Chapter 14

MICROBIAL NITRIC OXIDE, NITROUS OXIDE AND NITROUS ACID EMISSIONS FROM DRYLANDS

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1 INTRODUCTION

Reactive nitrogen compounds (N_r, which include NO_x (i.e. $NO+NO_2$), N_2O, ammonia and HONO) have a large impact on atmospheric chemical composition and thus, on climate. Nitric oxide (NO) is a chemically reactive trace gas that reacts with ozone (O_3) to form NO_2 (Crutzen, 1979). The formation of O_3 depends on a sensitive relationship between NO_x ($NO+NO_2$) and volatile organic compounds (VOC) (Sillman et al., 1990). Thus, even trace levels of NO_x can activate O_3 production. O_3 itself can enrich the troposphere and as a short-lived climate pollutant (SLCP) can affect the climate (Shoemaker, et al., 2013). Nitrous oxide (N_2O) is among the most important greenhouse gas, together with H_2O, CO_2 and CH_4. N_2O has a relatively long lifetime, is enriched in the troposphere and impacts the earth's radiative balance (Ciais et al., 2013). When N_2O enters the stratosphere, it reacts with O_3 to NO, thereby depleting the ozone layer (Crutzen, 1979).

In 2005, a total of about 187 Tg N reactive nitrogen compounds (N_r) were emitted into the atmosphere (Galloway et al., 2008). Deposition of atmospheric N_r in a dryland ecosystem was 29.3 kg N ha^{-1} yr^{-1} (Sickman et al., 2019). The deposition of N-acids, which is commonly referred to as acid rain, leads to an increase in acidification in terrestrial and aquatic ecosystems (Galloway, 1995). Globally, 8.9 Tg N yr^{-1} NO_x and 9.4 Tg N yr^{-1} N_2O (natural soils and agriculture) are released from soils into the atmosphere (Denman et al., 2007). NO_x emissions from soils are on the order of about one third of overall anthropogenic sources, which originate from burning of fossil fuel from car engines and industrial processes (Denman et al., 2007). The N_2O emissions from soils are the strongest global source where 0.7% and 0.9% of N-fertilizer is released as NO_x and N_2O, respectively (Bowman et al., 2002b). Continuous acceleration of the nitrogen cycle will result in an increased pollution of air, soils, and water and mitigation strategies for sustainable protection of the environment and human health are needed (Galloway et al., 2008).

A global inventory of NO emissions from soils, based on 112 studies with 583 NO_x emission rates worldwide, has been provided by Steinkamp and Lawrence (2011). Their estimate of the global NO soil source strength is 8.6 Tg N yr^{-1}, which is very close to the most recent IPCC (2007) estimate of 8.9 Tg yr^{-1}. Data from field measurements for NO emissions from desert soils are limited (McCalley and Sparks 2008; Hartley and Schlesinger, 2000). However, more than 40% of the surface area of the earth is covered by drylands (UNEP, 1997) and thus, the study of N_r emissions from semi-arid and arid ecosystems is of great importance. Recently it was discovered that especially alkaline soils from semi-arid and arid ecosystems can emit

nitrous acid, HONO (Oswald et al., 2013). When exposed to solar radiation (and more specifically to radiation at the wavelength of $\lambda=578$ nm), HONO is an indirect source of NO in the atmosphere due to photolysis to the hydroxyl radical (OH) and NO.

Additionally, soils from irrigated agriculture in all drylands are heavily fertilized and release high NO emissions, thereby affecting regional air quality (Behrendt et al., 2017). In this chapter, a description of recent discoveries and advances in the processes of the biogeochemical N-cycle and their relationship to environmental parameters is presented, followed by a discussion pertaining to current advances in NO and N_2O emissions from semi-arid and arid lands.

2 BIOGENIC EMISSION OF NO, N_2O AND HONO FROM SOILS, CRYPTOGAMIC COVERS AND PLANTS – GENERAL ASPECTS

Microbes are able to enzymatically produce and consume both, NO and N_2O in soils (Conrad, 1996). It is widely accepted that nitrification and denitrification are the predominant processes responsible for NO and N_2O release. However, the re-cycling of N_r within soils due to simultaneous microbial consumption, is likely to be small. For natural dryland soils, studies have detected only very low rates of NO consumption (Behrendt et al., 2014). There is evidence that thin biofilms of lichens and mosses pre-dominantly covering the top soil layer in drylands, which are called cryptogamic covers or biocrusts, release globally 0.6 Tg N yr^{-1} HONO, 1.1 Tg N yr^{-1} NO (Weber et al., 2015), and about 0.3 Tg N yr^{-1} N_2O (Lenhart et al., 2015). These biocrusts are micro-scale films and are habitat for various microbes. With an increase in crust development, inorganic nitrogen typically increases (Kidron et al., 2016), consequently affecting gaseous N-oxide-emissions. It was also found that the abundance of ammonia oxidizing Archaea (AOA) increases with aridity as indicated by quantification of their *amoA* (encoding the ammonia monooxygenase, AMO) genes (Delgado-Baquerizo et al., 2016). Recently, it was found that biocrusts can drive NO emissions from dryland soils under limited soil moisture (Behrendt et al., 2017). A moisture dependent response of nitrifying microbial communities to wetting of dry soil was also reported by an earlier study (Placella and Firestone, 2013), where the samples dried in the laboratory. More of such timely studies, where flux measurements are combined with molecular techniques, are needed to identify the biogeochemical processes responsible for sources and sinks of N-gases (see Chapter 3). This newly emerged research field is referred to as gas metabolomics or "volatilomics" (e.g. Insam and Seewald, 2010).

NO and N_2O fluxes are controlled by various environmental parameters such as: (i) gaseous diffusion (e.g., oxygen, carbon dioxide), (ii) substrate diffusion, (iii) soil temperature, (iv) soil moisture, (v) ambient mixing ratio of NO and N_2O, (vi) soil properties, e.g. pH, carbon content, redox potential (Butterbach-Bahl et al., 2013; Pilegaard, 2013). There is an urgent need to understand the potential negative and positive contributions of soil microbes to soil-atmosphere exchange of trace gases and complex microbe-microbe, microbe-environment and microbe-plant interactions with a focus on climate change (Bardgett et al., 2008). In dryland soils, soil temperature and soil moisture are highly variable and affect microbial activity (Chapter XX; Moyano et al., 2013; Behrendt et al., 2014; Behrendt et al., 2017), thereby causing variability in NO and N_2O fluxes in time and space. Since the focus of this review is on NO and N_2O emissions from drylands, where coverage of plants is sparse or absent, emissions from plants will only be briefly discussed. There is indication that plants emit N_2O during photosynthesis (Lenhart et al., 2018; Smart and Bloom, 2001; Hakata et al., 2003; Dean and Harper, 1986; Goshima et al. 1999), but this process is not yet considered on a

global scale (Denman et al., 2007). While earlier studies report compensation point concentrations (production and consumption are balanced resulting in a zero net flux) for NO_2 from plants, recent studies provide evidence that these compensation point concentrations are very low if at all existing (Breuninger et al., 2012 and references therein; Chaparro-Suarez et al., 2011). This suggests that plants act predominantly as a small NO_2 sink.

