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Gaseous nitrogen emmissions from undisturbed terrestrial ecosystems: An assessment of their impacts on local and global nitrogen budgets

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Abstract. There is increasing interest in the importance of nitrogen gas emissions from natural (non-agricultural) ecosystems with respect to local as well as global nitrogen budgets and with respect to the effects of nitrogen oxides on atmospheric ozone levels and global warming. The volatile forms of nitrogen of common interest are ammonia (NH_3), nitrous oxide (N_2O), dinitrogen (N_2), and NO_x (principally $NO + NO_2$). It is often difficult to attribute emissions of these compounds from soils to a single process because they are produced by a variety of common biogeochemical mechanisms. Although environmental conditions in the soil often appear to favor nitrogen gas emissions, the potential nitrogen gas emission rate from undisturbed ecosystems is rarely approached. The best estimates to date suggest that nitrogen gas emission rates from undisturbed ecosystems typically range from < 1 to perhaps 10 or 20 kg N ha^{-1} yr^{-1}. Under certain conditions, however, emission rates may be much higher. For example, excreta from animals in grasslands may elevate ammonia volatilization up to 100 kg N ha^{-1} yr^{-1} depending on grazer density; tidal input of nutrients to coastal wetlands may support denitrification rates of several hundred kg N ha^{-1} yr^{-1}. Excepting such cases, gaseous nitrogen losses are probably a small component of the local nitrogen budget in most undisturbed ecosystems. However, emissions from undisturbed soils are an important component of the global source strengths for ($N_2O + N_2$), N_2O and NO_x (50%, 21%, and 10% respectively). Emission rates of N_2O from natural ecosystems are higher than assumed previously by perhaps 10 times. Large-scale disturbance may have a stimulatory effect on nitrogen emission rates which could have important effects on global nitrogen budgets. There is a need for more sophisticated methods to account for natural temporal and spatial variations of emissions rates, to more accurately and precisely assess their global source strengths.

Introduction

Losses of nitrogenous gases from soil-plant systems have been a central issue in ecosystems research for at least three decades (Allison 1955, Porter 1975, Freney and Simpson 1983). The pioneering work in this field was done by agricultural scientists who were concerned about the agronomic consequences of nitrogen loss by volatilization from productive soils, especially after fertilization. More recently, ecologists have questioned whether nitrogen volatilization is an important component of the nitrogen budget in natural ecosystems, especially when nitrogen appears to be the limiting nutrient (Bormann and Likens 1979). Atmospheric scientists have questioned whether nitrogen emissions from natural lands have an impact on stratospheric ozone chemistry and global warming trends (Crutzen 1974, McElroy et al. 1977, Marland and Rotty 1985, Crutzen and Andreae 1985).

The transformations that lead to volatile nitrogen losses from agricultural land are common to all ecosystems and can occur under widely differing environmental conditions, suggesting that volatile losses of nitrogen could be important in a variety of natural ecosystems. In addition, since ammonium and nitrate are precursors for most volatile nitrogen compounds, high nitrogen gas emission rates could have a direct affect on biomass production in nitrogen limited systems. However, until recently there were very few data available to assess the importance of these suggestions.

The purpose of this paper is to review the state of our knowledge about the magnitude and ecological consequences of nitrogenous gas losses from undisturbed, non-agricultural land. The nitrogenous gases of primary concern here are ammonia (NH_3), nitrous oxide (N_2O), dinitrogen (N_2) and nitrogen oxides ($NO_x = NO + NO_2$). Nitrogen gas emission rates from other sources have been discussed elsewhere, e.g. oceans (Hahn 1981, Kahlil and Rasmussen 1983), inudustrial and urban combustion (Pierotti and Rasmussen 1976, Weiss and Craig 1976, Freyer 1978, Logan 1983), and agriculture (McElroy et al. 1977, Freney and Simpson 1983).

Nitrogen gas emissions will be considered in two contexts: the local nitrogen mass balance in specific ecosystems and the global, atmospheric nitrogen budget.

Mechanisms of nitrogen gas emission

The biogeochemistry of the terrestrial nitrogen cycle was thoroughly reviewed recently in Clark and Rosswall (1981). However, a brief description of the mechanisms that lead to nitrogen gas losses from ecosystems is relevant here. The gaseous nitrogen compounds described in this review (Figure 1) are the products of both biotic and abiotic transformations of inorganic nitrogen compounds. The significance of volatile organic nitrogen compounds in the nitrogen balance of ecosystems is less well-known (see for example, Farquhar et al. 1983).

Ammonia volatilization

The production of ammonium from organic matter is an ubiquitous property of decomposer microorganisms. In addition, the enzyme urease (urea aminohydrolase [EC 3.5.1.5]) produces ammonium from urea. This is an important source of ammonium when animal urine inputs are large, for example in feedlots or in dense herds of animals. It is far less important in natural ecosystems, such as grasslands and forests, where grazer density is low and patchy.

The ion ammonium (NH_4^+) is not volatile and must be de-protonated to

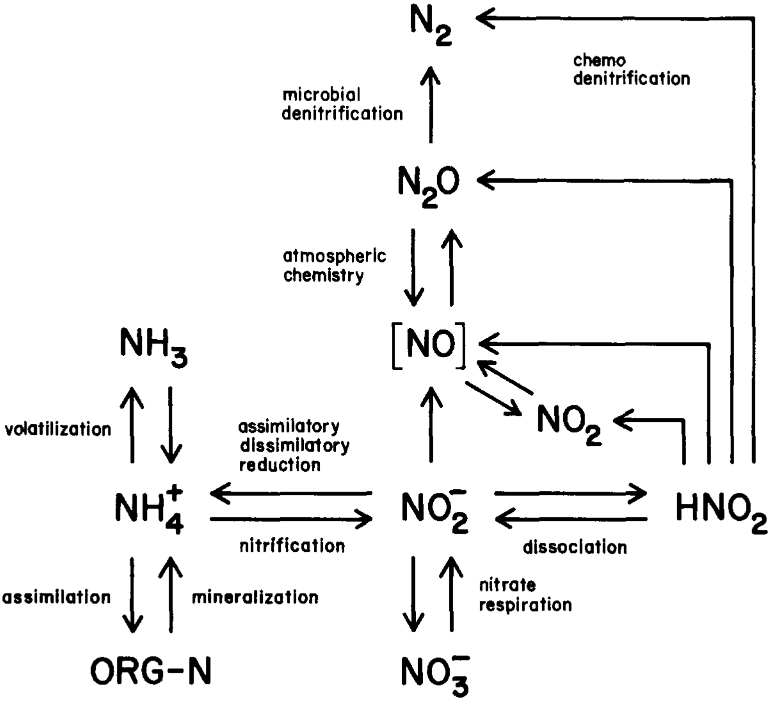

Figure 1. Components of the nitrogen cycle. Compounds in the upper half of the graph are the principle nitrogen gases emitted by ecosystems. The status of nitric oxide (indicated by [NO]) as an intermediate in biological denitrification remains uncertain. However, it has a major role in atmospheric chemistry.

