REVIEW

Soils, a sink for N_2O? A review

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Abstract

Soils are the main sources of the greenhouse gas nitrous oxide (N_2O). The N_2O emission at the soil surface is the result of production and consumption processes. So far, research has concentrated on net N_2O production. However, in the literature, there are numerous reports of net negative fluxes of N_2O, (i.e. fluxes from the atmosphere to the soil). Such fluxes are frequent and substantial and cannot simply be dismissed as experimental noise.

Net N_2O consumption has been measured under various conditions from the tropics to temperate areas, in natural and agricultural systems. Low mineral N and large moisture contents have sometimes been found to favour N_2O consumption. This fits in with denitrification as the responsible process, reducing N_2O to N_2. However, it has also been reported that nitrifiers consume N_2O in nitrifier denitrification. A contribution of various processes could explain the wide range of conditions found to allow N_2O consumption, ranging from low to high temperatures, wet to dry soils, and fertilized to unfertilized plots. Generally, conditions interfering with N_2O diffusion in the soil seem to enhance N_2O consumption. However, the factors regulating N_2O consumption are not yet well understood and merit further study.

Frequent literature reports of net N_2O consumption suggest that a soil sink could help account for the current imbalance in estimated global budgets of N_2O. Therefore, a systematic investigation into N_2O consumption is necessary. This should concentrate on the organisms, reactions, and environmental factors involved.

Keywords: denitrification, gas diffusion, global N_2O budget, greenhouse gas, N_2O consumption, negative flux, nitrification, nitrous oxide

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Introduction

Nitrous oxide (N_2O) is a relatively stable greenhouse gas (GHG) that also plays a significant role in atmospheric photochemical reactions that contribute to stratospheric ozone destruction. The atmospheric N_2O concentration has been increasing since about 1750 (Intergovernmental Panel on Climate Change, 2001). Since 1988, the rate of increase has been $0.8\,ppb\,yr^{-1}$, and in 2004 the concentration reached 318.6 ppb (World Meteorological Organization, 2006), exceeding the concentration of preindustrial times by 18% (ca. 270 ppb).

The total annual emission of N_2O has been estimated to be 16.4 Tg in the late 1990s (Intergovernmental Panel on Climate Change, 2001). Soils are the largest contributors to N_2O emissions, with $6.0\,Tg\,yr^{-1}$ from natural soils and $4.2\,Tg\,yr^{-1}$ from agricultural soils (Intergovernmental Panel on Climate Change, 2001). Biomass burning also produces N_2O directly, but frequently enhances the soil biogenic production of this gas as well (Mosier, 1994; Mosier et al., 2004). In soils, N_2O production is mainly governed by two microbial processes, nitrification and denitrification (Granli & Bøckman, 1994; Bremner, 1997; Barnard et al., 2005).

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Although soils are usually considered as net sources of atmospheric N_2O, they can also act as sinks, at least temporarily (Ryden, 1981; Slemr & Seiler, 1984; Minami, 1997). The sink strength depends on the potential for N_2O reduction to N_2, the ease of N_2O diffusion within the soil profile and its dissolution in soil water. We will elaborate on this further below. The flux of N_2O obtained at the soil/atmosphere interface is the result of dynamic production and consumption processes in the soil. Gross N_2O consumption has been a well-recognised process for a long-time (Nõmmik, 1956; Firestone & Davidson, 1989). However, as production rates are usually larger than consumption rates, most studies concentrate on the net production of N_2O and neglect the possibility of net consumption (i.e. negative fluxes of atmospheric N_2O). Nevertheless, much of the N_2O that is produced within the soil column may never reach the soil surface (e.g. Seiler & Conrad, 1981; Arah *et al.*, 1991). Arah *et al.* (1991) suggested that low N_2O emissions may be explained by a decrease in gas diffusivity leading to N_2O consumption. Cicerone (1989) was one of the first in the literature to underline the potentially important consequence of net soil sinks of N_2O on the estimate of its atmospheric residence time.

The term 'uptake' is used in atmospheric science to describe a net or gross flux of a gas from the atmosphere to the soil, (i.e. a negative flux). In this review, uptake also includes the disappearance of N_2O from the soil gaseous phase by reduction of N_2O to N_2, as well as the absorption of N_2O in soil water. We use the terms 'uptake' and 'consumption' synonymously to describe these processes. The term 'reduction', however, will be reserved for the description of N_2O reduction to N_2.

This paper provides a review of the current knowledge of soils as an N_2O sink. How have net negative N_2O fluxes at the soil surface so far been considered in the literature? What are the main drivers of N_2O uptake? Is N_2O uptake a potentially important process? Despite numerous reported incidents of net negative fluxes of N_2O, a systematic investigation of this phenomenon is still missing. By pointing out lacks in our understanding, this review should be a first step on our way to better understand the N_2O budget, helping to assess how important net N_2O uptake is globally in soils.

N_2O consumption: theory

The conceptual 'hole-in-the-pipe' model considered three levels of controls regulating the emissions of N_2O from the soil to the atmosphere. These were (1) factors controlling the rates of denitrification and nitrification; (2) factors regulating the proportions between the gaseous end products of these processes and (3) factors controlling the consumption of these gases in the soil matrix (Firestone & Davidson, 1989; Davidson, 1991). We will here consider the second and third point.

Net consumption of N_2O has been reported in different ecosystems, including grasslands and forests, but also lakes, seas and aquifers (Mengis *et al.*, 1997; Mühlherr & Hiscock, 1998; Cavigelli & Robertson, 2001; Glatzel & Stahr, 2001; Butterbach-Bahl *et al.*, 2002; LaMontagne *et al.*, 2003; Punshon & Moore, 2004a). It is generally assumed that denitrification, the electron-transport-linked reduction of nitrogen oxides during respiration of heterotrophic bacteria, is responsible for N_2O consumption (Bremner, 1997; Yu *et al.*, 2000). Beijerinck & Minkman (1910) first identified N_2O as an intermediate in denitrification following initial investigations of NO_3^- reduction in the late 19th century (Gayon & Dupetit, 1886; Breal, 1892). The ability to reduce N_2O to N_2 is wide-spread in denitrifiers: Okereke (1993) reported that 59 out of 71 denitrifiers isolated from various environments utilized N_2O as terminal electron acceptor. One denitrifier has even been found to be able to grow with N_2O as the sole electron acceptor (Bazylinski *et al.*, 1986).

Bacteria are thought to be the dominant organisms responsible for denitrification. However, fungi are also capable of denitrification, although many lack N_2O-reductase (NOR; Shoun *et al.*, 1992). Only nine out of 39 fungi tested by Shoun *et al.* (1992) exhibited complete denitrification to N_2. In most cases, the production of N_2 was low. However, the fungi tested only covered a small proportion of fungal groups able to denitrify. More work on this aspect is, therefore, required as other fungi might show greater ability to reduce N_2O to N_2.