Given the small quantities of NO and N_2O emissions from drylands, monitoring of these emissions poses a challenge because monitoring of these emissions requires a large instrumentation setup. The most frequent techniques to measure NO and N_2O are: (i) dynamic and static chambers in laboratory incubations (Behrendt et al., 2014), dynamic and static chambers in the field (Pape et al., 2009; Hutchinson and Moiser, 1981), and eddy covariance (Rummel et al., 2002; Eugster and Merbold, 2015). Recent developments in instrumentation provide highly sensitive chemiluminescence trace level analysers (Behrendt et al., 2014), quantum cascade laser absorption spectroscopy (including the measurement of isotopologues for N_2O) and fiber-enhaned Raman spectroscopy (Keiner et al., 2015), as well as ground based and satellite born sensors (Mamtimin et al., 2015; Mamtimin et al., 2016). Comparisons between the methods showed a good agreement between e.g. (i) soil chambers with gradient method (Parrish et al., 1987), (ii) soil chambers with laboratory incubations (Ludwig et al., 2001), and (iii) laboratory incubations with remote sensing techniques (Mamtimin et al., 2015).

2.1   SOIL-ATMOSPHERE EXCHANGE OF NO, N₂O AND HONO: PROCESSES

Soil processes are classified into abiotic (reactions based on chemical and physical principles) and biotic processes (that involve microbial metabolism). Abiotic formation of NO occurs in acidic and organic rich soils (Homyak et al., 2017), whereas abiotic formation of N_2O is based on the interaction between pH, organic matter, and MnO_2 (Liu et al., 2016). However, there is still a need to combine flux measurements with additional analysis of composition and diversity of microbial community characteristics (Butterbach-Bahl et al., 2013; Pilegaard, 2013) to gain a full understanding of abiotic processes. Linking flux measurements to the activity of certain microbial groups (Behrendt et al., 2017; Kolb and Horn, 2012) may be useful to improve biogeochemical processes in models. Within the N-cycle, microbes utilize a set of oxygen-demanding and oxygen sensitive enzymes, which either produce or consume NO and N_2O (Klotz and Stein, 2011). Thus, NO and N_2O are intermediates of the N-cycle subject to rapid microbial turnover. The expression of specific genes, e.g. bacterial *amoA,* or *narG/nosZ* (encoding nitrate and nitrous oxide reductases) can be used as a proxy for the activity of ammonia oxidizing and denitrifying bacteria, respectively (e.g. Behrendt et al., 2017; Palmer et al., 2016). Such proxies have been established for all major microbial groups involved in the N-cycle in soils. However, there is still an ongoing discussion to what extent these results reflect enzyme synthesis (Rocca et al., 2015; Blazewicz et al. 2013). The soil-atmosphere exchange of NO and N_2O is a result of the metabolism of various microbial groups, and variations that occur in gas exchange at the microsite scale consequently matter. Nevertheless, regional gas exchange is controlled by variations in environmental parameters. Therefore, abiotic and biotic processes (for overview see fig. 1) and environmental parameters are considered next.

2.1.1   *Chemodenitrification*
The abiotic production of NO and N_2O, but also other reactive N-gases such as NO_2 and methyl nitrite, was reported for soils with low pH (pH < 5.5), and high concentrations of iron cations (Fe^{2+}) and organic matter (Van Cleemput and Samater, 1996). There is evidence that

in drylands, where water is limited, a shift from biotic to abiotic processes for NO production occurs (Homyak et al., 2017; McCalley and Sparks 2009). About two decades ago, Venterea et al. (2000) stated that for improved NO/N_2O modelling, it is necessary to understand the abiotic reactions involving liquid NO_2^-/HNO_2 and gaseous NO_2/HONO. A recent study suggests that quinone redox chemistry is mediating NO_2 conversion to HONO and highlights abiotic processes at the soil surface (Scharko et al., 2017). Microbially produced hydroxylamine can react in the gas phase on mineral surfaces to form HONO (Ermel et al., 2018). Manganese dioxide (MnO_2) acts as a strong oxidant in soils and therefore pays a central role in N_2O formation from hydroxylamine (Liu et al., 2016).
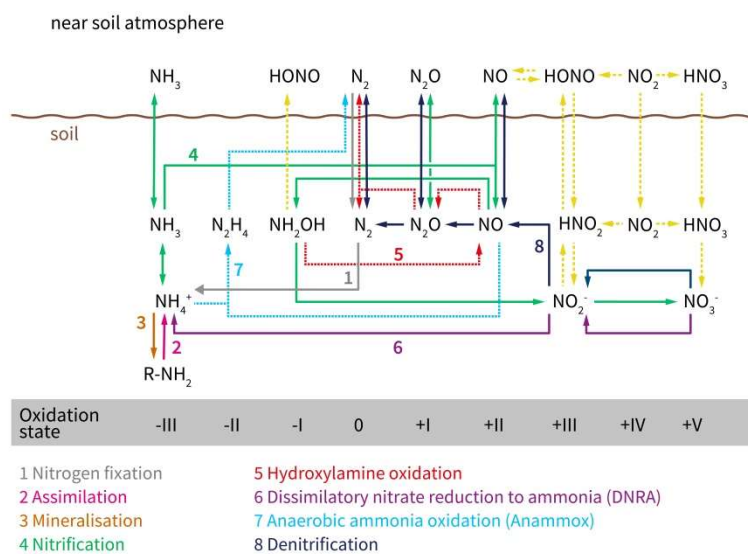

Figure 1:   *The major processes of the biogeochemical nitrogen cycle (modified from Su et al., 2011 and Klotz and Stein, 2011). Note that arrows for hydroxylamine oxidation and HONO release mechanisms are in dots, since the portion of abiotic and biotic contribution are unclear. The anaerobic ammonia oxidation (Anammox) arrows are dotted, since the importance of this process in soils is unclear.*

2.1.2   Biological nitrogen fixation (BNF)

The atmosphere provides a stable pool of N_2 for biological N-fixers. However, the large investment of energy required for BNF (Madigan et al., 2012) might be a reason why N-fixing microorganisms (i.e., diazotrophs) are not successful in utilizing their advantage compared to non-diazotrophs even in N-limited ecosystems. N-assimilation outweighs N-depositions by far in many ecosystems like N-limited wet- and drylands (Knorr et al., 2015; Borken et al., 2016; Larmola et al., 2013; Aranibar 2003; Su et al., 2011). Such ecosystems depend on N-fixing microorganisms (i.e., diazotrophs) that provide N_r to other organisms including plants for assimilation. Symbioses of diazotrophs with plants might accelerate N fixation dramatically. BSC of drylands host a symbiotic microbial community that likewise depends on the transfer N from diazotrophs that are active over a wide range of temperatures and moisture contents (Aranibar et al., 2003) contribute to ecosystem resilience in drylands. Diazotrophy can indeed be the major source of reactive N in such systems (Su et al., 2011),

demonstrating that diazotrophs are corner stone organisms in drylands. The increase of biological N fixation from 44 Tg N yr^{-1} in the pre-industrial period to about 195 Tg N yr^{-1} (Cleveland et al., 1999) suggests that anthropogenic alteration of the N-cycle has been larger than previously assumed (Vitousek et al., 2013). Land-use change in drylands decreases biological nitrogen fixation from natural soils, especially from conversion of late to early successional stages of biological soil crusts that routinely show diazotrophic activities (Housman et al., 2006; Belnap, 2002).