form ammonia (NH_3) before it will diffuse from soils. The dissociation constant (pK) for the reaction

$$NH_3 + H_2O \leftrightarrow NH_4^+ + OH^-$$

is approximately 4.75 to 4.85 in the temperature range from 0 to 30 °C (Freney et al. 1983). It is apparent that the ratio NH_3/NH_4^+ is highly dependent on pH. At pH 5.6 (the pH of pure water in equilibrium with air) this ratio is 0.00025 or less. The NH_3/NH_4^+ ratio is greater than 0.1 only above pH 8.2 but rises quickly to 0.5 at pH 8.9. Consequently, soils must be relatively alkaline for there to be much NH_3 available for volatilization.

Several other factors also influence ammonia volatilization (Freney et al. 1983) (Figure 2). For example, ammonium is readily adsorbed onto soil particles and fixed into clay lattices (Mortland 1966) and so is protected from deprotonation to more volatile ammonia. Also, since ammonium is a major plant nutrient, plants tend to remove ammonium before it can diffuse away to potential sites of volatilization. Finally, ammonia is highly soluble

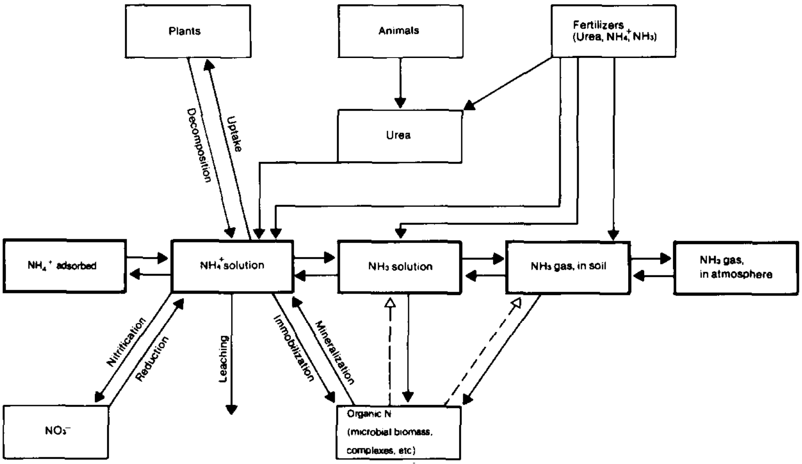

Figure 2. Some biological and chemical reactions affecting ammonia volatilization (from Freney et al. 1983).

in water (38% v/v at 15 °C [Merck 1976]) and its diffusion coefficient in moist soil (0.034 to $1.2\,cm^2 \cdot d^{-1}$) is orders of magnitude slower than its diffusion coefficient in air ($1.4 \times 10^4\ cm^2 \cdot d^{-1}$)(Gardner 1965). Consequently if the soil is moist, ammonia diffusion will be greatly retarded.

Nitrification

Until recently it was thought that nitrification had an indirect influence on nitrogen volatilization. Since the ultimate product of nitrification (nitrate) is the substrate for denitrification, factors that control nitrification should also control nitrogen gas losses via denitrification (see next section).

Recently, however, several investigators have shown that nitrous oxide is also a direct by-product of nitrification in soils and in the ocean (Bremner 1978, Bremner and Blackmer 1978, Cohen and Gordon 1978, Delwiche 1978, Freney et al. 1979, Blackmer et al. 1980, and Goreau et al. 1980). This work, and microbiological culture research that proceeded it, has been reviewed recently by Bremner and Blackmer (1981).

Evidence for the direct production of N_2O during nitrification is based on several observations. Bremner and Blackmer (1981) report that N_2O is produced from well aerated soils and that N_2O production is higher with added nitrifiable nitrogen (ammonium, urea, amino acids) than with added nitrate. These observations both indicate that significant amounts of N_2O can be produced under conditions that should not favor denitrification.

Other, strong evidence that N_2O is a by-product of nitrification comes from experiments with acetylene and "N-Serve" (2-chloro-6-[trichloromethyl] pyridine). Both of these compounds inhibit the oxidation of ammonium to nitrate and so eliminate N_2O production by nitrifiers (Bremner and Blackmer

1979). Acetylene also inhibits the reduction of N_2O to N_2 during denitrification (Yoshinari and Knowles 1976). The lack of N_2O evolution under aerobic conditions with acetylene indicates that N_2O production by denitrification in anaerobic microniches was negligible in the experiments observed by Bremner and Blackmer (1981).

Finally Bremner and Blackmer (1981) reported that they did not observe N_2O production in sterilized aerobic soil amended with ammonium until they added an inoculum of a nitrifier from pure culture. Each of these experiments indicates that N_2O is a direct by-product of nitrification.

In the field, N_2O production via nitrification is controlled by the oxygen status of the soil, by a readily available supply of nitrifiable nitrogen, by moisture content, and by temperature. It is difficult, however, to partition N_2O losses in the field between nitrification and denitrification because the distribution of aerobic and anerobic sites in the soil is usually unknown. Even in well aerated soil there can be localized areas (e.g. within soil aggregates) that support anaerobic microbial activity. The properties of these anaerobic "microniches" have been discussed recently by Stolzy and Fluhler (1978), Tiedje et al. (1984), and Sexstone et al. (1985).

Consequently, while popular field approaches (open and closed chambers) can quantify total N_2O emission rates, they can not separate nitrification from denitrification as sources of N_2O. The field acetylene-perfusion approach of Ryden et al. (1979) is an improvement that can partition the sources of N_2O *in situ*, but this technique may be difficult to implement at remote locations with rocky, untilled soil. The most unequivocal (though technically difficult) approach to partition nitrification and denitrification as sources on N_2O would be to use ^{15}N-isotopes of ammonium and nitrate and to analyze for oxides of nitrogen tagged with ^{15}N.

There are reports (Lipschultz et al. 1981, Johansson and Galbally 1984) that oxides of nitrogen other than N_2O (primarily NO but also NO_2) are produced by soil nitrifiers. Johansson and Galbally (1984) detected NO production, presumably from nitrifiers, in reconstructed soil cores held under aerobic conditions in the laboratory. Tests showed that the NO production could not be attributed to abiotic reactions (but see Chemodenitrification, below). The importance of biological NO_x production during field nitrification is unknown.

