et al., 2011) (Equation (8)).



(8)

It is assumed that the codenitrification pathway is based on biotically mediated N-nitrosation via enzyme (E) bound NO complexes (e.g., E-NO, $E\text{-}NO^-$ and $E\text{-}NO^+$) (Stamler et al., 1992; Kumon et al., 2002; Spott et al., 2011 and references therein). Both NO_2^- and NO are considered as nitroso donors for nitrosating agents (e.g., E-NO, $E\text{-}NO^-$ and $E\text{-}NO^+$) and the reaction is catalyzed by *cd1* NIR (Averill, 1996; Kim and Hollocher, 1984; Weeg-Aerssens et al., 1988). Thus, NO_2^- as well as NO can be directly involved in the biological formation of hybrid N-N gas, and under certain conditions the reaction between NO_2^- and NO can be reversible (Su et al., 2004; Spott et al., 2011 and references therein). This is in-line with the statement by Averill (1996) that NIR and NOR enzymes of many denitrifiers are likely to be strongly coupled and may function as multi-enzyme complexes and, therefore, are likely to play a key role as biotic catalysts of the codenitrification process.

Evidence for codenitrification has been found in archaea (order *Sulfolobales*) (Immoos et al., 2004), bacteria (orders *Actinomycetales, Burkholderiales, Enterobacteriales, Pseudomonadales, Rhizobiales* and

Rhodobacterales) (e.g., Garber and Hollocher 1982a,b; Goretski and Hollocher, 1991; Ye et al., 1991; Okada et al., 2005) and fungi (order *Hypocreales*) (e.g., Shoun et al., 1992; Tanimoto et al., 1992; Usuda et al., 1995, Sameshima-Saito et al., 2004; Su et al., 2004). Codenitrification seems to be a widely distributed process across terrestrial as well as aquatic ecosystems. But only a few studies provide direct evidence of codenitrification in natural environments, for example in grassland (Laughlin and Stevens, 2002) and agricultural soils (Spott and Stange, 2011; Long et al., 2013).

Controlling factors for codenitrification appear to be closely related to those for denitrification. Accordingly, oxygen availability, pH and availability of respirable organic carbon substrates are the main controllers of codenitrification (Spott et al., 2011), and as for denitrification, may occur under micro-aerobic conditions (Kumon et al., 2002; Okada et al., 2005).

Assuming that most denitrifiers are heterotrophic microorganisms, Spott et al. (2011) have suggested that codenitrification as well as denitrification are related to the availability of respirable organic carbon substances. Short-term experiments showed that decreasing availability of organic carbon compounds (e.g., succinate) diminish denitrification rates, but enhance the codenitrification/denitrification ratio of N_2 produced (Weeg-Aerssens et al., 1998).

In studies where NH_2OH (as naturally occurring nucleophilic compound) was added to denitrifier cultures (Garber and Hollocher, 1982b; Kim and Hollocher, 1984; Weeg-Aerssens et al., 1987, 1988; Goretski and Hollocher,

1991) or soil (Spott and Strange, 2011) 98% of the N_2O produced was formed by codenitrification.

The importance of codenitrification as a key process of N_2O and N_2 production has also been shown under natural conditions. Laughlin and Stevens (2002) showed that up to 92% of released N_2 in grassland soils was produced by codenitrification.

In addition, increasing NO production by denitrification has been observed in the presence of codenitrification (e.g., Garber and Hollocher, 1982a,b, Goretski and Hollocher, 1991). Goretsky and Hollocher (1991) have pointed out that azide (as a nucleophilic compound) partially inhibited NOR activity, thus resulting in NO accumulation. It is quite possible that others nucleophilic compunds could act analogically on NOR enzymes. In addition, it may be also attributed to a sort of abortive reaction of denitrification (Spott and Strange, 2011) as well as may indicate the underconsumption of NO_2^- and NO by a microbial N-nitrosation (i.e. codenitrification).

3.2.5. Dissimilatory nitrate reduction to ammonium

Nitrate ammonification or dissimilatory nitrate reduction to ammonium (DNRA) is a fermentative process, using NO_3^- as electron acceptor during its conversion via NO_2^- to NH_4^+ (Cole and Brown, 1980; Cole, 1990):

$$NO_3^- \rightarrow NO_2^- \rightarrow NH_4^+ \qquad (9)$$

$\downarrow$

$NO \rightarrow N_2O$

Two types of DNRA have been determined, acting in different subcellular compartments. 1) Periplasmic, energy-conserving (respiratory) nitrate reduction to ammonium, which catalyzes the electron transport from formate or H_2 to NO_2^- (using NAP-NRF (nitrite reduction to formate dehydrogenase or hydrogenase enzymes) was described in *Escherichia coli*, *Desulfovibrio*, and *Wolinella* spp. (Simon, 2002; Simon et al., 2003; Cabello et al., 2012). 2) Cytoplasmic dissimilatory NO_3^-/NO_2^- reduction to NH_4^+, which functions as both electron sink and detoxification of NO_2^- formed in NO_3^- respiration in the cytoplasm (using NAR-NIR enzymes). Both processes can result in NO as well as N_2O production. These processes have been reported for *E. coli* and *Klebsiella* spp. (Moreno-Vivián et al., 1999; Cabello et al., 2012), but may also occur in other microorganisms.

DNRA can be performed by different groups of bacteria, including obligate anaerobes (e.g. *Clostridium* spp.), facultative anaerobes (e.g. *Enterobacter* spp.) and aerobes (e.g. *Bacillus* spp.) (Tiedje, 1988). Very reduced and carbon rich environments (C/N ratio >4) favour DNRA (Buresh and Patrick, 1978; Tiedje et al., 1982; Tiedje, 1988; Fazzolari et al., 1998). Positive correlations of DNRA rates with soil pH, C/NO_3^- ratio, bulk soil density, sand content and NO_2^- concentration were reported by Schmidt et al. (2011) for temperate arable soils.

The DNRA pathway was reported to be responsible for up to >99% of the NO_3^- consumption in forest soils (Bengtsson and Bergwall, 2000; Silver et al., 2001, 2005; Pett-Ridge et al., 2006; Huygens et al., 2007; Rütting et al., 2008; Templer et al., 2008), and for up to 21% of NO_3^- consumption in rice paddies (Chen et al., 1995a, b; Yin et al., 2002). DNRA was attributed to NO_3^- consumption in calcareous agricultural soils following glucose addition (Wan et al., 2009), and in temperate arable soils, depending on the presence of low weight C sources (Schmidt et al., 2011). Based on correlation and regression analyses, Rütting et al. (2011) concluded that highest gross DNRA rates can be expected in soils with high organic matter content in humid temperate regions in soil with lower soil moisture.

Since NO_2^- was suggested as an intermediate during the reduction of NO_3^- to NH_4^+ (Cole, 1990; Baggs, 2011) in both periplasm and cytoplasm, evidence is increasing that N_2O is produced during DNRA (Stevens et al., 1998; Baggs, 2011; Rütting et al., 2011). Therefore, it may be assumed that NO (e.g. as an intermediate for N_2O) is produced during reduction of NO_2^- in the cytoplasmic or/and the periplasmatic space. Thus, DNRA may be considered as an additional source not only for N_2O, but also for NO in soils. However, the role of DNRA, as a source for soil NO, remains to be investigated.

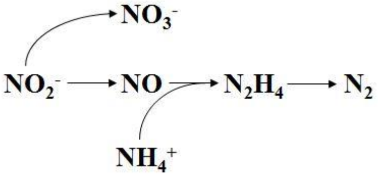
3.2.6. Anaerobic ammonium oxidation

Anaerobic ammonium oxidation (anammox) is a biological process where NH_4^+ serves as electron donor and NO_2^- as electron acceptor to form N_2 (van de Graaf et al., 1990, 1995; Strous et al., 1996; Kuypers et al., 2003; Kuenen, 2008). The anammox pathway is restricted to some slow-growing, strictly anoxic, and lithotropic bacteria belonging to the order

Planctomycetales of the phylum *Planctomycetes* (Kartal et al., 2011, 2013). Up to date 10 species of five genera (*Candidatus Brocadia* (Strous et al., 1999a; Kartal et al., 2008; Oshiki et al., 2011), *Candidatus Kuenenia* (Strous et al., 2006), *Candidatus Scalindua* (Schmid et al., 2003; Woebken et al., 2008; van de Vossenberg et al., 2013), *Candidatus Anammoxoglobus* (Kartal et al., 2007b) and *Candidatus Jettenia* (Quan et al., 2008; Hu et al., 2011)) have been described. Representatives of four from five genera, except *Candidatus Anammoxoglobus*, have been identified in terrestrial ecosystems (Humbert et al., 2010; Long et al., 2013; Wang and Gu, 2013).