2.1.3   Nitrification

Nitrification is the microbial oxidation of ammonia to nitrate. Most nitrifiers are autotrophic organisms and thus use carbon dioxide as their source of carbon. The first microbial group is ammonia oxidizing bacteria (AOB), which performs the oxidation of ammonia, via hydroxylamine, to nitrite (Ward et al., 2011). The enzymes are ammonia monooxygenase (AMO) and hydroxylamine oxidoreductase (HAO). Hydroxylamine has been discovered as an obligate intermediate long ago (Lees, 1952), whereas NO as an obligate intermediate was discovered just recently (Lancaster, 2017). Thus, the search for a third enzyme in the biological oxidation of ammonia to nitrite continues. The second group is ammonia oxidizing archaea (AOA), which is challenging to cultivate (Könneke, et al., 2005; Jung, et al., 2011). Differences in metabolism, kinetics, and specialization to ecosystems and environmental parameters lead to the question of niche differentiation of AOB and AOA (Prosser and Nicol, 2012; Hatzenpichler, 2012; Martens-Habbena et al., 2009). AOB can utilize enzymes that are homologous to denitrifier enzymes that reduce NO_2^- to NO and further to N₂O (Casciotti and Ward, 2001; Casciotti and Ward, 2005). This process is referred to as nitrifier denitrification (Wrage-Monnig et al., 2018; Kool et al., 2011). The third group is nitrite oxidizing bacteria (NOB), which convert nitrite to nitrate via the enzyme nitrite oxidoreductase, NXR (Sorokin et al., 2012). It is thought that AOB and AOA are main producers of NO and N₂O compared to NOB. The exhalation of NO and N₂O is being investigated for decades (Galbally and Roy, 1978; Lipschultz et al., 1981). HONO, a new indirect source of NO, was discovered (Su et al., 2011; Oswald et al., 2013). The latter is a product of AOB and AOA metabolism (Scharko et al., 2015), but produced from a heterogeneous reaction of gaseous hydroxylamine on the soil surface (Ermel et al., 2018). Recently, complete ammonia oxidizers (COMAMMOX) have been discovered, which are capable of complete nitrification (Van Kessel et al., 2015; Daims et al., 2015). For completeness, heterotrophic nitrification (HN) is included here. Dominant HN was found most likely due to saprophytic and fungal activity in acidic coniferous forest soils (Zhang et al., 2011), where conditions for other nitrifiers are unfavorable. In such ecosystems HN could dominate NO and N₂O exchange.

2.1.4   Denitrification

Complete denitrification is the microbial reduction of nitrate (NO_3^-) to N₂ via nitrite (NO_2^-), NO and N₂O as the obligatory intermediates (Knowles, 1982). Denitrifiers are facultative organisms that preferentially respire oxygen and switch to denitrification when oxygen becomes limiting and N-oxides are available (Zumft, 1997). In soils, various groups of denitrifiers have been identified, including a phylogenetically highly diverse group of mostly heterotrophic bacteria (Philippot et al., 2007; Philippot et al., 2009; Palmer et al., 2010; Palmer et al., 2012; Palmer and Horn, 2012; Palmer and Horn, 2015), fungi (Kobayashi et al., 1996), some archaea (Zumft, 1997), as well as algae, lichens and mosses in soil crusts (Barger et al., 2013). The denitrifying enzymes are nitrate reductase (NAR), nitrite reductase (NIR), NO reductase (NOR), and N₂O reductase (NOS, Philippot, 2002; Zumft, 1997). The study of the activity of these enzymes in soils and their controls is partly limited by experimental

methods (Gross and Bemner, 1992; Bollmann and Conrad, 1997). For example, it is almost impossible to differentiate denitrification from nitrification derived N_2O production in the field. For details about diversity, structure and size of the denitrifier community, the reader is referred to a more comprehensive review (Braker and Conrad 2011, and references therein). The regulation of the expression of denitrification associated genes, which have been identified for N_2O production and consumption, is dependent on oxygen and NO concentration (Spiro, 2012; van Spanning et al., 2007). Denitrification is promoted under microaerophilic and anoxic conditions, e.g. in anoxic microsites. pH is an important parameter affecting gene abundance, transcription and denitrification kinetics (Liu et al., 2010) as well. There is indication that water absorption on decomposing plant residues and the presence of pores > 35 μm in diameter create N_2O hotspots on a microscale in soil (Kravchenko et al., 2017; Schlüter et al., 2018). N_2O consumption and the different microbial groups capable of this process and their controls by environmental parameters is not yet well understood (Kolb and Horn, 2012; Chapuis-Lardy et al., 2007). Recent flux measurements are now more often accompanied either by molecular analysis and/or ^{15}N and ^{18}O isotopic measurements to increase the understanding of which process dominates the NO and N_2O exchange.

2.1.5   Other microbial processes relevant for N-gas exchange
One prominent example is the aerobic consumption of NO performed by methanotrophs, which links the N and C cycle in the gas phase (Stein and Klotz, 2011; Ren et al., 2000; Krämer et al., 1990; Bender and Conrad, 1994). Anaerobic ammonia oxidation is a process similar to denitrification, where ammonia is converted via NO_2^- to produce N_2 (Strous et al., 2006; Strous et al., 1999), which has an important role in the N-cycle in the oceans (Ward, 2003). The importance of this process for N-cycling in soils is not yet known. Codenitrification (Spott et al., 2011) and dissimilatory nitrate reduction to ammonia (DNRA) are mentioned here for a complete review, but due to low organic matter and lack of moisture their importance in dryland soils is expected to be low and thus is not further discussed.

2.1.6   Transport processes in soil, canopy and surface boundary layers
For microbial activity (as approximated by CO_2 production here), a single optimum function at intermediate soil moisture (volumetric water content approximately $\theta_v = 0.5 \times \varepsilon$, where ε equals the total porosity, saturated water content) was found (Skopp et al., 1990; Moyano et al., 2013). This single optimum function is shifted to low soil moisture for NO and HONO emissions (Oswald et al., 2014). Thus, it seems likely that this pattern in NO and HONO emissions is controlled by abundance and activity of the nitrifying community. An additional controller might be CO_2 diffusion, since most nitrifiers are autotrophs. For some soils, a bimodal distribution of NO emission was observed, with one maximum at low water content and the other at high water content (Yu et al., 2008; Behrendt et al., 2017). It was demonstrated by gene expression that nitrifier and denitrifier contribute to this bimodal distribution (Behrendt et al., 2017). More energy-rich organic substrates are available under high moisture conditions, thus promoting activity of heterotrophs including denitrifiers, and NO and O_2 diffusion coefficients are very low at about 2×10^{-9} m^2 s^{-1} (see Table1). The latter promotes the enrichment of NO and consumption of O_2 and thus conditions ideal for onset of denitrification.

Once the gases are released from the soil into the atmosphere, they may chemically react, interact with plant canopy, and dilute via mixing and transport. Within the canopy, NO reacts rapidly with O_3 and forms nitrogen dioxide (NO_2). The so-called canopy reduction factor

(CRF) is used to describe the amount of NO_x, which is used to reduce the soil emissions into the free atmosphere due to reactions within the canopy, e.g. stomatal uptake.

Table1: Compilation of diffusion coefficients (D) for oxygen (O_2) and nitric oxide (NO) in air and water.