Verstraete and Alexander (1973), Duggin (1984), and Schimel et al. (1984) have suggested that a major portion of the nitrification in some ecosystems may be heterotrophic, rather than autotrophic. Although Kaplan and Wofsy (1985) argue that the potential exists for N_2O production during heterotrophic nitrification, there is little evidence, yet, that they do so in the field. However, Castignetti and Hollocher (1982) have demonstrated that an *Alcaligenes* sp. isolated from soil produces N_2O when grown as a nitrifier on hydroxylamine in aerobic culture.

Microbial denitrification

The largest body of literature on gaseous nitrogen losses from soils concerns the loss of N_2 and nitrogen oxides during nitrate reduction, principally by denitrification. Denitrification is a microbiological process in which nitrate substitutes for oxygen as a terminal electron acceptor when oxygen is unavailable. The ultimate product is N_2 with various oxides of nitrogen as intermediates (Figure 1).

The physiology, genetics, ecology, and bioenergetics of denitrification are well known and have been reviewed extensively (Payne 1973, Stouthamer 1976, Focht and Verstraete 1977, Delwiche 1981, Knowles 1982, Fillery 1983, Firestone 1984). For the purposes of this review it is sufficient to recall that denitrification requires low oxygen conditions. Oxygen need not be completely absent in the bulk soil, however, for denitrification to proceed. The concept of anaerobic "microniches" is usually invoked to explain the co-occurrence of denitrification and generally oxic conditions. In addition, denitrification requires a ready supply of reduced carbon for energy and nitrate as a substrate. In otherwise favorable environments, nitrogen gas losses by denitrification may be limited by a lack of available carbon (Stanford et al. 1975, Jacobson and Alexander 1980, Burford and Bremner 1975) or by a lack of sufficient nitrate (Firestone et al. 1979, Firestone et al. 1980).

Other important environmental controls include temperature, soil moisture, and pH. Denitrification is strongly influenced by temperature, with Q_{10}'s reported from 1.4 to 16 depending on temperature range (Focht and Verstraete 1977). Continuous saturation (waterlogging) can reduce denitrification if it also restricts nitrification, which produces the substrate nitrate. In constrast, Patrick and Wyatt (1964) and Mulvaney and Kurtz (1984) noted that denitrification losses could be greatest in environments with large fluctuations in soil moisture (e.g. during irrigation). Presumably, water stimulates denitrification by temporarily limiting oxygen diffusion into soil and by solubilizing reduced carbon and nitrate. Binstock (1984) and Sexstone et al. (1985) have noted that, in uncultivated ecosystems with natural moisture regimes, losses of nitrogen by denitrification may increase for short intervals (hours to days) after rain storms.

Decreasing pH has an uncertain effect on the overall rate of denitrification (Fillery 1983) but dramatically alters the distribution of end products. Wijler and Delwiche (1954) and Nommik (1956) among others have noted that increasing soil acidity increases the mole fraction of N_2O production ($N_2O/[N_2O + N_2]$). This suggests that N_2O may be the dominant product in acidic soils, e.g. forest spodosols (Melillo et al. 1983, W.B. Bowden unpublished data).

There is considerable confusion in the literature about the ability of denitrifying microbes to produce oxides of nitrogen other that N_2O. One source of confusion revolves around the issue of whether NO is a free intermediate in the denitrification process. Payne (1981) argues that NO is a free intermediate while Averill and Tiedje (1982) have advanced an alternative hypothesis that excludes NO as a true intermediate. A second source of confusion is whether the major source of NO_x is attributable to abiotic transformations (see Chemodenitrification, below) rather than biotic transformations.

Chemodenitrification

Clark (1962) suggested the term "chemo-denitrification" for chemical reactions of nitrite that lead to gaseous nitrogen compounds like those found during microbial denitrification. These gaseous compounds include dinitrogen (N_2), nitrous oxide (N_2O), nitric oxide (NO), nitrogen dioxide (NO_2) and less familiar nitrogen compounds such as methyl nitrite (CH_3NO_2). The literature on chemodenitrification has been reviewed recently by Chalk and Smith (1983).

In general, chemodenitrification is most likely when conditions of high nitrite and low pH coexist. Such conditions prevail after application of alkaline-hydrolyzing fertilizers to crops. Various mechanisms by which nitrite (or nitrous acid) can react to form gaseous nitrogen compounds are listed in Table 1. In non-agricultural ecosystems nitrite does not usually accumulate because during complete nitrification, the nitrite oxidation rate is generally limited by the ammonium oxidation rate (Focht and Verstraete 1977). Consequently, even though soil pH can be quite low in some natural ecosystems, chemodenitrification should be limited by available nitrite. Nevertheless, in his review of microbial denitrification, Fillery (1983) concluded that while microbial denitrification produces most of the N_2O and N_2 in soil-plant systems, most of the NO_x (NO and NO_2) produced in soils may be due to chemodentrification. In support of this, some investigators (e.g. Bulla et al. 1970, Smith and Chalk 1980a, b) have demonstrated that NO_x is produced in significant amounts from sterilized and unsterilized soils amended with nitrite. In constrast, other investigators (e.g., Johansson and Galbally 1984, McKeeney et al. 1982) suggest that chemodenitrification is not quantitatively important and that most NO_x and N_2O is biogenic.

Non-denitrifying nitrate reducers

Rigorously defined, denitrification refers to the respiratory reduction of NO_3^- to free nitrogen gases. However, there are other forms of nitrate reduction, both assimilatory and dissimilatory, that may lead to nitrogen gas losses (Figure 1).

Smith and Zimmerman (1981) found that 163 of 209 soil bacterial isolates they studied (primarily *Bacillus* and *Enterobacter* species) reduced nitrate and produced N_2O. However, the N_2O production was not linked to respiration and these organisms could not reduce nitrogen past N_2O. In addition to N_2O, these organisms produced NO_2^- or NH_4^+. Chemodenitrification of NO_2^- to N_2O was thought to be small. Smith and Zimmerman (1981)

Table 1. Various mechanisms for the chemical reduction of nitrous acid or nitrite ion to gaseous products. After Chalk and Smith (1983). Gaseous products are in bold type

Mechanism	Representation	Reference
Self-decomposition of nitrous acid	$3HNO_3 \rightleftharpoons HNO_3 + \mathbf{2NO} + H_2O$	Chalk and Smith (1983)
	$2HNO_2 \rightleftharpoons \mathbf{NO} + \mathbf{NO_2} + H_2O$	Nelson and Bremner (1970)
Reaction with amino acids (Van Slyke)	$R\text{-}NH_2 + HNO_2 \rightleftharpoons R\text{-}OH + H_2O + \mathbf{N_2}$	Allison (1966)
Reaction with ammonium	$HNO_2 + NH_4^+ \rightleftharpoons \mathbf{N_2} + 2H_2O + H^+$	Ewing and Bauer (1966)
Reaction with soil organic nitrogen	$\text{phenolics} + HNO_2 \rightarrow\rightarrow \mathbf{N_2O, N_2}$	Stevenson et al. (1970)
Reaction with metal ions	$M^{++} + NO_2^- + 2H^+ \rightleftharpoons M^{+++} + \mathbf{NO} + H_2O$	Wullstein and Gilmour (1966)

concluded that these non-denitrifying nitrate reducers (or nitrate respirers) could be a potentially important souce of atmospheric N_2O.