In addition to denitrifiers, nitrifiers may also play a role in the consumption of N_2O. In 1986, nitrifiers were reported to be able to produce N_2 from nitrite (NO_2^-; Poth, 1986). This pathway, called nitrifier denitrification, is now known to proceed from NO_2^- via nitric oxide (NO) and N_2O to N_2 (Casciotti & Ward, 2001; Beaumont *et al.*, 2002, 2004; Schmidt *et al.*, 2004). It has been suggested that under anoxic conditions, *Nitrosomonas europaea* can gain growth energy either from NO_2^--dependent ammonia oxidation or from nitrifier denitrification (Schmidt *et al.*, 2004). A range of nitrifiers has already been found to possess the ability to denitrify, suggesting it might be a universal trait of β-proteobacterial ammonia oxidizers (Shaw *et al.*, 2006). It is not yet known, however, how common the ability to reduce N_2O to N_2 is in nitrifiers. Although the complete genome of *N. europaea* has been sequenced, the enzyme (or enzymes) responsible for N_2O reduction in nitrifiers has not yet been identified (Chain *et al.*, 2003; Schmidt *et al.*, 2004).

NOR is responsible for the reduction of N$_2$O during denitrification. The enzyme is inhibited at low pH and is more sensitive to O$_2$ than the other denitrification enzymes (Knowles, 1982), although this sensitivity to O$_2$ varies widely among different denitrifiers (Cavigelli & Robertson, 2001). The antecedent water regime of soil may also favour the synthesis of reduction enzyme and affect the N$_2$O/N$_2$ ratio (Dendooven et al., 1996). Furthermore, Menyailo et al. (1997) observed a decrease in N$_2$O consumption with increasing salinization of salt-affected soils, suggesting NOR is also highly susceptible to salts. A decrease of NOR activity leads to an increase in the ratio N$_2$O/N$_2$. This ratio is also increased if NO$_3^-$ is abundant, since NO$_3^-$ is preferred as an electron acceptor over N$_2$O (Schlegel, 1985). Therefore, negative N$_2$O fluxes are often supposed to be confined to N-limited ecosystems (e.g. Glatzel & Stahr, 2001).

It is highly probable that gross N$_2$O consumption is often masked by higher rates of N$_2$O production. For example, Wrage et al. (2004a) carried out soil incubation studies with additions of mineral N. In some incubations, net N$_2$O production was very low or levelled off after a period of time. This was linked with an increasing natural abundance of ^{15}N and ^{18}O in N$_2$O. Such results could only be explained by gross consumption of N$_2$O (Wrage et al., 2004a), which discriminates against ^{15}N- and ^{18}O-N$_2$O, leading to an enrichment of the remaining N$_2$O. If only the N$_2$O concentrations had been measured, the observed N$_2$O fluxes would probably have been interpreted as low rates of gross N$_2$O production and not as a combination of production and consumption.

Differences in microbial community composition can potentially influence N$_2$O consumption rates, and therefore N$_2$O fluxes from soils. For example, Cavigelli & Robertson (2000) reported that net N$_2$O consumption occurred in a never-tilled successional field, as well as in a conventionally tilled agricultural field, but the amount of active NOR was larger in the denitrifying community from the successional field. The denitrification enzymes, including NOR, from the successional field were more sensitive to pH changes than those from the agricultural field, which were more susceptible to inhibition by O$_2$ (Cavigelli & Robertson, 2000).

Knowns and unknowns about negative N$_2$O fluxes

Almost 30 years ago, Blackmer & Bremner (1976) demonstrated in laboratory experiments that the capacity of a soil to take up N$_2$O is in certain soils larger than its capacity to produce N$_2$O. For nine cultivated Iowa soils, they reported over a 14-day period more or less constant N$_2$O reduction rates of between -0.57 and $-1.11\,\mu g\,N\,g^{-1}\,soil\,day^{-1}$, (i.e. -0.024 and $-0.045\,\mu g$

N$\,g^{-1}\,soil\,h^{-1}$). Some subsequent publications reported uptake in field studies and strongly supported the hypothesis of Blackmer and Bremner on the potential of soil as a sink for atmospheric N$_2$O (Cicerone et al., 1978; Freney et al., 1978; Ryden, 1981).

Since then, both significant and frequent net negative N$_2$O fluxes have been reported (in figures or text), but without any consideration in the discussion other than an occasional remark on the lack of information on the extent to which soils act as a sink for N$_2$O (Fenn et al., 1996; Klemedtsson et al., 1997; Smith et al., 1998; Kamp et al., 2000; Davidson et al., 2001; Butterbach-Bahl et al., 2002; Longoria Ramírez et al., 2003; Xu et al., 2004). Hénault et al. (1998) also detected small negative fluxes, and outlined that the soil was able to trap atmospheric N$_2$O, but with a very weak efficiency, as supported by Granli & Bøckman (1994). Verchot et al. (1999) reported negative N$_2$O fluxes in 30–40% of observations during the wet season and in 55–65% of measurements during the dry season but did not discuss these values. Jordan et al. (1998) reported negative fluxes and pointed out the need for further research on the mechanisms of N$_2$O uptake.

Net N$_2$O consumption has also been observed in incubation studies with large N$_2$O concentrations (Freney et al., 1978; Bandibas et al., 1994; Swerts et al., 1996). Owing to this, it has sometimes been regarded as an artefact without consequences for in situ situations. We will deal with uncertainties concerning the measurements in the next part of the manuscript. Net N$_2$O consumption has not yet been systematically studied. However, the results available so far suggest that it might be important in several systems and, thus, should be taken into account in further studies.

Table 1 gives an overview of negative N$_2$O fluxes that have been measured in situ at the soil surface under a large range of conditions (temperate and tropical, natural and agricultural systems). This highlights that N$_2$O consumption is not limited to pristine ecosystems, but can also occur in agricultural land. Maximum net negative N$_2$O fluxes reported in the literature vary widely, from -0.0014 to $-484\,\mu g\,N_2O\text{-}N\,m^{-2}\,h^{-1}$ (Table 1).