	D_{O2}	D_{NO}	References
water	2.13×10^{-9} m² s⁻¹	2.21×10^{-9} m² s⁻¹	Goldstick and Fatt (1970); Zacharia and Deen (2005) at 25°C and atmospheric pressure
air	1.82×10^{-5} m² s⁻¹	1.80×10^{-5} m² s⁻¹	Massman, (1998) at standard pressure

2.2 SOIL-ATMOSPHERE EXCHANGE OF NO, N₂O AND HONO:

ENVIRONMENTAL PARAMETERS

In the following sub-sections the most dynamic environmental parameters affecting the production and consumption processes of NO and N₂O will be discussed. Other environmental parameters, such as soil properties (e.g. pH, carbon content, texture) may affect NO and N₂O emissions too, but their dynamics are commonly investigated on a larger scale in time and space (Chapter XX). Agricultural practices (e.g. irrigation, ploughing, liming, burning, herbicide/fungicide applications), however, are commonly only applied at field scale. While for NO emissions from soil into the atmosphere only the top layer of soil is of relevance (Rudolph et al., 1996), much deeper layers are also of relevance for N₂O emissions. In middle to upper soil layers the produced N₂O is partly consumed and only a fraction is released into the atmosphere (filter function).

2.2.1 Nitrogen availability and fertilization
Fertilizer application to increase yields is a common practice to secure food for a growing global population. However, the microbial processes, especially nitrification and denitrification, are dependent on NH_4^+, NO_3^-, and NO_2^- as substrates. Application of fertilizers thus results in agricultural fields emitting more N₂O and NO than natural soils. Within the available literature, various correlations between different nitrogen species and N-gases can be found, however, they are not consistent and very soil specific. One reason may be that nitrogen availability affects N₂O and NO emissions in several ways: (i) the amount of fertilizer (FA), (ii) the amplification factor defined as a dimensionless increase in gaseous emissions compared to a non-fertilized control soil, (iii) an increased temperature response based on fertilization ($Q_{10}F$), and the type of fertilizer (Mosier et al., 1998; Mamtimin et al., 2016). Urea is the predominant nitrogen fertilizer with 54% of overall nitrogen fertilizer used (IFA, 2018). Mixtures of fertilizers, such as diammonium phosphate and coated forms (e.g. polyolefin-coated fertilizers, POCFs) tend to yield lower gaseous emissions (Fechner, unpublished data; Shoji and Kanno, 1994). Based on the N demand the total amount of fertilizer applied in one growing season should be divided with largest amounts applied in stages of rapid growth (Chen et al., 2011). A fertilization factor was applied to laboratory NO measurements, assuming an exponential decay function, to model net potential NO emissions for the growth season 2010 in the field (Mamtimin et al., 2016). Also urine applications (Khan, 2009), wet and dry deposition (Jia et al., 2016) and plant residuals (Harrison et al., 2002) increase gaseous N emission. About 1.0% of N-fertilizer was emitted as NO in a recent study (Steinkamp and Lawrence, 2011), which is similar to 0.9% of N-fertilizer released as

N$_2$O reported from earlier studies (Bouwman et al., 2002a, 2002b). Recent and future focus of studies should be the establishment of management practices for constant yields under optimal N-fertilization to decrease gaseous N emissions (Matson et al., 1998; Ju et al., 2009; Chen et al., 2011).

2.2.2   Soil water content

The relative fluxes of nitrogen trace gases depend on the soil water content (expressed as water holding capacity, WHC, and water filled pore space, WFPS) (Figure 2; Oswald et al., 2013). This conceptual model was proposed by Firestone and Davidson (1989) for NO, N$_2$O, and N$_2$. Diffusion is dependent on soil water content (Skopp et al., 1990), which therefore is an indirect controller of denitrification (e.g. O$_2$ and NO concentration) and nitrification (e.g. O$_2$ and NH$_3$ concentration).
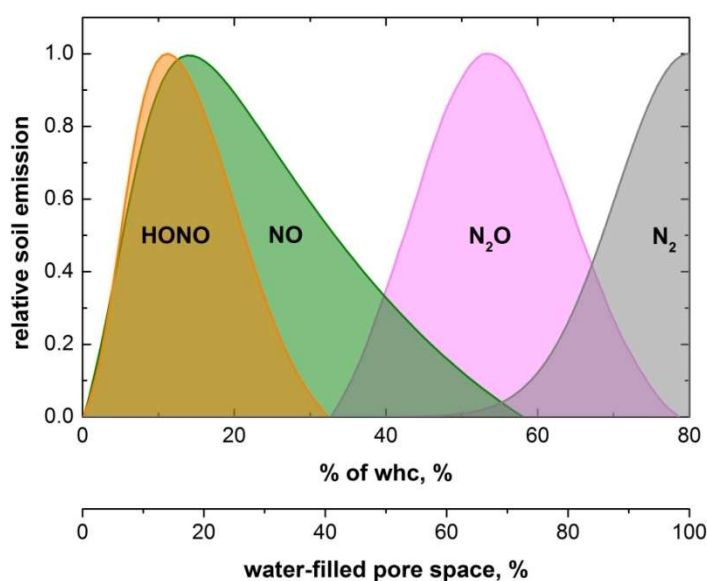

Figure 2:   The relationship between percent soil moisture (expressed as water holding capacity, WHC, and water-filled pore space, WFPS) and the relative fluxes of nitrogen trace gases (from Oswald et al., 2013, adopted from Firestone and Davidson, 1989). Recently a second HONO maximum at high soil moisture was discovered (Wu et al., submitted)

It is well known that at WFPS > 60% denitrification dominates, while at WFSP < 60% nitrification dominates (Davidson 1993). Interestingly, the initiation of HONO emissions was reported at about 33% WHC or 40% WFPS, when N$_2$O emissions decrease to zero (Oswald et al., 2013). There is evidence for a delicate balance between microbial oxidation of Mn$_2^+$ and reduction of Mn oxides (Sparrow and Uren, 2014). It was shown for artificial soil mixtures that the abiotic formation of N$_2$O from NH$_2$OH depends on the Mn-form, pH and organic matter (Liu et al., 2017). However, such studies are lacking to date for natural soils. Thus, it is hypothesized that in natural soils the availability of Mn-form depends on soil moisture and soil temperature (Sparrow and Uren, 2014), affects N$_2$O and potentially HONO formation, and deserves future research. It is also noteworthy that some dryland agricultural soils do not follow the conceptual model of a single NO optimum, but rather show two distinct NO emission maxima (Behrendt et al., 2017).

2.2.3 Soil temperature

Production and consumption of NO and N$_2$O is catalyzed by various microbial enzymes (see sections 2.1.3 and 2.1.4). It is well known that enzymatic reactions can be described with Michaelis-Menten kinetics (Michaelis and Menten, 1913), and are exponentially dependent on temperature. One way to model the relationship of temperature and NO and N$_2$O emissions is the use of a temperature amplification factor, known as the Q$_{10}$-value. It is generally accepted that Q$_{10}$ values for (micro) biological processes under non-limiting conditions (here: water availability and soil substrate) are in the order of 2 to 3 (Schipper et al., 2014). Exponential relationship of soil temperature and NO emissions was first demonstrated in a laboratory experiment (Yang et al., 1996).
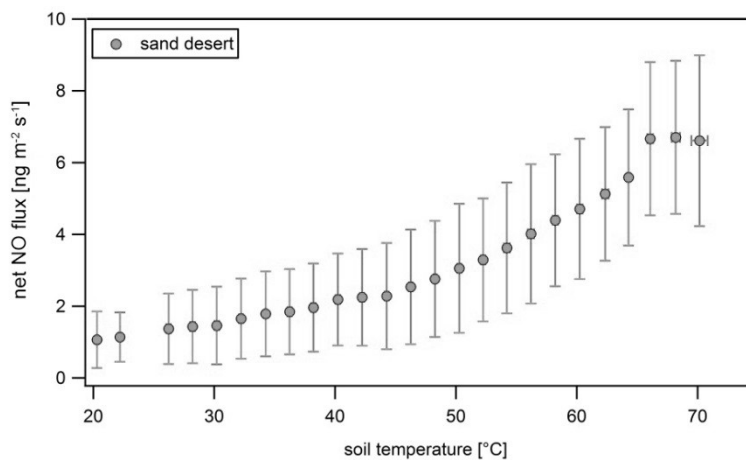

Figure 3: The relationship between soil temperature and the net flux of nitric oxide (NO) determined by laboratory incubation of a bare soil taken from the semi-arid Taklimakan Desert at 0.81% gravimetric soil moisture (close to Sache oasis, Xinjiang, China, N=3).