Anammox bacteria were first discovered in probes from wastewater treatment bioreactors (van de Graaf et al., 1995, 1996; Mulder et al., 1995; Jetten et al., 1997; Strous et al., 1997), but since then have been found in various ecosystems such as marine oxygen-limited zones and sediments (Rysgaard et al. 2004; Dalsgaard et al. 2005; Kuypers et al. 2005; Lam et al. 2007; van de Vossenberg et al. 2008; Hong et al. 2011), marine surface sediments (Hietanen and Kuparinen, 2008; Rich et al., 2008), sea ice (Rysgaard et al., 2008), estuaries (Trimmer et al., 2003; Dale et al. 2009), freshwater ecosystem (Schubert et al. 2006; Rich et al. 2008), oil reservoirs (Li et al. 2010a), marshlands (Koop-Jakobsen and Giblin 2009; Li et al., 2011a), wetlands (Jetten et al. 2003; Zhu et al. 2010; Humbert et al., 2012), permafrost soils (Philipot et al., 2007; Humbert et al., 2010), peat soils (Hu et al., 2011), rice paddy soils (Zhu et a., 2011; Wang and Gu, 2013), grassland soils (Humbert et al., 2010), agricultural soils (Long et al., 2013), and the rhizosphere (Humbert et al., 2010)

The anammox process occurs in a special intracytoplasmic compartment (organelle), the anammoxosome, which is surrounded by ladderane lipids (Lindsay et al., 2001; van Niftrik et al., 2004; Kuypers et al., 2003; Kartal et al., 2011). The reaction pathway is likely structured in three distinctive steps Strous et al., 2006) (Equation (10)): During the first stage NO_2^- is reduced to NO by cytochrome *cd1* NIR. Subsequently, the reaction between NH_4^+ and NO to hydrazine (N_2H_4) is catalyzed by a hydrazine synthase (HZS). Finally N_2H_4 is enzymatically dehydrogenized by a hydrazine dehydrogenase (DHD) resulting in N_2 production. Meanwhile a part of NO_2^- is oxidized for carbon fixation with NO_3^- formation.



(10)

Kartal et al. (2010b; 2011) showed that N_2H_4 and NO are obligatory intermediates of anammox, that anammox bacteria are tolerant to extremely high concentrations of NO (3500-5000 ppm), and that the reduction of NO is exclusively linked to the catabolic activity of the anammox pathway (Kartal et al., 2010).

Data describing controlling factors of the anammox process are scarce. Strictly anoxic condition and substrate availability (Kartal et al., 2013) under stable environmental conditions are assumed to favour anammox bacteria in natural ecosystems (Dalsgaard et al., 2003; Humbert et al., 2010). Anammox bacteria can grow at very low substrate concentrations, but require NO_2^- as well as NH_4^+. Interestingly, NO_2^- serves as both the electron acceptor for the ammonium oxidation and the ultimate electron donor in the reaction with bicarbonate (HCO_3^-) for biomass formation and NO_3^- production as a by-product (Strous et al., 1998; Kartal et al., 2013). Substrate consumption for anammox, including that for carbon fixation, are 1.27 moles of NO_2^- (including conversion of 1 mole via NO for NH_4^+ oxidation and 0.27 moles for carbon fixation) and 1 mole of NH_4^+ per 0.066 mole of fixed carbon (Strous et al., 1998; Kartal et al., 2013). Therefore, for the fixation of one mole of carbon into biomass 15 catabolic cycles of ammonium oxidation, resulting in significant N_2 production, are needed, which explains the slow growth rate of the bacteria (Kartal et al., 2013). N_2O production has not been observed so far, despite targeted experiments using a range of NO concentrations (Kartal et al., 2010). Anammox bacteria can also grow heterotrophically thereby converting organic compounds, e.g. formate, acetate, propionate, methanol, mono- and dimethylamine into biomass C (Strous et al., 2006; Kartal et al., 2007a,b, 2008, 2013) or even to CO_2 (Kartal et al., 2007a,b, 2008, 2013).

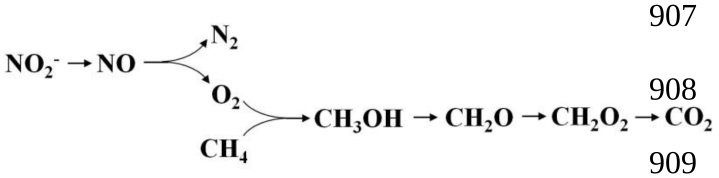
Dalsgaard and Thamdrup (2002) reported that the temperature optimum for NH_4^+ oxidation by anammox bacteria isolated from marine sediments was ca. 15 °C, though it may vary from 6 °C (Dalsgaard and Thamdrup, 2002) to temperatures >50°C (Jaeschke et al., 2009; Byrne et al., 2009; Li et al., 2010).

High NH_3 concentrations as found at high pH values may inhibit anammox (Aktan et al., 2012; Yang et al., 2014), while accumulation of heavy metals (e.g., As, Cd and Pb) in sediments affects the diversity of anammox bacteria (Li et al., 2011a; Yang et al., 2014). Generally, the diversity of anammox bacteria is higher in terrestrial systems as compared to marine systems (Humbert et al., 2010). Also increased soil or sediment aeration is negatively affecting anammox activity (Long et al., 2013) while reported effects of increasing N availability remains controversial: Koop-Jakobsen and Giblin (2009) did not find statistically significant differences between fertilized and unfertilized marsh lands while Hu et al. (2011) found that in NO_2^- and NH_4^+ amended peat soils the abundance of *Ca. Jettenia asiatca* increased.

However, it remains unknown if anamox bacteria are significant sources of NO or possibly even sinks in terrestrial ecosystems.

3.2.7. Nitrite-dependent anaerobic oxidation of methane

Nitrite-dependent anaerobic oxidation of methane (N-AOM) is an “intra-aerobic” pathway of methane (CH_4) oxidation to CO_2 by O_2. However, in this reaction the O_2 is produced by NO_2^- reduction via NO dismutation to O_2 and N_2 (Equation (11)) (Ettwig et al., 2010).



(11)

The process itself requires a set of enzymes: methane monooxygenase (MMO), methanol dehydrogenase (MDH), formate dehydrogenase (FDH) and nitrite or nitric oxide reductase, which has been found in slow-growing Gram-negative bacteria *Candidatus ‘Methylomirabilis oxyfera’* belonging to the phylum NC10 (Ettwig et al., 2010). *M. oxyfera* has been enriched from freshwater sediments (Raghoebarsingetal, 2006; Ettwig et al., 2008, 2009), and its complete genome has recently been published (Ettwig et al., 2010). Ettwig et al. (2010) have speculated that NOR may be involved in NO detoxification. Exogenous NO as well as NO_2^- has been demonstrated to be rapidly reduced to N_2 and O_2, thus stimulating CH_4 oxidation.

Very recently Harron et al. (2013) described an anaerobic, methane-oxidizing and nitrate-reducing archaeon *Candidatus 'Methanoperedens nitroreducens'*, which was enriched from a mixture of freshwater sediments and anaerobic wastewater sludge. This archaeon has been demonstrated to oxidize CH_4 to CO_2 while reducing NO_3^- to NO_2^-. Moreover *M. nitroreducens* was able to oxidize CH_4 in the presence of NH_4^+ through a syntrophic relationship with the anaerobic ammonium oxidizing bacteria *Kuenenia* spp. (Harron et al., 2013). Anammox bacteria have been shown to utilize NO_2^-, reduced by *M. nitroreducens* for NH_4^+ oxidation, thereby producing NO_3^- as byproduct (Harron et al., 2013).

Occurrence of N-AOM has been widely reported for freshwater sediments (Deutzmann and Schink, 2011; Kampman et al., 2012; Kojima et al., 2012; Shen et al., 2014a), estuarine sediments (Shen et al., 2014b), wastewater sludge (Luesken et al., 2011a), peat lands (Zhu et al., 2012), wetlands (Hu et al., 2014) and rice paddy soils (Wang et al., 2012; Shen et al., 2013; Hu et al., 2014).

Generally, oxic/anoxic interfaces with high CH_4^+ and NO_3^-/NO_2^- concentrations are favourable for the N-AOM process (Oremland, 2010; Shen et al., 2012). For example, highest N-AOM activity has been found at a depths of 50-60 cm for wetlands (Hu et al., 2014), 80-85 cm for peatlands (Zhu et al., 2012) and 90-100 cm for paddy soils (Hu et al., 2014).