Uncertainties concerning the measurement

Net N$_2$O emissions are variable in space and time, and the uncertainty of field-scale budgets is large, especially when fluxes are measured using manually operated chambers, the most commonly used system. Many authors have emphasized these sources of uncertainty and not commented on the observed negative fluxes any further. Some authors assumed that the apparent net uptake occurred when measurements had been carried out close to detection limits (Kamp et al., 2000;

Table 1 Published data of net negative N$_2$O fluxes from soils reported from field measurements

Place	Land-use/vegetation	Reported N$_2$O fluxes			Minimum	Occurrence of negative events	Reported soil information	Available information on the conditions of N$_2$O net uptake	Reference
		Original unit			μg N m^{-2} h^{-1}				
		Minimum	Maximum	Original unit	Minimum				
Temperate or Mediterranean climates									
China	Waterlogged rice	−0.031	4.4	mg N-N$_2$O m^{-2} h^{-1}	−31	II	Aqu-alkalic halosol		Xu et al. (2004)
China	Waterlogged rice	(A) −0.63		μg N-N$_2$O m^{-2} h^{-1}	−0.63	III	Loamy clay soil	Early rice period, top position of the slope	Xu et al. (1997)
NE China	Waterlogged rice	−39	164	μg N-N$_2$O m^{-2} h^{-1}	−39	I	Meadow brown soil	Flooding	Chen et al. (1997)
	Maize	−11.9	557		−11.9			No measurement in winter	
	Soybean	−20.3	218		−20.3				
	Spring Wheat	−9.5	46		−9.5				
SW Sweden	Norway spruce forest	(A) −10*		μg N-N$_2$O m^{-2} h^{-1}	−10	III	Acidic, well drained, orthic podzol	August, low water content	Klemedtsson et al. (1997)
Ballyhooly, Ireland	Spruce forest	−0.55	2.1	μg N-N$_2$O m^{-2} h^{-1}	−0.55	III	Very acidic, deep weathered haplorthod	November to July, <2 mg NO$_3$-N kg^{-1} soil	Butterbach-Bahl et al. (1998)
Rothamsted, UK	Wheat	−3.3	46	ng N-N$_2$O m^{-2} s^{-1}	−11.8	1/68	22% clay-26% silt, drained, limed (pH = 7)	High temperature, low soil moisture, low mineral N soil content	Yamulki et al. (1995)
Rothamsted, UK	Grassland	−4.2		ng N-N$_2$O m^{-2} s^{-1}	−15.1	2/11	22% clay-26% silt, drained, unlimed (pH = 3.9)	Soil temperature <10 °C, mid-November to mid-March	Yamulki et al. (1997)
Berkshire, UK	Ryegrass	−11.6		ng N-N$_2$O m^{-2} s^{-1}	−41.8	III	Loam ochraqualf	Moderate to high water content, very low nitrate content and temperature above 5–8 °C	Ryden (1981)
Berkshire, UK	Ryegrass	−0.009	0.2	Kg N-N$_2$O ha^{-1} day^{-1}	−37.5	III	Loamy soil, pH = 6.3	In fertilized soil and in control (no fertilization) Similar conditions as for Ryden (1981)	Ryden (1983)
NE Germany	Scots pine forest	(A) −4.1	34.1	μg N-N$_2$O m^{-2} h^{-1}	−4.1	III	Very acidic, sandy cambisol	Spring and autumn	Butterbach-Bahl et al. (2002)
SW Germany	Meadow	−41.2	73.2	μg N-N$_2$O m^{-2} h^{-1}	−41.2	III	Gleyi-cumulic anthrosol	Winter and summer, Soil temperature >8 °C unfertilized and fertilized plots	Glatzel & Stahr (2001)

Location	Land use/cover			Units			Soil type	Season and conditions	Reference
Darmstadt, Germany	Deciduous forest	−0.25	4.09	ng N$_2$O m^{-2} s^{-1}	−0.57	II	Sandy cambisol	February	Dong et al. (1998)
Belgium	Arable land	−4.2	41	g N-N$_2$O ha^{-1} day^{-1}	−17.5	III	Loamy sand to silt loam, soil 5.4–7.6	Autumn and winter	Goossens et al. (2001)
	Grassland	−2.4	340	g N-N$_2$O ha^{-1} day^{-1}	−10.0	II	Sandy loam, pH 7.3	Spring	
	Deciduous temperate forest	−16	2.6	g N-N$_2$O ha^{-1} day^{-1}	−66.6	68%	Sandy, very acidic (pH 3.8) soil	Almost whole year, WFPS >35%, low NO$_3^-$-N content	
NE France	Bare and rapeseed crop	−0.35	27	g N-N$_2$O ha^{-1} day^{-1}	−1.5	8/54	Typic rendzic leptosol	Autumn and winter	Hénault et al. (1998)
Central Switzerland	Artificial grassland (grass/clover mixture)	−109	2402	ng N$_2$O m^{-2} s^{-1}	−250	40%	Stagnic cambisol	Whole year, in unfertilized plot or towards the end of the fertilizer period in intensive systems, wet and dry soil conditions	Flechard et al. (2005)
Switzerland	Artificial grassland (grass-clover mixture)	100†		ppb		III	Mineralized soil on a drained marshland	During the growing season, at different soil depths (2–100 cm), WFPS 50–90%	Neftel et al. (2000)
Tuscany, Italy	Pine plantation	−10.9	−1.3	μg N-N$_2$O m^{-2} h^{-1}	−10.9	III	Sandy calcareous regosoil	Dry and hot spring, wet and mild autumn, soil temperature 14–20°C, inorganic N limited soil	Rosenkranz et al. (2005)
Spain	Cropland and sown pasture	−20*	125	μg N-N$_2$O m^{-2} h^{-1}	−20	II	Dystric cambisol	Fertilized, high soil moisture	Merino et al. (2004)
Ontario, Canada	Grassland	(A) −0.08	0.32	kg N-N$_2$O ha^{-1} month^{-1}	−10.9	III	Gleyed melanic brunisol	March to September	Wagner-Riddle et al. (1997)
Ontario, Canada	Undisturbed and managed Black Spruce forest	−8.0	3.1	μg N$_2$O m^{-2} h^{-1}	−5.1	III	Very poorly drained peat soil	In summer, for all sites, largest uptake in a drainage ditch at the clear-cut drained site	Schiller & Hastie (1996)
Saskatchewan, Canada	Mixture of grass	−0.2	25.3	ng N-N$_2$O m^{-2} s^{-1}	−0.72	II	Calci/halpo/argi-borolls and cryaquolls	Summer, in vegetated depressions	Yates et al. (2006)
NE USA	Temperate forest and pine plantation	−3.7	5.2	μg N-N$_2$O m^{-2} h^{-1}	−3.7	III	Sandy loam, acidic and well-drained entic haplorthod	No consistent relationship with soil parameters or air temperature, in fertilized soil and in control (no fertilization)	Bowden et al. (1991)
Chesapeake Bay, NE USA	Riparian forest	−2.2	16	μg N-N$_2$O m^{-2} h^{-1}	−2.2	II	Fine sandy loam, typic hapludult	Winter	Jordan et al. (1998)