For a soil sample from the Taklimakan Desert, where gravimetric soil water content in the field was around 0.81%, a similar exponential relationship of NO emissions and soil temperature was found (Figure 3). Q$_{10}$ values for NO emissions from that soil were in the range of 1.4 to 1.6. It is still under debate if these NO emissions at very low soil moisture are of abiotic or microbial origin (Sullivan et al., 2012; Behrendt et al., 2017; McCalley and Sparks, 2009). There is also evidence that different end-products, e.g. N$_2$O and N$_2$, generated by different enzymatic reactions differ in their Q$_{10}$ values by about 2 and 1.4, respectively (Phillips et al., 2014).

2.2.4 Ambient mixing ratio for NO, N$_2$O and HONO

The compensation concentration, c$_{comp}$, bellow which net emissions to the atmosphere occur, was introduced as a critical variable that controls the flux of trace gases in soil-atmosphere exchanges (Conrad, 1994). The use of c$_{comp}$ was suggested for scaling trace gas fluxes in soil-atmosphere exchange (Conrad and Dentener, 1999) and was frequently applied in modelling NO emissions (Bargsten et al., 2010; Feig et al., 2008; Yu et al., 2008; Kirkman et al., 2001). Behrendt and co-workers (2014) have concluded that only NO production can be detected from dryland soils. For a soil sample from a blueberry covered spruce forest (pH 3.2; 41.00%

carbon) they found the lowest c_{comp} of 47 ppb, whereas for a soil sample from the Mongolian Desert they estimated c_{comp} to amount to about 6590 ppb (pH 7.9; 0.96% carbon). It is well known that fungal activity dominates in acidic and organic rich coniferous forest soils (Pennanen et al., 1998). Often heterotrophic activity is related to denitrification (see Section 2.1.4) and therefore c_{comp} might be correlated to different microbial processes. N_2O consumption occurs in soils, even at low pH and atmospheric N_2O concentrations (Kolb and Horn, 2012; Palmer and Horn, 2015; Palmer et al., 2010). N_2O consumption is generally not well understood (Chapuis-Lardy et al., 2007), because N_2O net fluxes are more commonly studied, where it is thought that N_2O production is the main contributor to N_2O emissions. Ultimately isotopic measurements are necessary to disentangle heterotrophic nitrification (Zhang et al. 2011), (complete) denitrification and co-denitrification (Kumon et al., 2002). However, high NO consumption already points towards denitrification and co-denitrification. Moderate c_{comp} values of 506 and 600 ppb have been reported from dryland farming soils in China (Behrendt et al., 2014) and Egypt (Saad and Conrad, 1993), respectively. In dryland agriculture, the lack of organic matter as well as water (irrigation regime, see Mamtimin et al., 2016: about 24h flooding followed by a 2 weekly phase of evaporation) may explain why low abundance and activity of (heterotrophic) denitrifiers have been found in such soils (Behrendt et al., 2017). Low denitrifier diversity and activity was also found for Chilean arid soils (Orlando et al., 2012). HONO fumigation experiments indicate that c_{comp} for HONO is likely the result of multiple processes possibly including microbial processes, chemical reactions on the soil surface and adsorption/desorption effects (Ermel, 2014). The study of compensation concentrations is important for scaling fluxes, and additionally to target the identification of separate biological and chemical processes involved in production and consumption of NO, N_2O and HONO.

2.3   SOIL-ATMOSPHERE EXCHANGE OF NO, N_2O AND HONO: NOVEL

ISOTOPIC TOOLS

Different isotopic approaches have recently been developed to follow the (microbial) pathways for production of NO, N_2O, and HONO. Slightly different methods have been developed using either chromium trioxide (CrO_3) or the excess of ozone (O_3) to convert NO into gaseous NO_2 which is trapped in a solution as NO_2^- and NO_3^-, after the denitrifier conversion method is used and $^{15}N_2O$ is measured (Yu et al., 2017; Kang et al., 2017). Labelling and stable isotopes and isotopomers of N_2O demonstrated the tracing of the source by either nitrification or denitrification (Wrage-Mönnig et al., 2018; Buchen et al., 2018; Park et al., 2011; Wrage et al., 2005; Pérez et al., 2000) and finally allowed the quantification of archaeal N_2O production (Jung et al., 2013). ^{15}N labelled Urea was applied and a method to follow the biogenic $HO^{15}NO$ emissions from soils was established (Wu et al., 2014). Isotopic methods have been also applied for separating NO production (Kang et al., 2017) and N_2O consumption (Lewicka-Szczebak et al., 2017; Wen et al., 2016). ^{15}N tracer experiments for NH_4^+, NO_3^- and NO_2^- (Russow et al., 2009) have validated the hypothesis of a diffusion limit for NO emissions (Firestone and Davidson, 1989; Skopp et al., 1990; Skiba et al., 1997). Thus, diffusion of NO out of the cell is limited under elevated soil moisture and anaerobic conditions (0-0.2% O_2) and almost all NO can be converted to N_2O before it escapes into the atmosphere (Russow et al., 2009). This explains why previous studies on NO have been conducted only for a thin layer of topsoil (Rudolph et al., 1996; Behrendt et al., 2014; Bargsten et al., 2010; Feig et al., 2008; Yu et al., 2008; Remde et al, 1989), which is not limited by constraints of molecular diffusion. Recent studies also highlight that this soil surface layer plays an important role for multiple chemical reactions, which impact various forms of gaseous N_r release into the atmosphere (Ermel et al., 2018; Liu et al., 2017; Scharko

et al., 2015; Oswald et al., 2013). ^{15}N isotopic fractionation factors for nitrification ($\alpha_{s/p}$) revealed an optimum function with maximum $\alpha_{s/p}$ at field capacity of about 1.031, which might be the result of N-transport in form of NH$_4^+$ supply within the microbial cells and NH$_3$ oxidation via enzymatic catalysis (Yun and Ro, 2014).