Temperature optimum for ‘intra-aerobic’ CH_4 oxidation has been detected to be 25-30 °C for bacteria (Ettwig et al., 2010) and a bit widely 22-35 °C for archaea (Harron et al., 2013). N-AOM microorganisms are mesophilic to pH with optimum of 7-8 (Raghoebarsingetal, 2006; Ettwig et al., 2010), although are still active at more acidic (5.9) pH (Zhu et al., 2012).

However, to date there is no evidence that N-AOM contributes to NO production in soils, though NO is an obligatory intermediate.

3.2.8. Unspecific enzymo-oxidative mechanisms related to soil NO contents

The similarity of biochemical processes in different groups of living organisms is not surprising. Therefore, we briefly outline the seven known pathways of NO production in plants (Table 2), as described by Gupta et al. (2011) and compare it with soil microbial processes of NO production were appropriate. In this context, different pathways of NO biosynthesis could be classified either as reductive or as oxidative (Table 2).

INSERT Table 2 HERE

The ‘hydroxylamine-mediated NO production’ in plants may be due to the same or a very similar biochemical mechanism as soil NO production during nitrification. In plants, hydroxylamine reacts directly with superoxide

(O_2^-) to form NO under aerobic conditions (Vetrovsky et al., 1996), whereas this conversion in nitrifiers (*Nitrosomonas* spp.) is catalyzed by the enzyme hydroxylamine oxidase (Lees, 1952; Hooper and Terry, 1979; Hooper et al., 1997). *In vitro* experiments adding hydroxylamine (NH_2OH) to plant cells confirmed that NH_2OH is indeed converted to NO and NO_2^- (Rümer et al., 2009a, 2009b; Gupta et al., 2011).

The enzyme superoxide dismutase (SOD) (Beyer et al., 1991) was considered to be essential for the conversion of NH_2OH to NO and NO_2^- in plant cells and cell-free laboratory experiments (Rümer et al., 2009a, b). In cell-free systems NO emissions increased up to 10-fold in air and 25-fold in a N_2 environment in the presence of SOD and hydroxylamine compared to controls where only hydroxylamine was added. As both, substrate (NH_2OH) and by-products (NO and NO_2^-) are able to penetrate membranes (Rümer et al., 2009a) and extracellular SOD (EC-SOD) can originate from excretion by bacteria (Tullius et al., 2001; Takahashi et al., 2003) as well as plant cells (Alscher et al., 2002), oxidation of both endogenous and exogenous hydroxylamine may take place inside or outside plant cells (Rümer et al., 2009a). Murphy and Sies (1991) reported that SOD can faciliate the reversible conversion of nitroxyl anion (NO^-) to NO *in vitro*. The actual mechanism of the SOD-catalyzed reaction of NO and NO_2^- production from hydroxylamine is still unclear and its presence in the soil so far has not been demonstrated. It is noteworthy, that soil NH_2OH concentrations (e.g., 0.3-34.8 μg N kg^{-1} dry forest soil) can be comparable with those of NO_2^- (Liu et al., 2014).

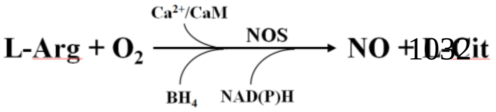
We assume that similar enzymatic environments as those described above, can be found in soils with high microbial activity and high nutrient concentrations, especially in the rhizosphere, when nutrients and enzymes are released into the soil, for example after rewetting/thawing of dry/frozen soils. Thus, theoretically, an unspecific enzymo-oxidative mechanisms could trigger NO and NO_2^- production in soils.

SOD is widely produced by most organisms (Beyer et al., 1991; Scandalios, 1997; Tullius et al., 2001; Alscher et al., 2002; Takahashi et al., 2003). In the soil, SOD is a rather thermo- and chemo-stable protein (Hunter et al., 2002; Khanna-Chopra and Sabarinath, 2004) that may originate from the active microbial community (Tullius et al., 2001; Takahashi et al., 2003), or recently decaying organisms. Considering these processes and mechanisms, we hypothesize that not only nitrifying (AOB and AOA) microbes are responsible for soil NO production, but that also other microbes via the release of extracellular SOD (directly) or SOD (after cell damage) contribute to soil NO production. More research is required to investigate activating factors for SOD in bacteria, since up to now only data for plant (Bowler et al., 1994; Scandalios, 1997; Babithaa et al., 2002; Baranenko, 2006) and animal cells (Yamakura and Kawasaki, 2010; Miller, 2012) are available.

3.2.9. Nitric oxide synthase

Nitric oxide synthase (NOS) is a common ubiquitous enzyme, which is responsible for NO synthesis in cells of bacteria as well as higher organisms, including mammals. NOS is present in protists, such as myxomycetes (Messner et al., 2009) and eukaryotic single cells (Fritz-Laylin et al., 2009). Active NOS enzymes are ubiquitously present in invertebrates, such as echinoderms, coelenterates, nematodes, annelids, insects, crustaceans and molluscs (Jacklet, 1997 and reference therein). In mammals, many cell types such as endothelial cells, neurons, myocytes, smooth muscle cells, and activated mune cells (e.g. leucocytes and macrophages) produce NO by both enzymatic and non-enzymatic pathways (Zweier et al., 1995; Velayutham and Zweier, 2013 and reference therein). Enzymatic NO synthesis by NOS appears to be much more important than non-enzymatic production (Zhou and Zhu, 2009; Chen et al., 2010; Forstermann and Sessa, 2012).

NOS-derived NO synthesis proceeds in a two step oxidation of the amino acid precursor L-arginine (L-Arg) via N-hydroxy-L-arginine to L-citrulline (L-Cit) (Griffith and Stuehr, 1995) in the presence of 5,6,7,8-tetrahydrobiopterin (BH_4), reduced nicotinamide-adenine-dinucleotide phosphate (NAD(P)H), molecular oxygen (O_2) and Ca^{2+}/calmodulin (CaM) (Zhou and Zhu, 2009; Chen et al., 2010; Forstermann and Sessa, 2012):



$$\text{L-Arg} + O_2 \xrightarrow[\text{BH}_4\quad \text{NAD(P)H}]{\text{Ca}^{2+}/\text{CaM}\quad \text{NOS}} \text{NO} + \text{L-Cit}$$

(12)

It is known that three phyla of Gram-positive bacteria (*Firmicutes, Actinobacteria, and Deinococcus-thermus*), at least one phylum of archaea (*Euryarchaeota*) and one representative of the *Proteobacteria* phylum of Gram-negative bacteria (*Sorangium cellulosum*) possess NOS-like enzymes that are highly homologous to the oxygenase domain of eukaryotic NOS (Stuehr, 1999; Gusarov et al., 2008; Sudhamsu and Crane, 2009 and reference therein; Crane et al., 2010 and reference therein). These specific proteins were found in pathogenic as well as in non-pathogenic soil bacteria (Gusarov et al., 2008, 2009). Indeed, a high level of functional and structural similarity between bacterial NOS (bNOS) and eukaryotic NOS was reported (Pant et al., 2002; Pant and Crane, 2006; Salard et al., 2006; Gusarov et al., 2008; Sudhamsu and Crane, 2009). Bacterial and archaeal NOS were thought to be unable to produce NO *in vivo* because of a lacking reductase domain (Adak et al., 2002) and only more recent studies have provided evidence of bNOS mediated bacterial NO production thereby using various nonspecific cellular reductases as their redox partners (Johnson et al., 2008; Gusarov et al., 2008; Shatalin et al., 2008). In the mentioned works it is proposed that NO, escaping from the cellular lumen, is readily oxidized in the culture medium under aerobic conditions forming NO_2^- and NO_3^-. Shatalin et al. (2008) and Schreiber et al. (2011) have demonstrated directly that NO was produced by *B. anthracis* and *B. subtilis*, using an NO sensitive dye. Furthermore, it has been shown in plant-pathogenic *Streptomyces* spp. that bNOS-derived NO production considerably exceeds the requirement of phytotoxin thaxtomin A nitration. Johnson et al. (2008) confirmed that surplus NO was produced by bNOS, and was detected in the gas phase above the culture medium by chemiluminescence. It is also known that other, NOS-independent mechanisms of L-Arg conversion to L-Cit in the urea cycle catalysed by arginine deiminase (Yamasaki and Sakihama, 2000, equation 12), arginase or ornithine carbamoyl transferase (Jansson and Lindblad, 1998; Viator et al., 2008) are present in bacteria (Sudhamsu and Crane, 2009).