Table 1 Published data of net negative N_2O fluxes from soils reported from field measurements

Place	Land-use/vegetation	Reported N_2O fluxes — Original unit — Minimum	Maximum	unit	$\mu g\,N\,m^{-2}\,h^{-1}$ Minimum	Occurrence of negative events	Reported soil information	Available information on the conditions of N_2O net uptake	Reference
NE USA	Spruce fir plantation	−6.7		$\mu g\,N\text{-}N_2O\,m^{-2}\,h^{-1}$	−1.1	III	Very acidic spodosol	Summer, high soil moisture, low NO_3^--N concentration	Castro *et al.* (1993)
Hidalgo, Mexico	Wheat	−484	385	$\mu g\,N\text{-}N_2O\,m^{-2}\,h^{-1}$	−484	34%	Loam soil, pH 6.8–7.2, organic matter 3.6%	Fertilization and irrigation, WFPS >70%, December to May	Longoria Ramírez *et al.* (2003)
Los Angeles, California	Pine plantation	−0.0004*		$ng\,N\text{-}N_2O\,m^{-2}\,s^{-1}$	−0.0014	I	Coarse-loamy, mixed, mesic, ultic haploxerolls	Summer-fall drought period	Fenn *et al.* (1996)
Tropical and sub-tropical climates									
Rondônia State, Brazil	Unfertilized (control) Pasture	−2.4	10.8	$\mu g\,N\text{-}N_2O\,m^{-2}\,h^{-1}$	−2.4	II	Ultisol	Dry season	Passianoto *et al.* (2003)
Rondônia State, Brazil	Pasture	−8.8	18	$\mu g\,N\text{-}N_2O\,m^{-2}\,h^{-1}$	−8.8	3/18	Ultisol	Wet and dry season	Garcia-Montiel *et al.* (2001)
Eastern Amazonia, Pará state, Brazil	Pasture	(A) −1	2.3	$ng\,N\text{-}N_2O\,cm^{-2}\,h^{-1}$	−10	30–65%	Kaolinitic yellow Latosol (haplustox)	Wet and dry season	Verchot *et al.* (1999)
Planaltina, Goiás State, Brazil	Degraded pasture	−0.3*	6.7	$ng\,N\text{-}N_2O\,cm^{-2}\,h^{-1}$	−3	II	Clayey red latosol (latossol vermelho in Brazilian classification)	Wet season, February to March, 6–9 mg NO_3-N kg^{-1} soil	Pinto *et al.* (2006)
São Paulo State, Brazil	Sugar cane	−6.8	23	$g\,N_2O\,ha^{-1}\,day^{-1}$	−18	II	Red latosol (orthic ferralsol)	March, end of wet season	Cerri *et al.* (2004)
Bolívar state, Venezuela	Savannah	−3.9	9.3	$10^9\,Molecules\,cm^{-2}\,s^{-1}$	−9.5	I	Sandy loam– sandy clay loam, poor in nutrients, soil pH = 4.7	Dry and rainy season	Sanhueza *et al.* (1990)
Bolívar state, Venezuela	Savannah	(A) −2.6		$10^9\,Molecules\,cm^{-2}\,s^{-1}$	−6.8	III	Sandy loam– sandy clay loam, poor in nutrients, soil pH = 4.7	Dry season	Donoso *et al.* (1993)
South Kalimantan, Indonesia	Upland field, paddy field and secondary forest	−0.04	0.03	$mg\,N\text{-}N_2O\,m^{-2}\,h^{-1}$	−40	8/33	Strongly acidic peat soils	January to June, (precipitations 240–320 mm month⁻¹; air temperature 26–28 °C)	Inubushi *et al.* (2003)

Location	Land use/crop	Negative flux	Positive flux	Units	Frequency	Soil type	Comments	Reference
South Kalimantan, Indonesia and Sarawak, Malaysia	Natural and converted peatlands (uncultivated uplands, and secondary forest)	(A) −0.03	0.16	mg N-N$_2$O m^{-2} h^{-1}	I	Strongly acidic peat soils, peat depth <100 cm		Hadi et al. (2000)
Malaysia	Groundnut-Maize rotation	−58	1400	μg N-N$_2$O m^{-2} day^{-1}	II	Typic paleudult	Low substrate availability or low soil moisture within N fertilization	Khalil et al. (2002)
Faisalabad, Pakistan	Maize	−0.94	1.53	g N ha^{-1} h^{-1}	10/29	Sandy-clay loam	Irrigated, WFPS 56–63%, 16–19 mg NO$_3^-$ - N kg^{-1} soil^{-1}	Mahmood et al. (1998)
	Wheat	−0.87	0.39		14/41			

Fluxes are presented as reported in the publication, i.e. the largest negative or positive values or an average (A) of negative, or positive, measurements during a sampling period (month or longer). Negative fluxes were converted to μg N m^{-2} h^{-1}, for easier comparison. The occurrence of negative fluxes is given as the number of events out of the total number of measurements (or as a percentage) as reported in the publication, unless estimated from published data; I, not available; II, singular or very occasional; III, frequent. Cell in the table has been left blank when no data was available in the publication.

*Approximate value as estimated from a figure.

†Equivalent to 220 ppb below the atmospheric concentration of N$_2$O (ca. 320 ppb).

WFPS, water-filled pore space.

Erickson et al., 2002; Pinto et al., 2006). However, Verchot et al. (1999) calculated the minimum detectable flux for their set-up ($6\,\mu g\,m^{-2}\,h^{-1}$), using the 95% confidence interval of fluxes in each individual chamber as recommended by Hutchinson & Livingston (1993). Using this threshold value, 10–20% of the net negative fluxes observed by Verchot et al. (1999) could be considered significantly different from 0.

As N$_2$O fluxes are often considered to be log-normally distributed in space (Velthof & Oenema, 1995), a frequent practice is to add an offset, making negative values positive (Hansen et al., 1993; Davidson et al., 2004). A subsequent log-transformation for statistical comparisons of treatment effects and site differences is legitimate as long as e.g. the mean flux is still presented as the mean of the untransformed data, including the effect of the negative fluxes. Singular net negative events should be reported (Smith et al., 1998) and transformations applied on the dataset clearly described. Log-normal statistics and classical confidence intervals for means based on the central limit theorem have been considered inapplicable when many significantly negative net fluxes are present in the dataset (Flechard et al., 2005).