In an extension of this study, Bleakley and Tiedje (1982) found that all of the nitrate-respiring (i.e. NO_3^- reduction to NO_2^- or NH_4^+) bacteria they tested, produced N_2O, but could not reduce it further. In addition, they found one assimilatory nitrate-reducing bacterium (*Azotobacter vinelandii*) and numerous yeast and fungi (e.g. *Aspergillus* and *Fusarium*) that produced N_2O. Burth et al. (1982) and Burth and Ottow (1982) also observed N_2O releases by non-denitrifying nitrate reducers.

In general it seems that nitrogen gas losses, at least of N_2O, may be widespread among organisms that are capable of any of a number of forms of nitrate reduction.

Foliar nitrogen volatilization

Farquhar et al. (1983) concluded that it is unlikely that oxidized forms of nitrogen are important in foliar volatilization. However, early studies (notably by Klein and Steiner [1928] and Steiner and Loffler [1931] as quoted in Farquhar et al. [1983]) established that reduced forms, such as ammonium and various amines, may be important sources of nitrogen for volatilization.

For ammonium to volatilize from leaves, there must be a free, intracellular pool of ammonium as a source. Although ammonium is rapidly assimilated by plants, general enzyme kinetics dictate that some free ammonium must by present to drive the assimilatory enzymes. Farquhar et al. (1983) argue that ammonium in this pool might as easily volatilize from the leaves as participate in an enzymatic reaction. However, as in the soil, the ammonium must first hydrolyze to NH_3 which will then be slowed from volatilization by the humidity and tortuosity of the leaf's interior.

The amount of volatile nitrogen compounds in leaves and flowers is highly correlated with the developmental stage of the plant so that nitrogen volatilization from foliage may have a strong seasonal pattern. For example, proteolysis after flowering and before complete senescence leads to periods of high ammonium content in leaves and possibly to periods of high ammonium volatilization. Evidence for such losses is scant (Hooker et al. 1980, Farquhar et al. 1979, Schimel et al. in press) and does not indicate that nitrogen volatilization during senescence is large.

Summary of mechanisms of volatilization

It is apparent from the proceeding discussion that gaseous nitrogen compounds can arise via a number of different mechanisms in natural ecosystems. It is important to realize that each of these compounds can arise via more than one mechanism and that different mechanisms function under different environmental conditions. As a consequence one can observe NO_x emissions, for example, under both aerobic and anaerobic conditions. Furthermore, experimental approaches based on the spatial or temporal characteristics of the emission rate of a particular compound (e.g. micrometeorological or chamber methods) can not typically provide detailed information about the emission mechanism. On the other hand, it is difficult to estimate quantitatively the total flux of nitrogen gases from rate estimates of individual mechanisms observed in the laboratory because the experimental conditions that are best suited to study the mechanisms may not be environmentally realistic. This leads to an ecological analog to "Heisenberg's Uncertainty Principle" in physics. That is, you can measure the net rate of a multicomponent phenomena but you cannot at the same time measure the rates of the individual components with certainty, and vice versa.

It is also apparent from the proceeding discussion that although there is a potential for nitrogen gas volatilization from natural ecosystems, the realization of this potential could be severely limited by natural factors. Clearly, factors such as temperature and soil structure ultimately control gas production by microbes and gas diffusion in soils, respectively; but other factors are also important. For example, ammonia volatilization in many natural ecosystems is probably limited by acid soils. Microbial denitrification may be limited by a lack of substrate NO_3^- or oxidizable carbon or both, while chemodenitrification is probably limited by a lack of NO_2^-. The yield of nitrogen oxides via nitrification and of reduced nitrogen via foliar emissions has been found to be naturally low. This limitation of potential nitrogen gas emission rates is discussed further in the section on measured emission rates, below.

This review deals exclusively with the emissions of nitrogen gases from natural plant-soil assemblages. There are, of course, mechanisms by which nitrogen gases are taken up by ecosystems, e.g. nitrogen fixation or dry deposition on vegetation. Furthermore, under different conditions, some of the emission mechanisms discussed here can become net sinks. For example, Farquhar et al. (1980) discuss the compensation point for ammonium volatilization from foliage and Blackmer and Bremner (1976) discuss conditions in which the soil is a net sink for N_2O (but not N alone since increased N_2O reduction causes a 1:1 increase in N_2 evolution). Simultaneous quantification of nitrogen gas input and output rates in natural ecosystems is a technically difficult but important area for research.

Rates of nitrogen gas emissions

Agricultural research has been invaluable to non-agricultural ecologists as a source for methods and for qualitative information about mechanims. However, quantitative rate estimates from agronomic experiments are often difficult to interpret in terms of natural ecosystems. Crop type, fertilization, irrigation, and tillage produce effects that have little relevance to forests, wetlands, or grasslands. There is a need therefore, to summarize the state of our knowledge about gaseous nitrogen emissions from natural ecosystems.

This section presents a compilation of measured nitrogen gas emission rates from undisturbed ecosystems. Rates are tabulated by compound (Tables 2–5) rather than mechanism since, as discussed earlier, it is difficult to reliably attribute a given emission to a single mechanism. The rates reported in Tables 2–5 tend to fall into common ranges for each ecosystem and each nitrogen compound. These ranges of "most likely" emission rates are summarized in Table 6.

All rates are expressed in standard units of kg N ha^{-1} yr^{-1} to facilitate comparisons. In many cases the rate reported in the original citation was not in these units so I have converted the reported rate to the standard unit. When rates were expressed on a short time interval (e.g. sec^{-1} or d^{-1}) this necessitated some assumptions about growing season or diel dynamics. These assumptions are noted in the tables.

For the purposes of this review I have not included reference to fertilized ecosystems or to "potential rate" estimates. Potential rate estimates in particular are valuable to explore specific mechanisms and their controls but can not easily be related to the field environment. For example, denitrification rate estimates are often made in soil slurries, under artificial atmospheres, and with large additions of nitrate and oxidizable carbon. Conditions in the field rarely approach these ideal conditions and so the rates measured have little relevance to the field.