3 MICROBIAL NO, N$_2$O AND HONO EMISSIONS FROM SEMI-ARID AND ARID SOILS

Earlier studies found an increase in NO and N$_2$O emissions on the order of 10 to 100 times after rainfall (Davidson and Kingerlee, 1997; Verchot et al., 1999; Ludwig et al., 2001; Hartley and Schlesinger, 2000). For soils from the Mojave Desert, 0.08 to 1.9 ng m^{-2} s^{-1} NO emissions were reported with a potential emission of up to 34 ng m^2 s^{-1} under simulated rainfall conditions in the laboratory (McCalley, 2008). A modelling study for atmospheric NO$_x$ emissions from bare soils found slightly higher values (Steinkamp and Lawrence, 2011). HONO emissions, which comprise a major fraction of gaseous nitrogen loss especially from dryland soils under low soil moisture, may explain this difference (Oswald et al., 2013). In contrast, when soils dry out, N substrates concentrate in hydrologically disconnected microsites, which generate, together with N uptake from plants, a hot spot character of NO and N$_2$O emissions in drylands (Homyak et al., 2016). Hence, the spatial variability of NO, N$_2$O and HONO emissions from drylands may be considerable. It is assumed that gaseous N emissions will further increase, predominantly in regions where dryland farming is intensified under fertilization and irrigation practices (Mamtimin et al., 2016). The type of fertilizer seems also important, since HONO (and N$_2$O) emissions depend on the microbial intermediate hydroxylamine (Ermel et al., 2018; Liu et al., 2017, Wu et al., 2014), which is thought to be produced in larger quantity from urea and NH$_4^+$ fertilizers than from fertilizer mixtures. For example, nitrate concentrations in air samples originated from the Taklimakan Desert under non-dust, floating dust, and dust storm conditions were 3.81 ± 1.24, 2.95 ± 0.69, and 4.99 ± 1.71 µg m^{-3}, respectively (Wu et al., 2014). It is still not known to which extent this nitrate is blown out from heavily fertilized soils or originated from chemical reactions in the desert atmosphere. However, similar elevated nitrate concentrations have been reported from other deserts (Turpin et al., 1997). The magnitude of biogenic soil NO emissions for dryland soils are on the lower range of NO emissions (Steinkamp and Lawrence, 2011), but the area is large (UNEP, 1997). Also the potential of NO emissions due to non-water rainfall inputs has not been studied yet. Therefore it is thought that the nitrogen cycle in drylands is of global relevance.

3.1 THE ROLE OF NON-RAINFALL WATER INPUTS AND SOIL TEMPERATURE

The limited rainfall in drylands has led the scientific community to assume that microbial abundance and activity in these areas is low. However, microbial life was even found in the middle of the Atacama Desert, the driest place on Earth (Maier et al., 2004). Recent studies demonstrate that physical vapor adsorption from the atmosphere by the desert soil, a form of non-rainfall water input, is very frequent (Agam and Berliner, 2006; Ravi et al., 2006). The adsorbed water penetrates the first few (3-5) centimeters of the topsoil (Agam and Berliner, 2004). There is strong evidence that these non-rainfall water inputs control CO$_2$ efflux (Hugh et al., 2015). New studies have found that high NO (and HONO) emission occurred in soils during very low soil moisture of < 2% gravimetric soil moisture (Behrendt et al., 2017; Behrendt et al., 2014; Mamtimin et al., 2016; Oswald et al., 2013, see also Fig. 4). Similar maximum NO emissions under very low soil moistures have been found in the Kalahari and

Chihuahuan Desert (Aranibar et al. 2004, Hartley and Schlesinger, 2000). Maximum CO_2 production was used as a proxy for activity of the overall microbial community, which was observed at about $\theta_v = 0.5 \times \varepsilon$ (Skopp et al., 1990; Moyano et al., 2013). This finding demonstrates that NO (and HONO) emissions from dryland soils at very low soil moisture are not correlated to the maximum relative soil emission at about 60% WFPS (Fig. 2). CO_2 production from soils under elevated soil moisture is predominantly the result of heterotrophic metabolism (Casals et al., 2011) and therefore using CO_2 production as a proxy for overall activity of the microbial community might not be suitable. It should be noted that the soil samples dried out significantly over the course of the experiment, thus, future research is needed to clarify if the activation is dependent on time after re-wetting or on soil moisture content. Rapidly responding bacteria can be linked to very strong increases of trace gases, which have been observed for N_2O (e.g. Davidson, 1992a) and CO_2 (Placella and Firestone, 2013; Placella et al., 2012) after addition of water to dry soils. Consequently, the trace gas emission from the soil into the atmosphere is not only a result of abiotic processes and transport, but additionally mixed with microbial processes modifying concentrations of the trace gas.

Under very low soil moisture, molecular gas diffusion in soils is accelerated (Skopp et al., 1990). Under < 2% gravimetric soil moisture, CO_2 from the atmosphere can easily diffuse into soil and thus is more easily accessible to microbes than organic matter. Thus, it is likely that under such low soil moisture conditions autotrophic processes dominate over heterotrophic processes. In soils from humid mid-latitude ecosystems, maximum NO emissions occurred under moderate soil moisture, and as the climate becomes drier, the maximum NO emissions shift towards lower optimum soil moistures (Behrendt et al., 2014; Behrendt et al., 2017). This highlights the importance of autotrophic nitrification for NO emissions in dryland soils. It is noteworthy that an increase in gravimetric soil moisture of up to 2.2% was frequently observed in the Negev Desert by non-rainfall water inputs (here: water vapor adsorption) (Agam and Berliner, 2004). This so-called hysteresis effect has not yet been studied for NO, N_2O, and HONO emissions. In comparison to fertilized agricultural soils from humid mid-latitude ecosystems, the NO emissions from dryland soils are very low. However, if water vapor adsorption could maintain NO emission at a low, but constant level, the large area covered by drylands (more than 40% of global land; UNEP, 1997) may result in a significant contribution to the overall global budget of NO (and eventually HONO) emissions.

The high NO emission under low soil moisture has also been investigated by molecular methods. Transcriptional activity of different microbial groups is correlated to soil moisture (Behrendt et al., 2017; Placella and Firestone, 2013), which suggests the hypothesis that under low soil moisture a specialized microbial community drives the nitrogen cycle in drylands. Dryland soils are hot spots for NO emissions (Homyak et al., 2016) and NO emission modeling suggests that dryland soils are a stronger source than previously recognized (Steinkamp and Lawrence, 2011). There is indication that ammonia oxidizing archaea (AOA) play a major role in the nitrogen cycle under extremely dry conditions (Sullivan et al., 2012). AOA are known to produce NO (Martens-Habbena et al., 2015), tolerate high temperatures (Adair and Schwarz, 2010) and low NH_4^+ (Stahl and de la Torre, 2012), and have an efficient aerobic carbon metabolism (Könneke et al., 2014). There is evidence that AOB dehydrate and quickly recover from drying out after re-wetting of soil (Ermel et al., 2018; Thion and Prosser, 2014; Gleeson et al., 2013). AOA dehydrate and recover slower, suggesting that they might stay active for a longer time than AOB under dry conditions. One reason for this is likely their smaller cell size and therefore their ability to colonize in fine soil pores, where water films are present even under low soil moisture. This might be an advantage for their survival under harsh conditions in dryland soils. However, other studies found evidence that

under low moisture, abiotic processes dominate gaseous N losses in drylands (e.g. McCalley and Sparks 2009). Thus, the processes responsible for gaseous losses under low soil moisture are still debated.