In mammals, three isoforms of NOS originating from separate genes have been described, i.e. endothelial NOS (eNOS), neuronal NOS (nNOS) and inducible NOS (iNOS). The first two types of NOS are constitutively expressed in the cells and are called cNOS; iNOS is typically expressed under infectious and inflammatory conditions at dramatically higher rates compared to cNOS (Wu, 1995; Siervo et al., 2011). Furthermore, NO_3^- and NO_2^- can also be reduced to NO via other enzymatic (NAP/NIR) and non-enzymatic reactions (e.g. via deoxygenated haemoglobin in acidic environment, via neuroglobin, by xanthine oxydo-reductase) in mammalian cells (Burmester and Hankeln, 2004; Gladwin and Kim-Shapiro, 2008; Jansson et al., 2008; Li et al., 2009). It is likely that eukaryotes have acquired the NOS enzyme from bacteria, which possess the most ancient primitive NOS type (Gusarov et al., 2008), by horizontal gene transfer, as supported by recent phylogenetic tree analysis (Sudhamsu and Crane, 2009).

In plant cells, a gene with significant homology to that encoding animal NOS has not been detected (Moreau et al., 2010; Gupta et al., 2011), and NOS-derived NO production has not been confirmed as an enzymatic pathway of Arg-derived NO production in plants (Zemojtel et al., 2006; Gas et al., 2009; Moreau et al., 2010). However, several studies showed evidence for an NOS-like enzymatic reaction in plants that is involved in various processes, based on a correlation between the supply with L-Arg and its analogs with NO production (Mackerness et al., 2001; Lum et al., 2002).

There are at least 6 other pathways of NO production in plant cells, mentioned in Table 2, but not described here, because in our opinion they most probably are not relevant for unspecific enzymo-oxidative pathways in soil.

3.2.10. Biotic consumption of NO in the soil

Soils are a net source of NO (IPCC, 2007), but also a sink for atmospheric of NO (IPCC, 2007; Slemr and Seiler, 1984, 1991; Ludwig and Meixner, 1994; Ludwig et al., 2001; Laville et al., 2009) or can be re-deposited as NO or/and NO_2 onto plant surfaces (Wesely and Hicks, 2000; Butterbach-Bahl et al., 2004; Horii et al., 2004; Seok et al., 2013; Shen et al., 2013). Plants can use atmospheric NO and NO_2 as additional nitrogen source (Neubert et al., 1993; Geßler et al. 2000; Butterbach-Bahl et al., 2004; Teklemariam and Sparks, 2006;). Plant uptake of atmospheric NO and NO_2 is a diffusive process through the stomata and flux rates depend on the compensation points of NO and NO_2 and their atmospheric gas mixing ratios. The atmospheric gas mixing ratios can vary significantly between ecosystems (Conrad, 1996; Geßler et al., 2000; Ludwig et al., 2001), and enhanced mixing ratios can stimulate the growth of chemolithoautotrophic nitrite oxidizers colonizing the phyllosphere (Geßler et al., 2002; Papen et al., 2002).

NO production during denitrification and nitrifier denitrification, is much larger than the NO emitted (Firestone and Davidson, 1989; Skiba et al, 1997), because a significant proportion of NO produced by denitrification is immediately consumed by denitrification for energy production (Zumft and Cardenas, 1979) and simultaneous detoxification (Zumft, 1997). Thus, the net NO emission rate from denitrification processes is typically very small.

Some heterotrophic bacteria can oxidize rather than reduce NO via aerobic co-oxidation reactions (Baumgärtner et al., 1996; Koschorreck et al. 1996; Rudolph et al. 1996; Koschorreck and Conrad 1997; Dunfield and Knowles 1997, 1998, 1999; Conrad, 1999). Increased NO consumption was demonstrated after manure or compost application (Dunfield and Knowles 1998). The magnitude of NO consumption in soils remains uncertain, but concentrations in the soil atmosphere can be significant. E.g., in temperate forest soils NO concentrations varied in a range of 60-180 ppbv at 0 to 10 cm soil depth (Dong, Simon and Rennenberg, unpublished data).

It is well known that NO is an important free diffusive signalling molecule in higher organisms with many direct and indirect functions, such as transcriptional gene regulation, post-translational protein modification, cytoprotection, cytotoxicity, pathogenesis, memory modulation and learning, or vasodilation (vascular smooth muscle relaxation) (for detailed information see section 2 below). For these specific purposes, NO is produced by the NOS enzyme or/and other enzymatic reactions, but also exogenous NO is consumed (Gusarov et al., 2013). The contibution of exogenous NO in intracellular signalling processes has rarely been studied and, therefore, is poorly understood. NO is also consumed for cell detoxification mainly via forming reactive N species (RNS), such as the NO radical (NO^*), nitroxyl (NO^-), S-nitrosothiols (RSNOs), NO-soluble guanylyn cyclase (NO-sGC), and dinitrosyl-iron complexes (DNICs). Not all NOS-derived NO is stored and converted to RNS and surplus will be emitted (Johnson et al., 2008); unfortunately, quantitative data are not available.

Many bacteria (including those not engaged in the N-cycle) are able to detoxify NO by a range of enzymes, such as NO dioxygenase (flavohemoglobin, *Hmp*), flavodiiron NO reductase (flavorubredoxin, *norVW*) and periplasmic cytochrome C nitrite reductase (*NrfA*), under both oxic and anoxic conditions (Poole et al., 2005; Koul et al., 2014; Mühlig et al., 2014). Under aerobic conditions *Hmp* catalizes the oxidation of NO to NO_3^- (Crawford and Goldberg, 1998; Gardner et al., 1998; Hausladen et al., 2001;); and *Hmp* was shown to protect *Salmonella typhimurium* against the growth inhibitory affect of NO (Mills et al. (2008). Meanwhile under anoxic conditions *Hmp* and *NorVW* facilitated the reduction of NO to N_2O (Kim et al. 1999; Gardner et al. 2002; Mills et al., 2005). The enzyme NrfA can catalize the five-electron-reduction of NO to NH_3/NH_4^+ undr anaerobic conditions (Poock et al., 2002; van Wonderen et al., 2008) and other proteins possessing an ability to mediate NO detoxification have been found across bacteria, e.g., truncated globin (HbN) in *Mycobecterium bovis* (Ouellet et al., 2002), vitreoscilla globin (Vgb) in *Vitreoscilla* spp. (Frey et al., 2002), cytochrome *c*' (CycP) in *Rhodobacter capsulatus* (Cross et al., 2001) and single-domain globin (Cgb) in *Campilobacter coli* and *C. jejuni* (Elvers et al., 2004).

For eucaryota the rate of NO consumption by cells is directly dependent on, and proportional to, the oxygen concentration. According to Thomas et al. (2001, 2008) this directly points to an important regulatory relationship between NO signaling and tissue oxygen concentration. Increased oxygen levels will increase NO consumption, and in reverse NO regulates oxygen consumption via inhibition of mitochondrial respiration. This important interdependent relationship between NO and O_2 provides a direct feedback mechanism to regulate their respective concentrations (Thomas et al., 2008). There are indications that such a mechanism may also regulate NO concentration in soil air, though simultaneous measurements of the dynamics of NO and O_2 concentrations in soil air are still needed for further judegement.

Quantification of the contribution of different NO consumption processes has so far not been achieved. However, Koschorreck and Conrad (1997) have measured a pseudo-first-order uptake rate constant (k) of NO consumption in soil samples from four differens ecosystems (primary forest, tree seedling plantation, flooded savanna, soil after tree burning). They reported that under aerobic conditions the consumption rate was low and varied between 12 and 28 $cm^3\ h^{-1}\ g^{-1}$, while at anaerobic condition the consumption rate was 1-2 orders of magnitude higher (227-3861 $cm^3\ h^{-1}\ g^{-1}$ dw). Further studies are needed to fill this large knowledge gap.

3.3. Interrelation between main abiotic and biotic processes of NO transformations in soils

Based on recently published literature, we have created a conceptual diagram of all known and theoretical microbial, chemical and enzymatic processes where NO is an obligatory player (Fig. 2). It is likely that NO_2^-, a precursor of NO, is the central intermediate connecting all microbial processes and processes associated with chemodenitrification.

INSERT Fig. 2 HERE

As shown in Fig. 2, all processes are interrelated, interacting, and can operate in parallel and/or partially stepwise, utilizing intermediates or products, which were formed during other processes. The unique integrity of interconnections between all components of the system *in situ*, presents the greatest challenge for research, in particular under field conditions.

Unraveling these interactions requires controlled laboratory experiments applying state-of-the-art methods such as multi-isotope tracing (e.g. Kool et al., 2009a, b) together with combined gene expression and functional analyses (e.g. Bru et al., 2010) of microbial mono-cultures and mixtures (e.g. Rümer et al., 2009a, b; Russow et al., 2009).