The rates reported here are based on direct measurement approaches (e.g. chambers, micrometeorology, tracer-level isotope additons, or unamended whole-cores). These methods have been critiqued to varying degrees by Mathias et al. (1978), Jury et al. (1982), Denmead (1983), Focht (1978), Ryden and Rolston (1983), Hauck and Bremner (1976), Tiedje et al. (1979), and Parkin et al. (1984).

Measured ammonia emission rates from natural ecosystems vary widely from 0 to over 100 kg N ha^{-1} yr^{-1} (Table 2). In general, emission rates from natural ungrazed ecosystems are very low and do not contribute substantially to the global emission rate of ammonia. However, ammonia emissions can be large in densely grazed grasslands, primarily due to volatilization from animal urine and feces. The importance of natural grasslands, prairies, and savanna as sources of ammonia can be expected to increase with animal density.

Data for ammonium volatilization from arid lands is scarce. J. Klopatek (personal communication) has found that soil pH is routinely about 8 in the Piñon-Juniper communities he has sampled in the arid southwest U.S. At this pH, ammonia volatilization could be significant if free ammonium is available.

Ammonia emission rates in temperate and tropical forests are assumed to be low due to acidic soil, but direct measurements are virtually nonexistent. The one report by Kim (1973) for a pine and an oak forest in South Korea is

Table 2. Ammonia emissions from natural soil-plant assemblages. The data in this and the following tables is arranged by ecosystem types

Ecosytem	Rate (kg N ha^{-1} yr^{-1})	Method	Comment	Reference
Oak forest South Korea	43	Closed chamber with H_2SO_4 trap	Unusually long (1 week) incubations with trap. Probably overestimates loss rate. Assume 20 week growing season	Kim (1973)
Pine forest South Korea	56			
Grassland South Korea	30			
Grassland Western, USA	3.5–16.5	various	Increases with increasing livestock biomass	Woodmansee (1978)
Grazed sheep pasture Australia	95 114 0	micrometerorology	50 sheep/ha 22 sheep/ha 0 sheep/ha	Denmead et al. (1974) Denmead et al. (1976)
Grazed sheep pasture New Zealand	40–60	chamber	20 sheep/ha short incubation	Ball and Keeney (1981)
Semi-desert Great Plains, USA	1	^{15}N studies		West and Skujins (1977)
Wet meadow tundra Barrow, Alaska, USA	0	not available		Van Cleve and Alexander (1981)

based on a continuous trapping method that could create a gradient from the soil to atmosphere and so overestimate the true emission rate. Even if emissions at the soil were this high it is unclear whether the ammonia could pass through the canopy without being resorbed by leaves (Denmead et al. 1976).

Measured denitrification rates ($N_2O + N_2$) range from near 0 to as much as 650 kg N ha^{-1} yr^{-1} (Table 3). The highest rates for natural areas are in coastal wetlands. Here, organic soils, waterlogged conditions, and a continuous supply of nitrate in tidal water promote denitrification. Denitrification rates in polar regions are probably uniformly low due to limitations of temperature and nitrogen inputs. Denitrification rates for forests and grasslands range from $<$ 1 kg N ha^{-1} yr^{-1} to about 50 kg N ha^{-1} yr^{-1}.

Denitrification rates from undisturbed lands are much lower than denitrification rates measured in intensely managed agricultural ecosystems. However, the relatively small area of the world that is so intensely managed reduces the global importance of high emission rates from agricultural land. In comparison, moderate emission rates (1 to 3 kg N ha^{-1} yr^{-1}) from the large area of natural land could be very important on a global scale.

Due to concern about possible reductions in stratospheric ozone by increased nitrous oxide emissions (Crutzen 1974) there has been much research on the various mechanisms and rates of N_2O production. Measured nitrous oxide emissions range from near 0 to as much as 20 kg N ha^{-1} yr^{-1}, with most measurements in the $<$ 1 to 2 kg N ha^{-1} yr^{-1} range (Table 4). These rates greatly exceed the CAST report (1976) estimate of 0.2 kg N ha^{-1} yr^{-1} for uncropped land. Addition of N_2O emission rates from fertilized, agricultural land to the measured natural rates increases the total estimated N_2O emission rates still further. If, in addition, the N_2O emission rates in tropical moist forests are especially high, as suggested recently by Keller et al. (1983 and in press), then total estimated N_2O emissions from land could be much higher than thought previously.

There are very few measurements of NO_x emissions from natural soils that can be used to estimate annual emission rates. Numerous laboratory and field studies show that, under favorable conditions, NO_x can be produced from soils by both biotic (McKenny et al. 1982, Johannson and Galbally 1984) and abiotic (Chalk and Smith 1983, Van Cleemput and Baert 1984) mechanisms. The data in Table 5 indicate natural emission rates of 1 to 2 kg N ha^{-1} yr^{-1} (excepting the extreme sites reported by Galbally and Roy [1981]) but represent only three independent studies by two research groups. Most research to date indicates that NO is more important than NO_2 as a component of NO_x.

Importance of nitrogen gas emissions

A distinction should be made between the "analytical significance" of a flux and its "ecosystem importance." For example, electron capture gas

Table 3. Denitrification (N_2 plus N_2O emission) rates from natural soil-plant assemblages. This table includes estimates based on acetylene blockage which includes N_2O emissions

Ecosystem	Rate (kg N ha^{-1} yr^{-1})	Method	Comment	Reference
Hardwoods (50 yrs) New Hampshire, USA	1.4	Acetylene block, mixed soil samples.	Aerobic incubation without C_2H_2. Negligible N_2	Melillo et al. (1983)
Oak-hickory forest North Carolina, USA	10.7	N_2O reduction to N_2	Probably a potential estimate	Todd et al. (1975)
Hardwoods (60–300+ yrs) Michigan, USA	0.27–49.9	acetylene block whole cores	6 month growing season	Robertson and Tiedje (1984)
Conifers (25–300+ yrs) Michigan, USA	0.32–2.21	acetylene block whole cores	6 month growing season	Robertson and Tiedje (1984)
Conifers California, USA	< 1	acetylene block whole cores	Assume 5 month growing season	Strauss and Firestone (in review)
Terra firma rain forest Venezuela	2.9	soil slurries	Probably a potential estimate	Jordan et al. (1982)
Old field/grass Michigan, USA	0.29–1.53	acetylene block whole cores	6 month growing season	Robertson and Tiedje (1984)
Grassland Colorado, USA	trace	not available	Limited by nitrate. (But see Moisier et al. 1981)	Woodmansee (1978)
Salt marsh Louisianna, USA	30	^{15}N balance		DeLaune and Patrick (1980)
Salt marsh Massachusetts, USA	144	chamber	Very high nitrate input from springs	Valiela and Teal (1978)
Salt marsh Georgia, USA	120	N_2 diffusion gradients	Possibly an overestimate	Haines et al. (1977)
Salt marsh Georgia, USA	650	acetylene block	Slurries, probably a potential estimate	Whitney et al. (1981)
Semi-desert Great Plains, USA	19	^{15}N tracer study	Intense nitrogen fixation exceeds plant demand	West and Skujins (1977)
Wet meadow tundra Barrow, Alaska, USA	0.024	^{15}N tracer study		Barsdate and Alexander (1975)