Taking the variability between replicates into account, Glatzel & Stahr (2001) considered fluxes between −20 and +50 $\mu g\,N_2O\text{-}N\,m^{-2}\,h^{-1}$ from soil under meadows as not significantly different from 0. However, singular negative fluxes (up to $-41.2\,\mu g\,N_2O\text{-}N\,m^{-2}\,h^{-1}$) larger than the analytical error of the gas chromatograph were still observed. Butterbach-Bahl et al. (1998) used decreasing N$_2$O concentrations from a headspace chamber to demonstrate that the measuring system used was sensitive enough to unequivocally detect net uptake of N$_2$O from the atmosphere into the soil. Flechard et al. (2005) continuously monitored N$_2$O fluxes at the soil/atmosphere interface using automatic chambers, and observed negative fluxes in ca. 40% of the measurements. The values were in some cases well above the flux detection limit ($-100\,ng\,N_2O\,m^{-2}\,s^{-1}$, which is equivalent to $-229\,\mu g\,N_2O\text{-}N\,m^{-2}\,h^{-1}$). They also reported a net sink activity that was consistent on a monthly average basis during a period of 6–7 months, even on a fertilized field.

Soil variables affecting the extent of N$_2$O uptake

Our understanding of N$_2$O reduction and the NOR enzyme leads to the expectation that N$_2$O uptake should mainly occur at high water-filled pore space (WFPS) and at low NO$_3^-$ availability. Indeed, many authors have reported links between net negative N$_2$O fluxes at the soil surface and very low concentrations of inorganic N, even in soils with an appreciable total

N content (Ryden, 1983; Clayton et al., 1997; Wagner-Riddle et al., 1997; Khalil et al., 2002). Atmospheric and/or soil gaseous N_2O may be the only electron acceptor left for denitrification when soil NO_3^- concentrations are very low (Butterbach-Bahl et al., 1998; Goossens et al., 2001; Rosenkranz et al., 2005). Furthermore, moderate to high soil water contents and soil temperature above 5 °C are conditions considered to promote N_2O uptake (Ryden, 1981; Glatzel & Stahr, 2001; Goossens et al., 2001). Ryden (1983) associated N_2O sink activity with soil NO_3^- levels of $\sim 1\,mg\,N\,kg^{-1}$, a soil moisture content $>20\%$ (w/w) and relatively low soil temperatures of 5–8 °C. However, net N_2O uptake has also been observed under different conditions, making it difficult to identify a set of conditions generally suitable for N_2O uptake. An impression of some of the conditions is given in the following.

Glatzel & Stahr (2001) observed net N_2O consumption in fertilized grassland, however, according to the authors, this might have been caused by quick N turnover caused by frequent cuts and large yields. Owing to this, N in the soil solution was low despite fertilization. Furthermore, O_2 concentrations might have been low following soil compaction from frequent mowing.

Rosenkranz et al. (2005) linked negative fluxes in Mediterranean forest soils to the very low N availability ($<1\,mg\,NO_3^-$-N and $2\,mg\,NH_4^+$-N $kg^{-1}\,soil^{-1}$). They also reported that the organic layer of the sandy soil was very well aerated even under wet conditions. To explain these observations, they considered aerobic denitrification as a possible pathway (Poth, 1986; Robertson et al., 1989, 1995; Wrage et al., 2001). However, high C contents could also have stimulated respiration, leading to anaerobic microsites where normal denitrification could have taken place. The availability of organic carbon in soils was correlated with the production of N_2 in soil core studies, hinting at more anaerobic conditions (Mathieu et al., 2006).

Some authors have linked the N_2O consumption occurring during N_2O incubation experiments to texture and/or redox potential (Letey et al., 1981; Chen et al., 1997; Włodarczyk et al., 2005) and pH (Letey et al., 1981; Ottow et al., 1985; Stevens et al., 1998). The enzyme NOR is inhibited at low pH (Knowles, 1982) and several authors found a strong negative relationship between soil pH and the mole fraction of N_2O [$N_2O/(N_2O + N_2)$; Nõmmik, 1956; Firestone et al., 1980; van der Weerden et al., 1999]. However, as some net negative fluxes occurred in very acidic soil (Table 1), the role of pH in the uptake process might not be so straightforward. For example, when denitrification was inhibited by aerobic conditions, Bremner & Blackmer (1980) found two to 20 times more N_2O production from soils with higher pH.

Although many authors have found a clear positive relationship between soil temperature and net N_2O production (e.g. Keeney et al., 1979; Öquist et al., 2004), contrasting results may illustrate a soil temperature effect on gross N_2O consumption. Donoso et al. (1993) observed that a larger N_2O uptake occurred during nighttime, and found a significant inverse correlation between soil temperature and net N_2O consumption. On the contrary, Yamulki et al. (1995) linked low emission rates, as well as net negative fluxes (Table 1, up to $-3.3\,ng\,N\,m^{-2}\,s^{-1}$) to high temperatures and low soil moisture contents. An increase in soil temperature positively influences microbiological activity and gas diffusion, while it negatively affects the solubility of N_2O (Heincke & Kaupenjohann, 1999). Thus, it is difficult to predict the impact of a change in soil temperature on gross N_2O uptake.

Mahmood et al. (1998) studied N_2O fluxes of an irrigated sandy-clay loam cropped to maize and wheat. During the wheat season, the authors reported a sink activity ranging from -0.01 to $-0.87\,g\,N\,ha^{-1}\,h^{-1}$ on 14 of 41 sampling occasions. During the maize season, sink activity was observed on 10 of the 29 sampling days over a range of -0.18 to $-0.94\,g\,N\,ha^{-1}\,h^{-1}$. In that study, N_2O sink activity was recorded at a WFPS of 56%, at relatively high soil temperatures (>23 °C), and respiration rates ($123\,kg\,C\,ha^{-1}\,day^{-1}$), and NO_3^- concentrations as high as $16–19\,mg\,N\,kg^{-1}$ (Mahmood et al., 1998). Khalil et al. (2002) underlined that in their study, net negative N_2O fluxes coincided with either low N substrate availability or low moisture content (WFPS $<50\%$), indicating that these fluxes are not necessarily connected with low mineral N availability, low temperatures and large moisture contents. Underlining the latter point, Neftel et al. (2000) detected N_2O negative fluxes from artificial grassland especially during the first growth period of the sward at a range of WFPS between 50% and 90%.

To sum up, N_2O uptake seems to be stimulated by low availability of mineral N. Soil temperature has an effect but this is not straightforward. Soil pH and O_2 content seem to be negatively correlated with N_2O reduction. However, these factors do not always act in the expected ways, probably depending on the main N_2O reducing processes in the soil and in relation to other factors. Besides denitrification, other N_2O reducing processes could be nitrifier denitrification and aerobic denitrification. The latter could explain the observed N_2O reduction in dry soil. However, other, possibly unknown processes, such as abiotic reactions with soil minerals, may also be involved with some of the observations of net N_2O consumption by soil. Based on current knowledge, it is not yet possible to clearly define a set of conditions promoting N_2O consumption.