Nitrification and denitrification are considered to be the main soil microbial processes leading to NO production. *In situ* and *in vivo* laboratory studies have suggested that nitrification rates can be estimated from initial and final substrate concentrations, assuming that oxidation of NH_4^+ via NH_2OH to NO_2^- and NO_3^- is prerogative for aerobic nitrification. However, we cannot ignore that part of the NH_2OH formed from NH_4^+ is decomposed chemically or by non-specific enzymo-oxidative mechanisms. Thus, we cannot answer the following simple questions due to a lack of knowledge:

i) - What is the relative contribution of oxidative (nitrification) and reductive (denitrification, codenitrification, DNRA, anammox, N-AOM) processes to NO_2^- production in soils; and can nitrifiers also utilize NO_2^- formed by other microbial processes?

ii) - What is the exact fate of NO_2^- in soils, i.e. to what extend is NO_2^- further oxidized to NO_3^- or reduced to NO, N_2O, N_2 or even NH_3?

iii) - What are the dynamics of N oxidizing and reducing processes in soils, since current lack of adequate measuring techniques limits the identification of individual processes in bulk soil?

iv) - What are the gross NO production and consumption rates and what is the contribution of different processes to this consumption?

In situ studies have enabled us to estimate with reasonable confidence rates of production and consumption of by- or end-products of nitrification/denitrification pathways under certain environmental condition. However, we can only speculate about the processes involved. In other words, we are studying ‘symptoms’ (substances), but not ‘diseases’ (processes). The future challenge is to characterize and quantify these processes with new experimental approaches to better understand drivers and processes leading to NO emissions from soil.

4. Physiological functions of NO in different groups of organisms

Generally NO-related signalling functions are attributed to various reactive N species (RNS), which are derivatives of NO, e.g. NO radical

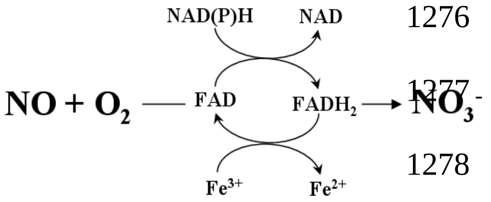
($NO^{\cdot}$), nitroxyl (NO^-), nitrosonium (NO^+), peroxynitrite ($ONOO^-$), S-nitrosothiols (RSNOs), NO-soluble guanylyn cyclase (NO-sGC), dinitrosyl-iron complexes (DNICs), N_2O_5, etc.

4.1. Functions of NO in bacteria

In Gram-positive bacteria (e.g. *B. subtilis*, *B. anthracis*), endogenous NO produced by bNOS as well as exogenous NO mainly possess the function of rapid protection against oxidative stress. Direct protection is achieved through catalase activation and transient inhibition of the rate of enzymatic reduction of free cysteine. This sulphur amino acid is involved in the re-reduction of Fe^{3+} to Fe^{2+}, thus suppressing Fe^{2+}-mediated formation of hydroxyl radicals (a Fenton reaction) (Gusarov and Nudler, 2005; Shatalin et al., 2008). In addition, it was demonstrated (Gusarov et al., 2009) that the enzyme bNOS protects bacteria (e.g. *B. subtilis*, *Staphylococcus aureus*) against a wide spectrum of antibiotics by endogenous NO production, either directly by nitrosation (acridines) or indirectly by NO-mediated suppression of oxidative stress (pyocyanin, cephalosporins, lactams). Corker and Poole (2003) showed that anaerobic NO accumulation in *E.coli* grown in the presence of NO_3^- but absence of *Hmp* inactivated the anaerobic regulator *Fnr* (fumarate and nitrate reductase). *Fnr* controls periplasmic cytochrome *c* nitrite reductase (NrfA), Nir and Nar, and thereby blocks further NO production from NO_3^- via NO_2^-. In addition, Mühlig et al. (2014) proposed that in *S. typhimurium* NO can initiate detoxification via inactivation of Fnr and/or NO-responsive regulator (NsrR) derepressing Hmp expression as well as via activation of an anaerobic nitric oxide reductase transcription regulator (NorR) derepressing NorV expression.

bNOS-dependent NO production is involved in the synthesis of a nitrated phytotoxin thaxtomin A and thereby plays a major role in the pathogenesis of *Streptomyces* spp., (Johnson et al., 2008). Endogenous NO produced by NOS indirectly protects *Deinococcus radiodurans* against ultraviolet radiation (Patel et al., 2009).

In bacteria, where NOS is expressed (e.g. *S. aureus*, *B. subtilis*, *B. anthracis*), flavohemoglobins (flavoHbs) are co-expressed and in the presence of O_2 may convert bNOS-derived NO to NO_3^- with electron transfer from NAD(P)H to the ferric heme iron ligand via FAD (Bang et al., 2006; Ilari and Boffi, 2008; Nobre et al., 2008):



(13)

Hence NOS-produced NO may be consumed by bacteria in a balanced way, although evidence for and the rate of NO consumption in a reaction with endogenous flavoHbs have to be elucidated in further studies (Rafferty, 2011).

Moreover, it was observed that also SOD A expression in *B. subtilis* is significantly increased by bNOS activity. From this observation it was speculated that NO can act as a transcriptional regulator, however, a mechanism of this regulation has not been revealed (details in Rafferty, 2011).

Recently, Schreiber et al. (2011) showed that biofilm dispersal of *B. subtilis* appears to be affected by NOS activity. The authors suggested that NO is involved in the fine-tuning decision between adaptation to anoxic conditions (in the biofilm) or dispersal from the biofilm. A role of NO for biofilm dispersion was reported for the pathogens *Pseudomonas aeruginosa* (Barraud et al., 2006, 2009a) and *S. aureus* (Schlag et al., 2007), the myxomycete *Candida albicans,* as well as in mixed-species biofilms (Barraud et al., 2009b). In contrast, in many Gram-negative bacteria, where NO is mainly synthesized as a by-product by NAR/NAP during denitrification, NO can play a signalling function to enhance biofilm formation. For instance, NO not only induces biofilm formation, but also up-regulates the genes involved in NIR and NAP synthesis and oxidative stress tolerance in *Neisseria gonorrhoeae* (Falsetta et al., 2011). Moreover, NO triggers the transcription of a gene obligatory for attachment and initial biofilm formation in a number of nitrifying bacteria (e.g. *Nitrosomonas europaea*, *Nitrosolobus multiformis* and *Nitrospira briensis*) (Schmidt et al., 2004).

Increasing the NO concentration in the medium induced the formation of biofilms by the Gram-negative rhizobacteria *Azospirillum brasilense*, whilst a gradual decrease of NO in the medium appears to mobilize cell motility (Arruebarrena Di Palma et al., 2013). The authors showed that both endogenously produced and exogenously added NO (e.g. GSNO as NO-donor) caused the same response. Apparently, NO-mediated effects on bacterial biofilm formation or dispersal are species-specific phenomena, depending on N availability (e.g. at the soil microsite or the host environment).

4.2. Functions of NO in protists

NOS activity in myxomycetes (e.g. *Physarum polycephalum*) is induced under nutrient limitation and is involved in sporulation, but the mechanisms responsible so far have not been described (Messner et al., 2009).

Recently, a NOS enzyme without a reductase domain, but resembling bacterial NOS, was found in the eukaryotic unicellular algi *Naegleria gruberi* (Fritz-Laylin et al., 2009). Characterization of the enzyme and its function has not been reported.

4.3. Functions of NO in animals

Invertebrates and vertebrates (i.e. worms, beetles,, rodents, moles,, ruminants) influence the physical and chemical composition of soil, by burrowing, compaction and deposition of nutrients (i.e. faeces, urine and saliva), thereby indirectly influence NO production and consumption processes.

4.3.1. Invertebrates

In invertebrates (e.g. roundworms) NO can prolong life and mediate stress resistance to heat (Gusarov et al., 2013), Cd^{2+} toxicity (Cui et al., 2007) and the response to pathogenic bacteria (e.g. *P. aeruginosa*) (Troemel et al., 2006).

In addition, in invertebrates (e.g. echinoderms, coelenterates, nematodes, annelids, insects, crustaceans and molluscs) NO is of ubiquitous importance as an orthograde transmitter and a co-transmitter in signalling cascades as well as a modulator of conventional transmitter release (Jacklet 1997). These signalling functions of NOS-derived NO include neuronal sensory, including chemosensory (Gelperin, 1994; Jacklet and Gruhn, 1994; Elphick et al., 1995), as well as signalling in learning processes (Robertson et al., 1995; Kendrick et al., 1997; Müller, 1997) and development (Davis and Murphey, 1994; Kuzin et al., 1996; Froggett and Leise, 1997; Jacklet, 1997; Meleshkevitch et al., 1997). In the bug *Rhodnius* NO mediated vasodilation (Nussenzveig et al., 1995); the exact mechanism is not clear, but may resemble that identified in mammals (Jacklet, 1997). Comprehensive studies carried out (Susswein and Chiel, 2012) on the sea slug *Aplysia* elucidated that NO plays a major role in neuron mediated control of food finding and food consumption. Thus, NO is associated with the neural function of the swallow-rejecting mechanism, i.e. the rejection and reposition of mechanically resistant food, and the formation of memories of food inedibility (learning function), when food could not be swallowed successfully (Susswein and Chiel, 2012).