The main focus of laboratory incubations is to study the impact of microbe-environment interactions on the soil-atmosphere exchange of trace gases to deduce a net potential NO flux, which can be validated against field NO fluxes; e.g. from dynamic chambers (Ludwig et al., 2001). Commonly, in these studies soil moisture, soil temperature, and the mixing ratio of the trace gas under investigation are changed (Laville et al., 2009; Feig et al., 2008; Yang et al., 1996). The unique advantage of laboratory studies versus field measurements is the investigation of the effect of single parameters, such as soil moisture, on the soil-atmosphere exchange of trace gases (Figure 4).
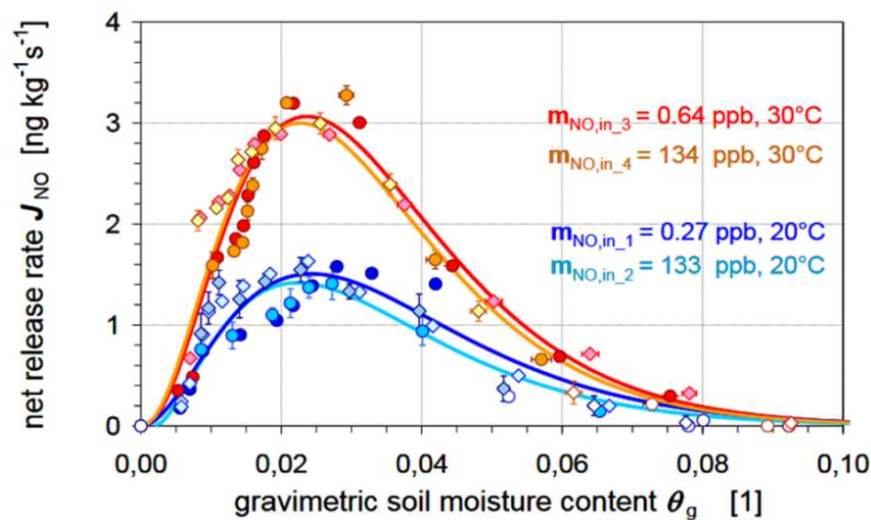

Figure 4: Effect of gravimetric soil moisture and soil temperature on net NO flux from a hyper-arid, unfertilized soil from Gobi Desert, Mongolia (results of laboratory experiments, see Behrendt et al., 2014). Blue and red color refers to 20 and 30°C and dark and bright color refers to NO-free and 133 ppb NO fumigation, respectively.

The net NO release rate follows an optimum function over the course of the drying-out of the soil sample and under low and elevated NO as well as at 20 and 30°C. For this hyper arid soil, only NO production was observed (Figure 4). For this hyper arid soil, NO consumption rate coefficients, k_{NO}, were estimated to be on the order of $< - 0.120 \times 10^{-5}$ m^3 kg^{-1} s^{-1}. This very low k_{NO} range indicates that NO consumption and potential conversion into N$_2$O and N$_2$ may be of minor importance in dryland soils. This agrees with one of the first few studies of NO and N$_2$O from semi-arid regions, where it was found that NO fluxes dominate and N$_2$O fluxes are of minor importance (Scholes et al., 1997). Low organic carbon contents and thus limited carbon substrate (availability of CO$_2$ dominates over (dissolved) organic matter under low soil moisture) and elevated temperatures may be the reasons why soils from semi-arid, arid and hyperarid ecosystems are a less favorable environment for denitrifiers. Low denitrifier diversity and activity was found for such soils (Orlando et al., 2012; Behrendt et al., 2017). The increase of NO production with soil temperature, here expressed as Q$_{10}$-value, is on the

order of 2. Indeed, previously developed algorithms (e.g. Feig et al., 2008) fit both the laboratory and the field data very well in most cases. In this algorithm, the net NO flux, F_{NO} (in ng m^{-2} s^{-1}) is described as a function of the relative soil moisture, S (or % of "Water Filled Pore Space"), by

$$F_{NO}(S) = a * S^b * \exp(-c * S).$$

The parameters a, b, and c are related to observed values by

$$a = \frac{F_{NO}(S_{opt})}{S_{opt}^{b} * \exp(-b)}$$

$$b = \frac{ln\frac{F_{NO}(S_{opt})}{F_{NO}(S_{upp})}}{ln\left(\frac{S_{opt}}{S_{upp}}\right) + \frac{S_{upp}}{S_{opt}} - 1}$$

$$c = \frac{-b}{S_{opt}}$$

where S_{opt} is the soil moisture at which the maximum net NO flux is observed; $F_{NO}(S_{opt})$ equals max[F_{NO}(S)]; and S_{upp} is the soil moisture at which F_{NO}(WFPS) = $F_{NO}(S_{upp}) \approx 0$ for S > S_{opt}. Numerical values of the parameters a, b, and c can be determined by minimizing the sum product of the difference between measured and fitted data points. Different temperature responses for NO release rate under low and high soil moisture indicate that different microbial groups contribute to the overall NO release rate from soil over the course of a dry-out.

3.2   MICROBIAL GROUPS VS. MICROBIAL GUILDS – EFFECT ON DRYLAND

SOIL PROCESSES

The activity of the overall microbial community in dryland soils drives the dynamics of biogeochemical processes, e.g. nitrification and denitrification (expressed in terms of the change in NO and N₂O fluxes from soil to the atmosphere). However, in order to understand how the microbial community affects biogeochemical processes, both microbial phylogeny and physiology need to be considered. The overall activity of the microbial community of a soil can be thought of as the sum of activities of various microbial groups. As a proxy for the activity of different microbial groups, e.g. ammonia oxidizing bacteria (AOB), ammonia oxidizing archaea (AOA) and denitrifiers, their gene expression can be studied and linked to NO, N₂O and/or HONO emissions from dryland soils. Under elevated and very low soil moisture, two maxima in NO release rate occur, which can be linked to the activity of phylogenetic different microbial groups: AOA under very low soil moisture, and denitrifiers under elevated soil moisture, respectively (Behrendt et al., 2017). For a better understanding of the overall microbial community response to changes in environmental parameters (e.g. pH, ammonia concentration and temperature) are linked to different physiological responses within a microbial group. This has been modelled by incorporating several microbial guilds into one microbial group (Bouskill et al., 2012). In such a model, the different microbial guilds are characterized based on differences in their traits, e.g., V_{max} and K_M values (physiology), for different species (phylogeny). V_{max} is the maximal velocity under which an enzyme can catalyze a reaction and K_M is the half-saturation constant. Both are parameters for modelling enzyme kinetics (Michaelis and Menten, 1913). A similar concept of microbial guilds was discussed for carbon cycling (Schimel and Schaefer, 2012; see Chapter XX), and for the temperature response of the microbial community consisting of different microbial

guilds (Schipper et al., 2014). The concept of microbial groups and microbial guilds is of great importance to modelling trace gas fluxes.

The primary evidence for two maxima in NO release rates during drying out has been reported for sodic soils from a semi-arid ecosystem, but only one maximum in NO release rate was used for modelling (Yu et al., 2008). This resulted in an underestimation of NO fluxes from semiarid sodic soils. Finally, there is evidence that the incorporation of phylogenetic microbial guilds via functional gene data into models can improve their results (Graham et al., 2016) and the understanding of how microbes affect ecosystem functioning in drylands. The knowledge about archaea is still limited, but they are thought to have a great ecological relevance in drylands, especially for NO emissions from soils. Thus, the biological nitrification model (Bouskill et al., 2012) may be extended in the future by several archaeal guilds to better understand the role of various AOA's in dryland nitrogen cycling. Finally, the concept of microbial groups and microbial guilds does not only focus anymore on the microbiological questions "who is there?" and "who is active?", but also on the question "how much detail of the overall microbial community structure and activity is needed to create accurate models?". The ultimate goal of this interdisciplinary research is to create models that are sufficiently detailed to represent the dynamics in biogeochemical processes conceptually rich enough to explore emergent behaviors. Focus of new research should be on the link between molecular methods and measurements of various trace gas fluxes. Since molecular analyses only provides a "snapshot" for specific time points and are destructive samplings, the online monitoring of trace gases is thought of as a powerful tool to get insight into the dynamics of the different microbial groups within the overall microbial community and into physiology/enzyme kinetics and metabolism of different microbial guilds. One prominent trace gas candidate may be methanol, which is produced during the microbial oxidation of methane (see Section 2.1.5). This is of interest, since methanotrophs are also capable of NO consumption (see Section 2.1.5). The NO consumption by methanotrophs is a third process in addition to activity from AOA and denitrifiers to model NO release rates from a dryland soil based on microbial activity deduced from functional gene expression (Behrendt et al., 2017). There is evidence that methane oxidation occurs in arid soils, but could not be detected in hyperarid soils from the Negev Desert (Angel and Conrad, 2009).