N$_2$O within soil profile and the role of diffusion processes

Several authors have reported that the depth of N$_2$O production influences the net positive or negative fluxes at the soil surface (e.g. Clough *et al.*, 1999; Verchot *et al.*, 1999; Brye *et al.*, 2001; Elmi *et al.*, 2003; Müller *et al.*, 2004). Production, consumption and diffusion of N$_2$O within the soil interact, creating a dynamic pattern of gas concentrations in the profile (Højberg *et al.*, 1994). Thus, the N$_2$O efflux from the soil surface is a function of the time and location of N$_2$O production/consumption in the profile. Hosen *et al.* (2000) demonstrated that the production depth of N$_2$O affects its emission rate and that the low concentration of N$_2$O found in soil could not be simulated with a simple process-oriented model unless a consumption term was included. Yoh *et al.* (1997) reported that most N$_2$O produced in the topsoil may easily escape to the atmosphere without a long residence time in the soil, while N$_2$O produced at depth does not necessarily reach the atmosphere (Neftel *et al.*, 2000).

Transport processes are part of the third level of regulation of N$_2$O production in the model developed by Firestone & Davidson (1989) and Davidson (1991). With decreasing WFPS, diffusion and transport of gases increase. Upward movement of N$_2$O produced in soils should, thus, increase as soil water content declines. Transport of O$_2$ into the soil will also increase, however, which may slow down production rates of N$_2$O. The net effect of decreased WFPS on N$_2$O flux will depend on the balance between transport out of the soil and the influence of O$_2$ on nitrification, denitrification, and partitioning of N between gaseous products. The movement and fate of N$_2$O in the subsoil have recently been reviewed (Heincke & Kaupenjohann, 1999; Clough *et al.*, 2005). Transport of N$_2$O within the soil profile occurs predominantly via passive diffusion, but convective fluxes can also occur (e.g. via the penetration of water during rainfall or irrigation). Based on N$_2$O concentration profiles and estimates of diffusivity, Davidson *et al.* (2004) reported modest rates of net downward flux of N$_2$O deep in the soil profile. Hence, downward diffusion could be a sink, at least temporarily, for N$_2$O produced within the surface layers of soil. Neftel *et al.* (2000) showed that the N$_2$O concentrations in a soil under sown grassland remained below atmospheric concentrations in the zone below the plough depth where diffusivity was low. Metay (2005) reported net N$_2$O concentration in a soil profile while slightly negative or very low positive fluxes were measured at the soil surface. This might have been linked to a lack in gas diffusion or a time lag as N$_2$O production at depth and at the surface were measured simultaneously. Thus, the relationship between N$_2$O concentrations measured in the soil and at the surface may not be direct, particularly if production occurs at depth.

Sink activity can be linked to the ease of diffusion of N$_2$O through soil rather than to the potential for N$_2$O reduction *per se* (Ryden, 1981), as high water contents may restrict N$_2$O diffusion (i.e. increase the residence time), leading to the microbial consumption of N$_2$O before emission (Letey *et al.*, 1980a, b; Arah *et al.*, 1991; Lessard *et al.*, 1996). Several authors reported that consumption of N$_2$O may occur when it diffuses upwards in the soil profile (Clough *et al.*, 1999; van Groenigen *et al.*, 2005). Soil physical factors, such as structure, compaction, fine texture, surface sealing, impeded drainage, or shallow groundwater may also affect the balance between diffusive escape of N$_2$O and its further consumption.

Infiltration of water into the soil may lead to entrapment and the temporary storage of N$_2$O, ebullition, or the transport of dissolved N$_2$O in soil leachates as reviewed by Clough *et al.* (2005). Nobre *et al.* (2001) underlined the connection between the movement of a water front into the soil and the change of N$_2$O concentrations within the soil. N$_2$O solubility in water decreases with increasing alkalinity, salinity and temperature (Heincke & Kaupenjohann, 1999). The uptake of N$_2$O in soil water increases the time for potential reduction of N$_2$O to N$_2$ as the time required for N$_2$O to diffuse from the soil profile to the surface is increased. N$_2$O dissolved in soil water may be taken up from soil by roots, leading to N$_2$O emission via plant transpiration (Mosier *et al.*, 1990; Chang *et al.*, 1998; Rusch & Rennenberg, 1998). Water-dissolved N$_2$O may also be transported with drainage to surface or ground waters and, thus, generate N$_2$O emissions elsewhere (Dowdell *et al.*, 1979; Bowden & Bormann, 1986; Sotomayor & Rice, 1996; van Cleemput, 1998; Heincke & Kaupenjohann, 1999; Well *et al.*, 2001). McMahon & Dennehy (1999) reported a supersaturation of river water with N$_2$O of 2500%, leading to median surface emission rates between 90 and 32 600 μg N m^{-2} day^{-1}. A recent study by Clough *et al.* (2006a) suggests that a significant proportion of N$_2$O fluxes from river surfaces may be due to antecedent N$_2$O, (i.e. N$_2$O already dissolved in groundwater flows). This further confounds the relationship between controlling factors in the soil and surface fluxes of N$_2$O.

Contrary to other soil variables potentially affecting N$_2$O reduction, the influence of the ease of diffusion seems to be straightforward. The longer N$_2$O remains in the soil, either due to production in deep soil layers or due to factors reducing diffusion, the more N$_2$O is consumed. There are, however, considerable uncertainties, difficult to quantify, when trace gas sources or sinks are not uniformly distributed in the soil or located

too close to the surface for gradients to be measured, or when nondiffusive transport is involved. The uptake of N_2O by plant roots or the transport by drainage water after its production in the soil may contribute to its local disappearance but generate emissions elsewhere.

Measurement of N_2O consumption

We have so far seen that net negative N_2O fluxes have frequently been reported and that they are usually neglected or interpreted as measurement errors. In contrast, N_2O consumption during denitrification is an accepted pathway that has been studied. Methods to investigate N_2O consumption during denitrification include inhibitor studies (Ryden et al., 1979; Klemedtsson et al., 1990; Garrido et al., 2002), stable isotope assays (Punshon & Moore, 2004b; Clough et al., 2005, 2006b), and microbial approaches (Chéneby et al., 1998; Cavigelli & Robertson, 2001; Mei et al., 2004). We will discuss the advantages and disadvantages of their potential to study gross N_2O consumption.