NO produced by bacteria (e.g. *B. subtilis*, *E. coli* with a NOS plasmid), previously eaten by the roundworm *Caenorhabditis elegans* (lacking its own NOS), diffuses into the worm's intestine tissues and triggers a cascade of signalling reactions causing a specific transcriptional response that promotes thermotolerance and prolongs life (Gusarov et al., 2013). The anti-aging effects of bacterial NO, were demonstrated by adding exogenous NO to the growth medium of the worm (Gusarov et al., 2013). The authors suggested that similar mechanisms may be relevant in higher organisms, one example may be the beneficial effect of 'normal' gastrointestinal microbiota. Such gastrointestinal microbes, predominately Gram-positive lactic acid bacteria (e.g. *Lactobacillus, Streptococcus, Lactococcus* spp.) possess NOS (Masson et al., 2011 and references therein) and NOS-derived NO may be used by the host. Thus, bacterial NO may diffuse into gastrointestinal tract cells and increase the level of available NO, which together with endogenous produced NO by the host may be involved in vasodilation, vasoprotection, cytoprotection, neuroprotection, etc. (Lundberg et al., 1994, 2008; Velayutham and Zweier, 2013 and references therein). However, this suggestion requires further investigations.

4.3.2. Mammals (including humans)

It has been clearly demonstrated that in mammals NO is involved in the regulation of synaptic signalling events, blood pressure, gut peristalsis, vasodilation, penile erection, developing retinal tissue at the level of gene transcription, mRNA translation and post-translational modifications of proteins (Forstermann and Sessa, 2012; Socodato et al., 2013). Zhou and Zhu (2009) indicated that NO is also engaged in modulating memory, learning and neurogenesis. The functions of NO in mammals include a whole set of both positive and negative effects listed in Table 3.

INSERT Table 3 HERE

The presumably healthy human population of Earth (7.22 billion in March, 2014 according to Worldometers, 2014) annually exhales approximately 92 Gg N-NO a^{-1} (estimated using Antczak et al. (2011), Davies and Moores (2003) and Levitzky (2003) data), which is equally to 1% of total soil emission (IPCC, 2007). Undoubtedly, this value is an underestimation, as people suffering from inflammatory diseases or physiological problems exhale higher rates of NO (Kharitonov et al., 1996; Fuchs et al., 2012). Exhaled NO has been proposed as an inflammatory disease marker for humans, since iNOS can be triggered to a greater degree by inflammatory cytokines, endotoxines and viral infections (Asano et al., 1994; Hunt et al., 2000; Antczak et al., 2011). We can speculate with confidence that NO is also exhaled by other mammals, including those living in the soil. Hence, the total exhaled NO rate of mammals is likely to be much higher than the estimate for the human population.

4.4. Functions of NO in plants

In plants NO is a ubiquitous endogenous key mediator of numerous physiological and developmental processes (Guo et al., 2003; Lamattina et al., 2003; Wendehenne et al., 2004; Delledonne, 2005; Besson-Bard et al., 2008; Neill et al., 2008). In the aboveground parts of the plant, it is, for example, involved in flowering, seed germination and floral development; in belowground parts in root organogenesis, lateral root development, and formation of root hairs and adventitious roots (see review by Mur et al., 2012 and references therein). NO also plays a role in plant-microbe interaction including host defense, pathogen virulence and symbiotic interaction (Mur et al., 2012). In addition, it fulfills functions in stomatal regulation (García-Mata and Lamattina, 2001; Desikan et al., 2002; Neill et al., 2002), root nitrogen uptake and metabolism (Simon et al., 2009; 2013) and adaptive responses to abiotic stress (Neill et al., 2003; 2008; Besson-Bard et al., 2008; Mur et al., 2012). Abiotic stress reactions with proven participation of NO signaling include drought (García-Mata and Lamattina, 2001; Desikan et al., 2002; Neill et al., 2002; Freschi et al. 2010), salinity (Zhang et al., 2004, 2006; Liu et al., 2007; Shi et al., 2007; Zhao et al., 2007; David et al., 2010; Chen et al., 2013), heat (Leshem et al., 1998; Gould et al., 2003), cold (Zhao et al. 2009) and flooding (Dean and Harper, 1986; Guo et al., 2003; Zhang et al., 2006; Ferreira et al., 2010; Gupta and Kaiser, 2010; Gupta et al., 2012). All these environmental factors cause oxidative stress in plants; it is therefore suggested that NO stimulates antioxidative defense mechanisms during periods of elevated production and abundance of reactive oxygen species (ROS) (Neill et al., 2008).

NO production by plants is of particular significance upon nitrate reduction in roots under hypoxia (Dean and Harper, 1986; Dordas et al., 2003, 2004; Igamberdiev et al., 2004; Igamberdiev and Hill, 2009; Gupta and Kaiser, 2010; Gupta et al., 2012). NO formation was determined in these studies directly in the tissue affected by hypoxia stress. Recently, NO emissions were measured fom the leaves of trees, where only the root system was flooded (Copolovici and Niinemets, 2010). Because NO emissions were highest in flooding sensitive and lowest in flooding tolerant species, NO emissions were suggested to be a marker of flooding tolerance. In addition, a regulatory function of NO in stomatal conductance of flooded plants was postulated (Copolovici and Niinemets, 2010). The significance of NO produced in plant roots upon hypoxia for other soil biota has so far not been elucidated. In addition, the contribution of plant derived NO for NO emissions from the soil and from aboveground parts of plants into the atmosphere has so far not been quantified.

In plants, NO is involved in protein modification as posttranslational regulator of enzymes both directly and indirectly via its derivatives (RNS). S-nitrosylation of cysteine, nitrosylation of transition metals and tyrosine nitration appear to be the main NO-associated protein modifications. S-nitrosylation is involved in gene regulation, modulates phytohormon signalling and can control programmed cell death (PCD) in opposing ways (promote or inactivate) (Hara et al., 2005; Melotto et al., 2006; Belenghi, 2007; Forman et al., 2008; Tada et al., 2008). NO regulation of gene expression via S-nitrosylation has been widely reported (Grün et al., 2006 and reference therein). However, the regulatory mechanisms involved in this regulation are still unclear (Grün et al., 2006; Leitner et al., 2009). NO appears to modulate the response of phytohormones, involved in pathogen-induced stomatal movements via S-nitrosylation of K^+ outward channels (Sokolovski et al., 2004; Melotto et al., 2006). An opposite function of NO-mediated S-nitrosylation in apoptosis is connected with cytosolic glyceraldehyde 3-phosphate dehydrogenase (GAPDH) inactivation. The role of metal nitrosylation in plants has not been revealed yet, but it seems that cytochrome P450s could be a target (Leitner et al., 2009). NO can easily neutralize harmful O_2^- to form peroxynitrite ($ONOO^-$); $ONOO^-$ can further react with tyrosine residues by nitration, thereby enhancing tyrosine residue containing proteins' susceptibility to proteolysis (Grune et al., 1998; Souza et al., 2000). Tyrosine nitration is associated with disease resistance response (Sailto et al., 2006; Romero-Puertas et al., 2007; Cecconi et al., 2009), plant resistance to abiotic and biotic stresses, but is also important for normal growth, fertility and reproduction of plants (Rusterucci et al., 2007; Lee et al., 2008; Leitner et al., 2009).

The following pathways of NO scavenging have been considered in plant cells. NO can be transformed to nitrate by non-symbiotic haemoglobins under hypoxic stress (Perazolli et al., 2004), providing cells with NO_3^-, an important nutrient which acts as a signal for plant growth and regulates of genes expression (Crawford and Glass, 1998 and reference therein; Stitt et al., 2002 and reference therein). NO can easily react with glutathione (GSH) to form S-nitrosolated glutathione (GSNO). Further, GSNO can be used as a NO storage pool and/or act a transnitrosylation agent, or can be reduced by S-nitrosoglutathione reductase (GSNOR), producing oxidised glutathione

(GSSG) and NH_3. Great significance is attributed to the reaction of NO with superoxide to form $ONOO^-$, which can be detoxified by peroxiredoxins with nitrite production or react with tyrosine residues. Resistance during biotic and abiotic stresses appears to be associated with NO-mediated GSNO formation and transport in systemic stress signalling, as well as tyrosine nitration (Saito et al., 2006; Corpas et al., 2008).