Table 4. Nitrous oxide emissions from natural soil plant assemblages. The emission rates below exclude nitrous oxide emissions in the presence of acetylene unless N_2 emissions were known to be small (see Table 3)

Ecosystem	Rate (kg N Ha^{-1} yr^{-1})	Method	Comment	Reference
Hardwoods (60 yrs) New Hampshire, USA	0.1	chamber	Average rate all year	Keller et al. (1983)
Organic forest soil New York, USA	0.9	chamber		Duxbury et al. (1982)
Deciduous forest Wisconsin, USA	0.19 and 0.80	chamber	1979 vs. 1980 growing season	Goodroad and Keeney (1984)
Hardwoods (60–300+ yrs)	0.18–19.4	acetylene block whole cores	6 month growing season	Robertson and Tiedje (1984)
Coniferous forest Michigan, USA	0.99 and 2.1	chamber	1979 vs. 1980 growing season	Goodroad and Keeney (1984)
Pines (25–300+ yrs) Michigan, USA	0.34–1.75	acetylene block whole cores	6 month growing season	Robertson and Tiedje (1984)
Tropical forests, Brazil Ecuador, Puerto Rico	2.9	chamber	Average rate all year	Keller et al. (in press)
Short grass prairie Colorado, USA	< 1	chamber		Moisier et al. (1981)
Prairie, unburned Wisconsin, USA	0.10 and 0.10	chamber	1979 vs. 1980 growing season	Goodroad and Keeney (1984)
Prairie, burned Wisconsin, USA	0.09 and 0.11	chamber	1979 vs. 1980 growing season	Goodroad and Keeney (1984)
Grass-weed field New York, USA	1.7 and 0.9	chamber		Duxbury et al. (1982)

Old field/grass Michigan, USA	0.56–1.57	acetylene block whole cores	6 months growing season	Robertson and Tiedje (1984)
Soil survey Iowa, USA	< 0.5	chamber	Personal communication from AM Blackmer and JM Bremner	Duxbury et al. (1982)
Salt marsh Louisiana, USA	0.31	chamber		Smith et al. (1983)
Brackish marsh Louisiana, USA	0.48	chamber		Smith et al. (1983)
Freshwater marsh Louisiana, USA	0.55	chamber		Smith et al. (1983)
Undrained marsh Wisconsin, USA	0.02 and 0.06	chamber	1979 vs 1980 growing season	Goodroad and Keeney (1984)
Drained marsh Wisconsin, USA	2.3 and 7.4	chamber	1979 vs. 1980 growing season	Goodroad and Keeney (1984)
Wet meadow Wisconsin, USA	1.1 and 1.4	chamber	1979 vs. 1980 growing	Goodroad and Keeney (1984)
Everglades organic soil Florida, USA	1	chamber		Duxbury et al. (1982)

Table 5. Nitrogen oxide (NO_x) emission rates from natural soil-plant assemblages

Ecosystem	Rate (kg N ha^{-1} yr^{-1})	Method	Comment	Reference
Oak forest South Korea	1.1	Closed chamber with NaOH trap	Long (1 week) incubation. Possibly overestimates rates	Kim (1973)
Pine forest South Korea	2.0			
Grassland South Korea	1.8			
Pasture soil Australia	1.0	chamber	Short incubation. Chemiluminescence detector	Galbally and Roy (1978)
Grazed legume pasture Australia	0.3–16	chamber	Extreme range for 12 sites. High values due to high mineral nitrogen at subsite. Assumes constant rate all year	Galbally and Roy (1981)

Table 6. Summary of most likely ranges for measured areal emission rates of volatile nitrogen compounds from undisturbed ecosystems based on compilations in Tables 2–5. Units are kg N ha^{-1} yr^{-1}. Trace emission rates (< 1 kg N ha^{-1} yr^{-1}) are indicated by "tr" or by "tr?" if the rate is unmeasured but can be presumed to be small. "ND" indicates no data are available

Ecosystem	NH_3	$N_2O + N_2$	N_2O	NO_x	Total[a]
Temperate hardwoods	tr?[b]	tr–10	tr–1	1	1–10[b]
Temperate conifers	tr?[b]	tr	1–2	2	2–4[b]
Tropical forests	ND	2.9	2.9	ND	3
Prairie/Grasslands	0–10[b,c]	tr	tr–2	tr–10	0–20[b]
Arid lands/Desert	1[d]	19[d]	ND	ND	1–20
Tundra/Boreal	0	tr	tr?	ND	tr
Wetlands/Marsh	ND	30–650	tr–10	ND	30–650

[a] This is not a sum but a "best approximation" based on the literature cited
[b] Ignores high rates reported by Kim (1973)
[c] Ungrazed to lightly grazed conditions
[d] Ammonium volatilization may be higher and denitrification lower in Piñon-Juniper communities (J. Klopatek, personal communication)

chromatography and chemiluminesence detectors allow estimation of N_2O and NO_x fluxes in field chambers in a range equivalent to a few hundredths of a kg N ha^{-1} yr^{-1}. Fluxes of nitrous oxide on the order of a few tenths of a kg N ha^{-1} yr^{-1} may be inconsequential to the ecologist interested in ecosystem budgets but may be noteworthy to the atmospheric scientist interested in the chemistry of stratospheric ozone.

To provide some perspective on the importance of gaseous losses with respect to local nitrogen cycling, Table 7 compares ranges for total nitrogen gas emissions from Table 6 with selected basic ecosystem fluxes in several different ecosystem types. The range of these estimates, both within and between ecosystems, is wide and yet several points may be made.

First, the range of gaseous nitrogen emission rates is roughly similar to the range of hydrologic export rates in forests and dominates hydrologic export in grasslands, deserts, and wetlands. It is unlikely, however, that nitrogen gas emissions by each of the various mechanisms discussed would be high simultaneously. Thus, gaseous outputs are probably skewed toward the low end of these ranges.