In inhibitor studies, acetylene (C_2H_2) is used in large concentrations (usually 10 kPa) to inhibit NOR (Yoshinari et al., 1977). Soil is incubated with and without C_2H_2. The difference between N_2O produced in the two treatments is supposed to be equal to the amount of N_2O that is reduced to N_2 without C_2H_2 addition (Ryden et al., 1979). Hénault et al. (2001) carried out incubations in the presence or absence of C_2H_2 with addition of N_2O as electron acceptor to test the capacity of soil to reduce N_2O to N_2. They reported gross reduction rates in denitrification up to $-0.30 \mu g N g^{-1} soil h^{-1}$ in arable and grassland soils. The advantage of the C_2H_2 method is that it is easy-to-use and cheap, but it also has several disadvantages. First of all, nitrifiers are inhibited by small concentrations of C_2H_2 (Berg et al., 1982; Wrage et al., 2004b). This can lead to substrate limitations for denitrification, especially in systems like grasslands, were N inputs occur mainly in the forms of organic N or ammonium (Klemedtsson et al., 1990). Furthermore, due to the inhibition of ammonia oxidation, N_2O reduction by nitrifier denitrification cannot be studied with C_2H_2. Second, C_2H_2 can be oxidized by different microorganisms (Klemedtsson et al., 1990), so that the C_2H_2 concentrations may decrease during incubations. Last, but not least, C_2H_2 leads to a decomposition of nitric oxide (Bollmann & Conrad, 1997a), an important intermediate of denitrification, thus causing an underestimation of denitrification rates (Bollmann & Conrad, 1997b).

In stable isotope studies of N_2O reduction or denitrification capacity, typically the NO_3^- pool is labelled and the production of both $^{15}N_2O$ and $^{15}N_2$ measured (Myrold, 1990; Well et al., 2005). The amount of $^{15}N_2$ produced then indicates how much $^{15}N_2O$ has been reduced. The amount of NO_3^- added should be as small as possible, since NO_3^- is preferred as an electron acceptor over N_2O and changing ratios between the two could, therefore, influence N_2O reduction (Firestone et al., 1979).

A possibility to measure N_2O reduction more directly is to add $^{15}N_2O$ and follow this pool over time (Punshon & Moore, 2004a, b; Clough et al., 2005, 2006b). This approach has been applied to coastal waters to determine N_2O consumption (Punshon & Moore, 2004b). A disadvantage is that N_2O has to be added, thus potentially changing reaction rates. Punshon & Moore (2004a, b) added an amount equal to 10% of ambient N_2O as tracer. In soil studies, addition of $^{15}N_2O$ permits the study of gross N_2O consumption, as well as its transport (Clough et al., 2005) if application can be achieved without changes in gas pressure. In a soil column study, Clough et al. (2006b) allowed ^{15}N-enriched N_2O to diffuse from a reservoir into a 100 cm long soil column at a depth of 60 cm over a 12-day period. Measuring samples from the soil profile and the headspace, as well as from the reservoir, they could calculate gross N_2O production and consumption rates. The passive introduction of N_2O into soil allows the study of its disappearance, especially when labelled N_2O is used. However, the increased N_2O concentration could induce changes in the processes involved in N_2O reduction.

Natural abundance studies have the advantage that no material needs to be added to the soil. Owing to the different fractionation occurring during the production and consumption of N_2O, these processes can be distinguished. The isotopic discrimination, or isotope effect, of N_2O production has been reported to be 35 ‰ for $\delta^{15}N$ in pure culture studies of nitrification (Mariotti et al., 1981), more than 60‰ in soil studies of nitrification (Yoshida, 1988), and 29‰ in denitrification (Barford et al., 1999). For N_2O reduction to N_2 in denitrification, an isotope effect of 13‰ has been reported for $\delta^{15}N$ (Barford et al., 1999). Perez et al. (2000) found large variation in $\delta^{15}N$ ($-34‰$ to $-23‰$ in Costa Rica, $-34‰$ to $+2‰$ in Brazil) and $\delta^{18}O$ of N_2O ($-2‰$ to $+11‰$ in Costa Rica, $-4‰$ to $+18‰$ in Brazil) emitted from tropical rain forest soils. They attributed these variations to different gross production and consumption of N_2O, with a larger fraction of N_2O reduction to N_2 in the Brazilian sites. Van Groenigen et al. (2005) measured vertical gradients of $\delta^{15}N$ and $\delta^{18}O$ in N_2O. They identified the subsoil at 90 cm as the main source of N_2O, which was subsequently consumed on its way to the topsoil. Enrichment in $\delta^{15}N$ and $\delta^{18}O$ of N_2O together with constant or decreasing N_2O concentrations revealed N_2O consumption in soil incubations

(Wrage *et al.*, 2004a). Thus, if N$_2$O production and consumption take place at different locations or if consumption is high, the natural abundance of δ^{15}N and δ^{18}O in N$_2$O allow detection of N$_2$O consumption. However, it is difficult to quantify N$_2$O consumption in natural abundance studies due to the simultaneous occurrence of several processes, which influence the isotopic composition of the different products.

Molecular methods do not aim to quantify N$_2$O consumption, however, they can help to explain differences in consumption behaviour of different soils (Chéneby *et al.*, 1998). In molecular approaches, the presence or absence of important genes, for example, the NOR (*nos*Z)-like gene (Zumft *et al.*, 1990), can be evaluated by polymerase chain reaction. However, the presence of a gene does not necessarily mean that the enzyme is present and active. Chéneby *et al.* (1998) found the presence of the *nos*Z-like sequence to be a poor predictor of N$_2$O reducing ability when they combined the molecular approach with community studies in which they isolated the NO$_3^-$-respiring bacteria from the soils and tested them separately for their ability to reduce N$_2$O.

In a community study, Cavigelli & Robertson (2000) controlled all known environmental regulators of N$_2$O production and consumption in soil incubations, using C$_2$H$_2$ methodology, or provided these regulators in unlimiting amounts. Thus, the only factor leading to different responses of two soils should have been community composition. With this approach, different reactions of the denitrifying communities of an agricultural and a successional field, respectively, to oxygen and pH were found, as reported above.

Mei *et al.* (2004) developed another method to study differences in N$_2$O production and consumption abilities between soil microbial communities. They prepared serial 10-fold soil dilutions similar to those used in the most probable number method (MPN) and added NO$_3^-$ or N$_2$O as the sole electron acceptor. With NO$_3^-$ as electron acceptor, both N$_2$O producers and consumers determined the final N$_2$O concentration. When N$_2$O was the sole electron acceptor, only N$_2$O consumption could take place. Thus, production and consumption could both be studied. Furthermore, the development of the N$_2$O concentration in highly diluted suspensions allowed conclusions to be drawn about the relative abundance of N$_2$O producers and consumers in the soil (Mei *et al.*, 2004). A problem of all community studies is the need to culture the microorganisms. Culture conditions might suppress the growth of some species that might be important in soil. Furthermore, it is not possible to study the effect of different groups, e.g. of nitrifiers and denitrifiers, simultaneously.