4.4.1. Microbial NO and plant pathogenesis

Plant-pathogenic *Streptomyces* spp. produce endogenous NO catalysed by the bNOS enzyme at the host-pathogen interface, and is induced by cellobiose, a disaccharide product of cellulose degradation (Johnson et al., 2008). In fact, bNOS-derived NO is used for nitration of thaxtomin A, a dipeptide phytotoxin), which inhibits cellulose biosynthesis (Johnson et al., 2008; Fry and Loria, 2002; Scheible et al., 2003). Since NO can easily diffuse through biological membranes and is also well known as a defence and signalling molecule in plants, the NO produced by *Streptomyces* spp. in response to the degradation of the host plant cell wall is likely to penetrate into plant tissues, thereby affecting the plant signalling systems (Johnson et al., 2008).

4.4.2. Soil microbial NO and plant root processes

NO plays a significant role in legume-rhizobium symbiosis, since both plant and bacteria are involved in production and metabolism of NO

(Meilhoc et al., 2011). NOS-like activity was observed in free living rhizobia under anaerobic condition (Pii et al., 2007) as well as during the symbiosis establishment phase (Meilhoc et al., 2011). In mature N_2-fixing nodules denitrification and the plant NR/mitochondrial electron transport chain (ETC) system seem to be basic NO sources under micro-oxic condition (Sanchez et al., 2010; Horchani et al., 2011). Signalling functions of NO are attributed to the expression of genes involved in nodule organogenesis, C- and N-metabolism, redox response, and cell division (Cooper, 2004; Frendo et al., 2005; Pii et al., 2007). It also has been shown that functional nodules of *Glycine max* (Meakin et al., 2007), and *Medicago truncatula* (Horchani et al., 2011) increased their NO production under oxygen limiting condition.

In greenhouse experiments it was shown that the rhizosphere NO concentration modulated uptake of N compounds by tree roots (Simon et al., 2009, 2013). It is therefore assumed that soil microbial NO is sensed by roots and acts as a signal determining the competitive strength of roots in the acquisition of N sources from the soil. At the ecosystem level, this signalling function of NO appears highly important, particularly in low N soils, since plant root and bacteria compete for the same inorganic and organic N sources (Stoelken et al., 2010). It is currently unknown if N acquisition by mycorrhizal fungi is also subject to bacterial NO mediated modulation. It is also unclear if this signalling process is based on root surface interactions or requires NO influx into the root. Since NO action is thought to take place at the level of posttranslational protein modification (Leitner et al., 2009), it is feasible that NO of microbial origin acts on the outer surface of the plasmalemma on transmembrane proteins responsible of N transport processes. If microbial NO would pass the plasmalemma, it would directly interact with plant responses to abiotic stress such as salinity, high temperature, high light intensity and anoxia. These environmental factors are all subject to signalling by posttranslational modifications mediated by NO internally produced by plants (Leitner et al., 2009). Therefore, it appears that a clear separation of external NO of bacterial origin and internally produced NO is highly desirable for the interaction of plants with its ever changing environment. Still NO influx into the roots is likely to take place, since other trace gases of soil microbial origin such as CH_4 and N_2O, are subject to root influx, plant mediated transport, and release from the shoot into the atmosphere (Schütz et al., 1991; Butterbach-Bahl et al., 1997; Machacova et al., 2013). The contribution of this pathway to the release of soil microbial NO into the atmosphere is currently unknown. It also remains to be analysed if some of the NO produced inside plant cells is emitted into the atmosphere.

5. Conclusions

New approaches and techniques, e.g. stable isotope labelling, inhibitor application, gas-flow-soil-core and chamber methods, “omics” technologies, have improved existing understanding and have discovered new mechanisms of N transformation leading to NO production. It is likely that archaea are important players involved in processes related to ammonia oxidation especially in NH_4^+-poor and/or acid environments. It has clearly been demonstrated that:

(a) nitrite is the main precursor for NO under both oxic and anoxic condition, but sources for NO_2^- can be linked either to oxidative or reductive microbial N transformation pathways;

(b) ammonium is the dominant (70%) source of NO under aerobic condition, which confirms previous reports that nitrification is the prevailing process responsible for soil NO production;

(c) nitrate is a dominant (87%) source of NO under anoxic condition, which elucidates the significant role of denitrification in NO production;

(d) nitric oxide is a free (and non-enzyme-bound) precursor for N_2O under anaerobic conditions, thereby confirming the “diffusion limitation” hypothesis.

Our literature review suggests that NO/N_2O emission ratios are possibly not good predictors of the NO production pathway (nitrification or denitrification). There is some evidence that periplasmic and cytoplasmic DNRA may produce NO, but the significance at ecosystem level needs to be studied. Codenitrification process has been shown to mediate NO production by denitrification. Significance of NO for the anaerobic processes anammox and N-AOM has been elucidated as well as the potential importance of NO loss/leakage; the latter urgent needs for further investigations.

We have described a theoretically feasible unspecific enzymo-oxidative mechanism of NO production in soils, which suggests that not only nitrifying and denitrifying microbes produce NO, but that also extracellular enzymes from a wide range of microorganisms could influence NO production.

NO is a signalling molecule due to its ability to diffuse freely across biological membranes, hence it can directly or indirectly (via RNS) modulate the activities of cellular and extracellular proteins in various groups of organisms, implementing significant physiological functions.

NOS seems to be a ubiquitous trans-species enzyme (although its presence in plants has not been confirmed yet), which is responsible for NO synthesis in various organisms. However, role of NO production via NOS in ecosystem functioning is unknown.

In bacteria NO production is associated with a defence function in early stages of infection. At the same time NO produced by the host organism is part of its protective system against pathogens. Furthermore bNOS-derived NO from non-pathogenic and opportunistic bacteria can diffuse to host cells and can be used by a host for a wide range of physiological purposes, i.e. cause beneficial effect on inter-organismic level.

A new role of soil microbial NO in determining the competition between microbial and plant use of soil nitrogen resources has been recently suggested, but still requires validation at the field and identification on the mechanisms involved. In addition, the role of plants in mediating the exchange of microbial NO into the atmosphere requires further investigations.

A wide range of prokaryotes and eukaryotes are able to produce NO by multiple pathways for its own purposes, since each cell needs a sufficient amount of NO for its normal physiological functioning. However it is unknown to what extent cells rely on NO produced by exogenous processes. Detailed studies of the cellular NO demand in physiological processes will provide a closer understanding of NO exchange at the cellular and the organismic level.

Many NO consumption pathways have been described, both abiotic (e.g., nitrosation and possible reaction with SOM in soil; reactions in soil-atmosphere surface) and biotic processes (e.g., denitrification, codenitrification, anammox, N-AOM, detoxification, for physiological purposes).

Detailed investigations are needed to clarify molecular mechanisms of NO production and consumption, its controlling factors, and the significance of NO as a regulator of microbial, animal and plant processes in order to gain a better understanding of soil NO emissions to the atmosphere.

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Figure captions and Tables

Fig. 1. Example of models simulating the temperature effect on nitrification rates (adopted from Stark, 1996). Curves were reconstructed using coefficients for temperature response functions, taken from Stark (1996) [Table 1, p. 440] for open grassy interspaces with the temperature optimum of 35.9 ˚C.