Second, most measurements indicate that gaseous nitrogen emissions do not constitute a large loss of nitrogen compared to commonly measured inputs such as precipitation and nitrogen fixation. A rigorous treatment of ecosystem nitrogen budgets requires attention to dry nitrogen deposition, accretion in biomass, deep seepage, etc. For example, the apparent input-output discrepancy in Table 7 for coastal wetlands is probably due to an additional input of nitrogen as nitrate in tidal water. Over long periods (decades to centuries), nitrogen outputs from healthy, stable ecosystems should not exceed nitrogen inputs (Odum 1969, Vitousek and Reiners 1975, Gorham et al. 1979). However, natural aperiodic events (hurricane blowdowns, fires, pest outbreaks) may cause transient excess losses of both gaseous and

Table 7. Comparison of selected ecosystem nitrogen fluxes with approximate total gaseous nitrogen emissions ($NH_3 + N_2O + N_2 + NO_x$). Gaseous emissions are from Table 6. All values are in kg N • ha^{-1} • yr^{-1}. Trace emission rates (< 1 kg N • ha^{-1} • yr^{-1}) are denoted "tr"

Ecosystem	Inputs		Interconversions		Outputs		Reference
	Precipitation	N Fixation[a]	Plant Uptake	Mineralization	Hydrologic	Gaseous	
Temperate Hardwoods	6.6–22.6	tr–12.1	72–153	24–400	3.1	tr–10[b]	Melillo (1981)
Temperate Conifers	2–14	5–10	30–50	30–50	0.5–1.5	2–4[b]	Gosz (1981), Boring et al. (in review)
Tropical Forest	tr–21	16–35	> 278[c]	> 278[d]	5–30	3–4	Bentley et al. (1982) Herrera and Jordan (1981)
Prairie Grasslands	1.5–10	tr–50	65–86	87–126	0	3–100[e]	Woodmansee et al. (1981), Jones and Woodmansee (1979), Woodmansee (1978)
Arid lands Desert	1–2	tr–13	10–40	60	0	1–20	West and Skujins (1977), Wallace et al. (1978), Skujins (1981)
Tundra Boreal	tr–2.5	tr–17	9–111	9–101	tr	tr	Van Cleve and Alexander (1981)
Wetlands Marshes	3–7.9[f]	67.9–149	183–700	183–700	–466–111[g]	30–650	Valiela and Teal (1979) Whitney et al. (1981)

[a] These rates can be considerably higher in ecosystems where symbiotic nitrogen fixation is important (Bormann and Gordan 1984, Boring et al. [in review]).

[b] Ignores high ammonia flux reported by Kim (1973).

[c] Amazon caatinga forest only. Estimated as sum of root turnover plus fine and woody litter fall. Does not include growth.

[d] At least equal to plant uptake?

[e] Assumes low grazer density. If grazer density increases, ammonia emissions alone could exceed 100 Kg N ha^{-1} yr^{-1}.

[f] Latter figure includes dissolved organic nitrogen.

[g] Tidal exchange. The magnitude and direction of this flux is the subject of some debate in coastal ecology. See for example Nixon (1980).

Table 8. Ranges for global emissions of volatile nitrogen compounds from undisturbed terrestrial ecosystems of the world. Land areas are rearranged slightly from Whitaker (1975, Table 5.2). Global emission rates are the product of land areas and measured areal emission ranges from Table 6. Areas are in units of 10^9 ha; emissions are in units of 10^{12} g N yr^{-1}. "tr" indicates global emission rates that are $<10^{12}$ g N yr^{-1}; "ND" indicates no data are available

		Global emission rate				
Ecosytem	Area	NH_3	$(N_2O + N_2)$	N_2O	NO_x	Total[a]
Temperate Hardwood	1.55	tr	tr–15.5	tr–1.5	1.5	1.5–15.5
Temperate Conifer	0.50	tr	tr	tr–1.0	1.0	1.0–2.0
Tropical Forests	2.45	ND	7.1	7.1	ND	7.4–9.8
Prairie/Grassland	2.40	0–24	tr	tr–4.8	3–24	4.8–48.0
Arid lands/Desert	4.20	4.2	0–80	ND	ND	4.2–84.0
Tundra/Boreal	2.00	0	tr	tr	ND	tr
Wetlands/Marsh	0.20	ND	6–130	tr–20	ND	6.0–130
Total[a]	13.30[b]	4–28	13–233	7–16	5–26	20–280

[a] Column and row totals may not sum due to rounding errors and differences in source data.

[b] Does not include cultivated land (1.4 × 10^9 ha) or lakes and streams (0.12 × 10^9 ha).

Table 9. Comparison of ranges for nitrogen gas emission rates from undisturbed terrestrial soils with estimated global emission rates from all terrestrial soils, oceanic sources, and combustion processes. The values in parentheses are "best approximations" based on the central tendencies of ranges reported in the literature. All values are in 10^{12} g N yr^{-1}

Source	NH_3	$(N_2O + N_2)$	N_2O	NO_x
Undisturbed soils[a]	4–28 (15)	13–233 (100)	7–16 (12)	5–26 (5)
All soils combined[b]	75–232 (125)	107–161 (120)	8.5–83[c] (< 30)	4–16 (8)
Oceans and seas[b]	negligible	25–179 (25)	5.7–80[c] (< 20)	negligible
Fossil fuel and biomass burning[b]	3.5–12 (5)	[2–6][d]	2–6 (3)	18–52 (23)
Total[be]	113–244 (150)	132–340 (200)	20–248 (55)	25–99 (50)

[a] Source: Table 8, this compilation.

[b] Sources: Burns and Hardy (1975), Peirotti and Rasmussen (1976), Soderlund and Svensson (1976), Delwiche (1977), McElroy et al. (1977), Hahn (1981), Galbally and Roy (1983), Khalil and Rasmussen (1983), Logan (1983).

[c] There is a strong decreasing trend in recent literature estimates of N_2O emissions from both terrestrial and especially oceanic sources.

[d] Presumed to be the same as N_2O emissions alone.

[e] These values are not necessarily the sum of values above due to miscellaneous sources (e.g. lightning for NO_x) and variations between independent estimates from the literature.

hydrologic outputs over atmospheric inputs. These occasional periods of net nitrogen loss make it difficult to quantify the true, long-term rate of nitrogen accretion in ecosystems, based on short-term measurements.

Finally, nitrogen gas losses are not usually large compared to internal conversions of nitrogen such as plant uptake or mineralization. This is consistent with Odum's (1969) suggestion that in mature ecosystems, internal nutrient turnover is maximized with minimum external loss.

While nitrogen gas emissions from natural ecosystems may not be important for local nitrogen mass balances, they are important for global atmospheric budgets, especially of N_2O and NO_x. Table 8 summarizes the estimated annual gaseous losses from the major biomes of the earth and supports several conclusions. First, the emission rate from wetlands and marshes is disproportionately high compared to the area occupied by these ecosystems (1.5% of total uncultivated land). This is due entirely to the large $(N_2O + N_2)$ flux from salt marshes. Note, however, that each of the salt marsh estimates used as a basis for this range (Table 3) may be an overestimate of the true emission rate.