To sum up, several methods exist to study N$_2$O consumption. However, so far no nonintrusive method allows to reliably quantify the gross amount of N$_2$O reduced *in situ*. Until a better method is found, stable isotope approaches, especially passive introduction of ^{15}N$_2$O into soil, as well as community and molecular approaches can help to detect N$_2$O consumption and to compare the consumption potentials of different soils.

Implications for global budgets

Periodic or net annual consumption by soil may have important repercussions for the global source and the atmospheric lifetime of N$_2$O. Goossens *et al.* (2001) reported slightly negative N$_2$O fluxes for 68% of observations of an unsaturated, very acid forest soil, accounting for a total net uptake of -500 ± 50 g N$_2$O-N ha^{-1} during a 314-day measurement period. Similar N$_2$O uptake rates from temperate forest soils have been reported by Klemedtsson *et al.* (1997) and Butterbach-Bahl *et al.* (1998). Donoso *et al.* (1993) extrapolated their results to the whole tropical savannah region and obtained a net negative N$_2$O flux of the same order as the production of N$_2$O due to biomass burning in the tropics. Rosenkranz *et al.* (2005) reported weak but significant negative N$_2$O fluxes in Mediterranean forest soils over a long time period, which represented a mean annual flux of approximately -0.5 kg N ha^{-1} yr^{-1}. So, the net negative N$_2$O flux at the soil/atmosphere interface could be significant on a global scale when considered on a cumulative basis. Cicerone (1989) concluded that a global soil sink of -1.5 to -3 Tg N per year may reduce the atmospheric lifetime by as much as 20% and included a small N$_2$O soil sink in model calculations of sources and sinks of atmospheric N$_2$O.

The Intergovernmental Panel on Climate Change (2001) reported that known total sources for 1994 (17.7 Tg N-N$_2$O yr^{-1}) do not equal known stratospheric sinks (12.6 Tg N-N$_2$O yr^{-1}) plus the atmospheric increase (3.8 Tg N-N$_2$O yr^{-1}). However, the unbalance necessary to close the budget (a sink of ca. 1.1 Tg N-N$_2$O yr^{-1}) is small compared with the range of the estimates and their associated error terms, e.g. total source estimates range from 6.7 to 36.6 Tg N-N$_2$O yr^{-1} (Intergovernmental Panel on Climate Change, 2001). Nevertheless, the stratospheric lifetime of N$_2$O seems to be shorter than previously thought (Intergovernmental Panel on Climate Change, 2001), indicating that the sinks may have been underestimated. N$_2$O emissions from soils are the largest term in the budget (10.2 Tg N-N$_2$O yr^{-1}, with 6 Tg N-N$_2$O yr^{-1} for natural soils and 4.2 Tg N-N$_2$O yr^{-1} for agricultural soils), but with large uncertainties (Mosier *et al.*, 1998; Intergovernmental Panel on Climate Change, 2001).

For soil IPCC values, the publication of Mosier *et al.* (1998) served as a reference, outlining that soil uptake of

N_2O will not be included in the budget for agricultural systems until better information becomes available. Although the Intergovernmental Panel on Climate Change (2001) noted that a soil sink exists, the guidelines (Intergovernmental Panel on Climate Change, 1997, 2000, 2003) on how to construct N_2O inventories only provide default emission factors for N_2O. As the estimates of N_2O sources from soils and the emission factors are based on means of net flux measurements, which may include some net negative flux, the net source estimates may include part of the sink component. However, if net negative flux measurements were not systematically included, a significant bias may have been introduced into the net N_2O emission estimate from soil.

Considering a total soil surface of ca. 134.4 million km^2, the global emissions from soils of ca. 10.2 Tg $N\text{-}N_2O\,yr^{-1}$ correspond to a mean flux of $8.7\,\mu g\,N\text{-}N_2O$ $m^{-2}\,h^{-1}$ or an instant flux of $2.4\,ng\,N\text{-}N_2O\,m^{-2}\,s^{-1}$. In absolute values, the observed negative N_2O fluxes (Table 1) were of the same order of magnitude. Depending on the periodicity of production and the so far neglected uptake, this means that the consideration of N_2O uptake by soils may considerably lower calculated net emissions, and perhaps allow closing of the global N_2O budget.

An increased understanding of soil N_2O uptake is fundamental if we wish to close the global N_2O budget, but also to evaluate the possibility to enhance this sink. We have seen that N_2O consumption can be quite large, making it a potentially important process on a global scale. To be able to consider it in budgets and models, it is necessary to get to know more about the processes involved and their driving factors.

Conclusion

Despite uncertainties of *in situ* N_2O measurements resulting from high heterogeneity in soil properties, as well as analytical error, the multitude and extent of reported negative N_2O fluxes makes it clear that they cannot be treated as mere measurement errors.

N_2O can be consumed by denitrifiers, but probably also by nitrifiers. Net negative N_2O fluxes have been found in a range of conditions, often, but not always connected to low N and low O_2. The rate of N_2O uptake (reduction to N_2 plus absorption by water) primarily depends on soil properties, such as the availability of mineral N (substrate for nitrification and denitrification), soil oxygen and water content, soil temperature, pH and redox conditions, and the availability of labile organic C and N. The diverse conditions stimulating N_2O uptake, including the enigma of uptake in dry soil, hint at various processes responsible for the uptake.

More process-oriented research is needed to understand what these processes are and how soil variables interact to control N_2O uptake in agricultural and natural soils in temperate and tropical regions. Generally, factors opposing diffusion of N_2O in soil seem to increase its consumption. Although we have concentrated on reports of net negative N_2O flux, N_2O consumption might also take place in soils with net N_2O production if gross production exceeds gross consumption. It is suggested that N_2O uptake is often masked by larger N_2O production and might, therefore, be more important than so far assumed. A nonintrusive method still needs to be found to clearly quantify the gross uptake of N_2O *in situ*.

The issue of soils acting as a sink for N_2O may be indirectly accounted for in the global N_2O budget when included in the estimate of net emissions, but this is uncertain as researchers may systematically discard their negative measurements before calculating reported mean fluxes. As pointed out by several authors cited in this review and by the IPCC (Intergovernmental Panel on Climate Change, 2001), soils may have to be considered as an additional sink next to stratospheric N_2O destruction. However, it must be stressed that the database from both field and laboratory studies must still be expanded before definite conclusions can be drawn about the magnitude of this possible additional sink and its contribution to the global N_2O budget.

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