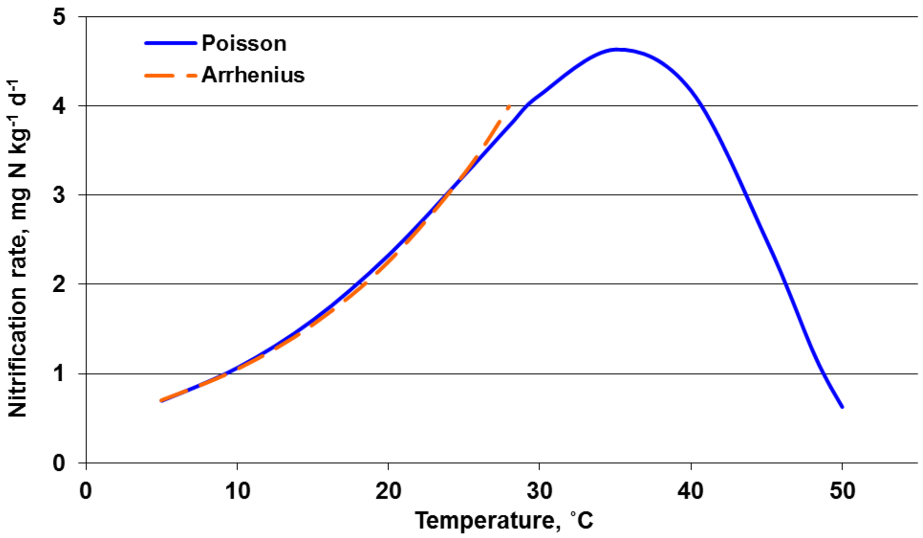
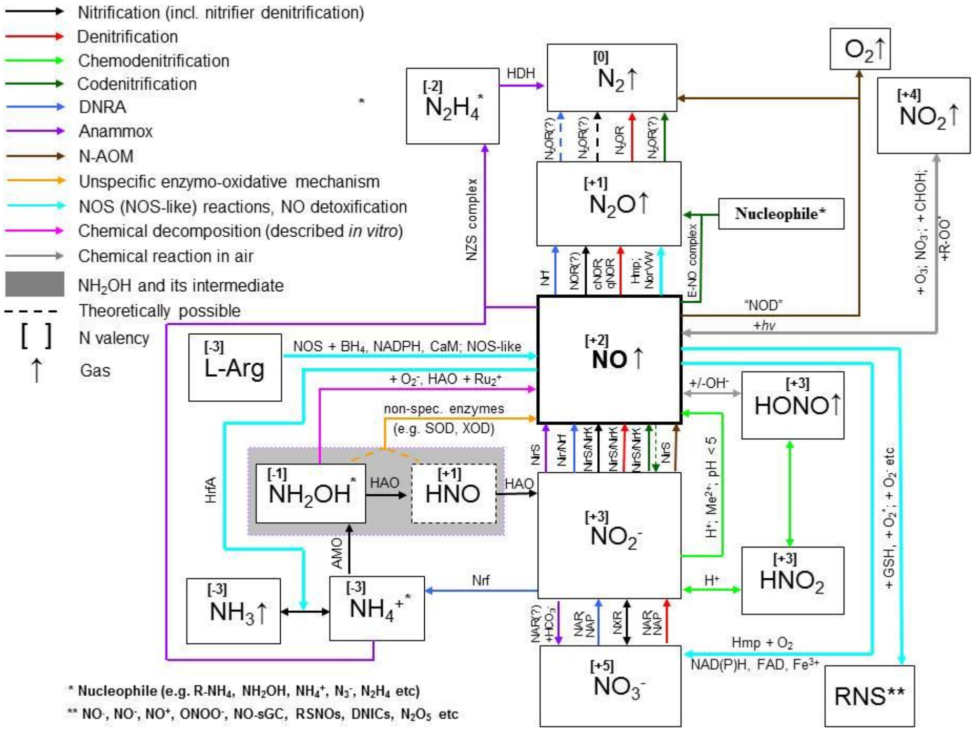


Fig. 2. Schematic diagram of NO transformations mediated by microbial, enzymatic and chemical processes in soils.

DNRA (dissimilatory nitrate reduction to ammonium); anammox (anaerobic ammonium oxidation); N-AOM (nitrite-dependent anaerobic oxidation of methane); RNS (reactive N species); enzymes: AMO (ammonia monooxygenase); HAO (hydroxylamine oxidoreductase); NAR (membrane-bound nitrate reductase); NAP (periplasmic nitrate reductase); NirK (copper-containing nitrite reductase); NirS (cytochrome *cd*1 nitrite reductase); NirB (cytoplasmic nitrite reductase); Nrf (cytochrome *c* nitrite reductase); NrfA (periplasmic cytochrome *c* nitrite reductase); NXR (nitrite oxidoreductase); cNor (nitric oxide reductase that accepts electrons from c-type cytochromes); qNor (nitric oxide reductase that accepts electrons from quinols); NorVW (flavorubredoxin), Hmp, (flavohemoglobins); N_2OR (nitrous oxide reductase); HZS complex (hydrazine synthase enzyme complex); HDH (hydrazine dehydrogenase); “NOD” (undefined hypothetical nitric oxide dismutase); NOS (nitric oxide synthase); SOD (super oxide dismutase); XOD (xanthine oxide dismutase); E-NO complex (enzyme (E) bound NO complexes, e.g. E-NO, E-NO^- and E-NO^+, which mediates biotical N-nitrosation).



* Nucleophile (e.g. R-NH_4, NH_2OH, NH_4^+, N_3^-, N_2H_4 etc)

** NO, NO^-, NO^+, $ONOO^-$, NO-sGC, RSNOs, DNICs, N_2O_5 etc

Table 1. Emission rates and sources of nitric oxide under a range of oxygen concentrations (from Russow et al., 2009).

O_2 content (vol. %)	Emission (µg N kg^{-1} h^{-1})	NO formation from[a]		
		NH_4^+ (%)	NO_3^- (%)	NH_4^+ + NO_3^- (%)
20.0	0.92±0.35	70	10	80
2.0	1.16±0.24	26	53	79
0.3	1.90±0.88	1.7	81	83
0	3.71±1.40	0	87	87

[a] standard error of the mean (1σ), n=6

Table 2. Pathways of NO production in plants (Gupta et al., 2011 and reference therein).

Reductive pathways	**Oxidative pathways**
Nitrate reductase (NR)	Nitric oxide synthase (NOS) -like activity
Plasma membrane-bound nitrite: NO reductase (NiNOR)	Arginine-dependent, polyamine-mediated NO Production
Mitochondrial nitrite reduction	Hydroxylamine-mediated NO production
Xanthine oxidoreductase in plant peroxisomes	

Table 3. Positive and negative effects of NO and its derivatives in mammals.

Effect/function	Agent	Location	Reference
Positive effect			
Vasodilation (vascular smooth muscle relaxation)	Formation of NO-sGC or (NO)$_2$-sGC complexes, with releasing of His-105 triggers various cellular signalling pathways (e.g. cGMP formation with further cGK, PDE and iongated channels regulation)	Endothelium eNOS-derived NO could immediately diffuse across the cell membrane to smooth muscle cells	Li and Forstermann, 2000; Derbyshire and Marletta, 2009; Martin et al., 2012
Neurotransmission			
Vasoprotection via inhibiting platelet aggregation			
Stimulating smooth muscle proliferation			
Protection against atherogenesis on its early stages, preventing leukocyte adhesion to the vascular endothelium			
Protective function via cytotoxic effect on intracellular bacteria, cancer cells and tumor tissues	NO-mediated	Activated macrophages	Nathan and Hibbs, 1991; Wei et al., 1995; MacMicking et al., 1997; Forstermann and Sessa, 2012; Rahmanto et al., 2012;
Cardioprotection (e.g. against ischemic and reperfusion injury)	NO-mediated	Cardiocytes	Bolli et al., 2007; West et al., 2008; Granfeldt et al., 2009; Talukder et al., 2010
Antitumor activity	NO-mediated via reduced glutathione (GSH)	multidrug resistance protein (MRP) 1 channel in various cells	Richardson et al., 1995; Li et al., 2011b;
Neuroprotection			
Regulating release of several neuromodulators in the developing retina (e.g. glutamate, gamma-aminobutyric acid (GABA), glutamine, ascorbate)	NO as an atypical retinal messenger	Retina	Ientile et al., 1996; Maggesissi et al., 2009; Portugal et al., 2012
Negative effect			
Cytotoxicity (e.g. reaction with proteins and nucleic acids), leading to apoptosis and cell death	Overproduction of NO	Various types of cells	Boje and Arora, 1992; Dimmeler and Zeiher, 1997; Kroncke et al., 1997; Gotoh and

			Mori, 2006; Erusalimsky and Moncada, 2007; Forstermann and Sessa, 2012;
Attenuation of energy production by inhibiting mitochondrial respiration and glycolysis	Overproduction of NO	Mitochondria and cytoplasm	Erusalimsky and Moncada, 2007; Brown, 2010;
Neurodegenerative disorders and cerebral infarction	Overproduction of NO by activated macrophages or microglia cells	Neurons	Chao et al., 1992; Kroncke et al., 1997; Ignarro, 2009;
Septic shock due to vasodilation and hypotension	Overproduction of NO	Vascular system	Wong and Billiar, 1995; Lange et al., 2009;
Pathogenesis of Type I diabetes due to NO induced islet cell death	Overproduction of NO	Endocrine system	Oyadomari et al., 2002
Apoptosis due to eliminating Ca^{2+} from endoplasmic reticulum	Overproduction of NO	Pancreatic β-cells	Oyadomari et al., 2001, 2002
Damaging DNA, proteins and lipids	NO-mediated oxidative reaction products (e.g. $ONOO^-$)	Various types of cells	Lee et al., 2003; Mikkelsen and Wardman, 2003; Ridnour et al., 2004
Brain pathology		Neurons	Brown and Neher, 2010
Myocardial injury		Cardiocytes	Wang and Zweier, 1996; Zweier and Talukder, 2006

3555