3.3   NITRIFICATION VS. DENITRIFICATION: OBSERVATIONS FROM DRYLANDS

There is indication that in dryland soils the activity of denitrifiers is limited (Orlando et al., 2012; Behrendt et al., 2017). Exceptions are dark cyanolichen biocrusts, which are characterized by high N fixation rates, but denitrification equals only about 3-4% of N fixation rates (Barger et al., 2013). These dark cyanolichen biocrusts have also been identified as important source for HONO (Weber et al., 2015). However, we want to recapitulate that nitrifiers are also capable of denitrification (see section 2.1.3) and thus produce NO and N_2O. Interestingly, there is evidence that this process is dependent on NO_2^- accumulation (Giguere et al., 2017; Behrendt et al., 2017). Despite NO_2^- levels that are commonly very low, there is evidence that these low NO_2^--levels drive NO (Behrendt et al., 2017) and N_2O production (Giguere et al., 2017) by both AOA and AOB. Interestingly, there is evidence of an abundance of atypical archaeal ammonia-oxidizing communities in desert soils, demonstrating that AOA are of great relevance (Marusenko et al., 2015). All the aforementioned studies raise the need for future studies focusing on changes in the NO_2^- pool in desert soils, potential nitrifier denitrification by AOA and AOB, and finally the role of nitrite oxidizing bacteria (NOB). Interestingly, a modelling approach for nitrification revealed

a 12 °C higher optimum temperature for AOA than for AOB (Taylor et al., 2016), supporting the role of AOA for NO and N$_2$O emissions from dryland soils under elevated temperatures. These findings may help to understand the counterintuitive larger potential nitrification rates observed in seasonally dry ecosystems (Sullivan et al., 2012). There is indication for a bacterial salt tolerant nitrifying community in soils from the Negev desert (Nejidat, 2005). This highlights the important role of salts in dryland soils, and the role of the deliquescence relative humidity (DRH). For NaCl-organic mixed aerosols, the point of DRH was determined at about 75% (Cruz and Pandis, 2000). For soils with high salt content, water vapor adsorption increases beyond 2.2% in gravimetric soil moisture. For HONO it was found that alkaline soils emit the largest amounts (Oswald et al., 2013), but the effect of salts on HONO formation from soils is still unkown. Microbial processes involved in ammonia oxidation for NO, N$_2$O and HONO emissions from dryland soils are not yet understood. Eventually in dryland soils conditions are less favorable for denitrifiers and in deserts they might be even bellow the limit of detection (Orlando et al., 2012). Thus, nitrification should be the predominant process in desert soils.

3.4 GLOBAL IMPORTANCE OF NO, N$_2$O AND HONO EMISSIONS FROM NATURAL DRYLAND SOILS

Most dryland soils are carbon-poor and lack substantial rainfall inputs, which results in predominantly low soil moisture (Chapter YY). These conditions are unfavourable for denitrification and the contribution to N$_2$O emissions from these soils is commonly low. However, under these conditions the processes of nitrification and nitrifier denitrification might be important and contribute largely to HONO and NO formation. Instead of focusing on rainfall as the main driver of microbial activity and trace gas release from dryland soils, future studies should focus on the role of water vapor adsorption. There is also evidence from a multi-satellite sensor study that already one day before rainfall, soil moisture increased and NO emissions are within the order of about 3.3 ng (N) m^{-2} s^{-1} from soils in the Sahel region (Zörner et al. 2016). In the same study, the NO emissions from rainfall pulses were found to be range from 6 to 65 ng (N) m^{-2} s^{-1} (assuming a life time for NO$_x$ of 4 h). While the short NO$_x$ pulses due to rainfall detected by remote sensing techniques are a validation of previous field measurements (Johansson and Sanhueza, 1988; Davidson, 1992b; Levine et al., 1996; Scholes et al., 1997), NO$_x$ emissions based on water vapor adsorption in the field have not yet been measured. Very low yearly average NO emissions of 2.18 to 3.46 ng (N) m^{-2} s^{-1} for the Sahel region (Delon et al. 2014) suggest that NO emissions due to water vapor adsorption might be the predominant process in regions where rainfall events are rare. Changes in land-use, desertification as well as the increase in dryland farming (including irrigation/soil moisture regime and C and/or N fertilization practices) are thought to accelerate the N cycle in drylands in the future. For example, a change in land-use from grassland to shrubland resulted in decrease of NO emissions (Hartley and Schlesinger, 2000), whereas a conversion of grassland into cropland resulted in an 8-fold increase in N$_2$O emissions (Mosier et al., 1996). While the contribution of natural dryland soils to global N$_2$O emissions is low (e.g. Scholes et al., 1997), the role of dryland soils for N$_2$O consumption is not yet understood. There is indication that not only denitrifiers, but also other bacteria and archaea might play an important role in N$_2$O consumption, like the recently detected clade II nitrous oxide reducers most of which don't denitrify (Jones et al., 2014; Sanford et al., 2012; Chapuis-Lardy et al., 2007). The effect of soil degradation (water or wind erosion or chemical/physical deterioration), which frequently occurs in dryland soils (Müller et al., 2014), on NO, N$_2$O and HONO emissions has not been studied yet. However, there is indication that especially at sites where the salt content is increasing, a nitrifying community with unique capabilities can establish (Nejidat, 2005). An overview examining the variability of HONO emissions under different land use is given by Oswald et al. (2013). There is evidence that the development of

bio crusts are capable of fixing sand dunes on a large scale of 16 km long and 0,7 km wide area where 1 x 1 meter straw checkerboard sand barriers were constructed (Li et al., 2002). However, a change from bare sand dunes into anthropogenic created soil surfaces where bio crusts have been established has not only the benefit of dune stabilization, but also the price of additional trace gas release. There is evidence that especially the late successional stage of dark cyanolichen crusts produce large amounts of HONO and NO (Weber et al., 2015). Despite maximal gaseous N-emissions from dryland soils are only low, recent HONO emissions from drylands (Oswald et al., 2013) suggest that these soils are important for N-cycling. Despite fluxes of N-oxides are several orders of magnitude higher under simulated rainfall conditions (McCalley, 2008), rainfall in drylands is limited. Of so far unknown importance in the water cycle in drylands are the non-rainfall water inputs, which have been shown to trigger trace gas emissions recently (McHugh et al., 2015). Non-rainfall water inputs are thought to occur in drylands on a more regular basis than rainfall and therefore might be important for N-cycling in these ecosystems.

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