The next highest global emission rate is for arid lands. This is due largely to the vast area occupied by this biome (31.6% of total uncultivated land). However, these emission estimates are very poorly constrained at the moment

(J. Klopatek, personal communication); the range for ammonia volatilization may be too low and the range for denitrification too high.

Finally, the emission rates from prairies and grasslands are occasionally quite high. The highest rates are associated with intense ammonia volatilization due to dense herds of grazing animals.

If one accepts Lovelock's (1979) premise about the tight coupling between atmospheric and biospheric processes (GAIA), then it should be apparent that natural ecosystems influence atmospheric nitrogen cycling. Additional questions concern the relative importance of anthropogenic versus natural, abiotic versus biotic, and oceanic versus continental influences.

It is apparent from Table 9 that, excepting ammonia volatilization, nitrogen gas emissions from natural terrestrial ecosystems are important on a global basis. Over 20% of the total global N_2O emissions and 50% of the total ($N_2O + N_2$) emissions may be due to natural terrestrial emissions. Despite the smaller area occupied by terrestrial ecosystems compared to oceans, they are the sole source of NH_3 and NO_x and probably dominate oceanic sources of both N_2O and N_2. Although over half of the NO_x emissions from soils are due to natural sources, undisturbed and total soils emissions make up only 10% and about 16%, respectively, of the global total. The balance is due primarily to fossil fuel burning, with small additions due to lightning and volcanism (Logan 1983). Ammonia volatilization from undisturbed soils is a relatively minor component of both total soils and global emissions.

It is important to emphasize that these estimated global emission rates are based on occasional measurements of emissions from a minute fraction of the total area of each biome. Extrapolation of these measurements from the local to the global scale is easy to do on paper, but is fraught with uncertainty. One of the most challenging tasks that ecosystems ecologists face, is to devise ways to account for local temporal and spatial variability so that local measurements can be scaled up accurately and precisely to the global level for comparison to the models devised by atmospheric chemists.

The effects of disturbance

There is very little information about the effects of disturbance on nitrogen gas emissions from natural ecosystems. The best documented effects are for fire and for grazing in grasslands, but it is reasonable to expect that other types of disturbance could have a stimulatory effect. Combustion of fuel oils and biomass produces nitrogen oxides (Weiss and Craig 1976, Pierotti and Rasmussen 1976, Smith 1981, and Logan 1983). The yield of nitrogen oxide from a unit of fuel can be as high as 7.7 kg N per ton of fuel (Malte 1975). Increasing development and industrialization is, therefore, a potential source of NO_x, as was shown in Table 9. In addition, however, fires used to clear land, especially in the tropics (Medina 1982, Logan 1983), may be an additional major source of nitrogen oxides.

As was pointed out in Table 2, grazing can increase emissions of ammonia from natural lands via animal wastes. It can be expected then that conversion of natural land to grazed land should increase atmospheric ammonia loading, but there are few data to quantify this expectation.

There are a few indications that physical disturbance (e.g. by development or clearcutting) stimulates losses of N_2O and N_2 via nitrification and denitrification. Destruction of plants reduces plant nitrogen and water demand and coincidentally the loss of canopy cover warms the soil and accelerates microbial activity. Increased microbial mineralization should produce more ammonium and since plant demand is low, this nitrogen may potentially be nitrified (Likens et al. 1969, Bormann and Likens 1979, Vitousek et al. 1982). Increased water availability (due to low transpiration) may solubilize substrates and restrict oxygen diffusion so that, given sufficient nitrate, denitrification may be stimulated also. In either case, N_2O or N_2 could be produced at an accelerated rate.

As reasonable as this scenario appears, evidence to support it is scant. Robertson and Tiedje (1984), using an acetylene block technique, found that $(N_2O + N_2)$ evolution rates from whole cores from a recent clearcut were higher than the evolution rates from nearby second growth forests. At other sites, however, $(N_2O + N_2)$ emission rates from old-growth forests were occasionally higher than from the recent clearcut. Strauss and Firestone (in review) concluded that N_2O (acetylene block) evolution from both undisturbed and clearcut conifer forests were uniformly low to negligible. I have found that nitrous oxide evolution rates into closed chambers are occasionally much higher in a clearcut northern hardwood forest at Hubbard Brook, USA (Watershed 5) than in the pre-cut or in adjacent reference forests. The variability between sites in the cut watershed is high, however. Interestingly, groundwater emerging at seeps carries a very high load of N_2O that quickly degasses to the atmosphere as the water collects in streams. The elevated N_2O concentration in groundwater is exclusive to the cut watershed and has persisted for two years. My best estimate is that $\sim 0.5\,\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$ is lost, primarily as N_2O, from both soils and groundwater in the cut watershed (Bowden and Bormann in press).

The measured nitrogen gas emission rates from Watershed 5 at Hubbard Brook are lower than might be expected. Soil solution and streamwater nitrate concentrations increase dramatically at Hubbard Brook when the forests are clearcut. The loss of nitrate in streamwater is typically 35, 22, and $10\,\mathrm{kg\,NO_3\text{–}N\,ha^{-1}}$ for the first three years after a clearcut (Bormann and Likens 1979, Martin and Pierce 1980). These nitrate loss rates provide a minimum estimate of the nitrification rates. If the yield of N_2O during nitrification is roughtly 1% of the nitrate produced, an assumption that is consistent with observations by Bremner and Blackmer (1981) and Goreau et al. (1980), then at least 0.35, 0.22, and $0.10\,\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$ are lost as N_2O each year. In addition, however, the observed increase in soil solution nitrate (Hornbeck and Kropelin 1982) should stimulate denitrification with N_2O as the dominant product (Melillo et al. 1983, W.B. Bowden unpublished data). The fact that I have not measured emission rates in excess of $\sim 0.5\,\mathrm{kg\,N\,ha^{-1}\,yr^{-1}}$ does not imply that nitrification is the major source of N_2O in Watershed 5. It does suggest that nitrogen gas emission rates are below the potential rates that might be expected.

Estimates of global emission rates of N_2O and NO_x have been a subject of intense debate in recent years (McElroy et al. 1977, Hahn and Junge 1977, Hahn 1981, Logan et al. 1978, Logan 1983, Kahlil and Rasmussen 1983) due to concerns over the effects of these compounds on global warming and on the stratospheric ozone content, which helps regulate harmful UV radiation (Crutzen 1974). Despite some argument about the absolute source magnitudes and origins, there is general agreement that N_2O is increasing in the atmosphere at the rate of 0.2 to 0.4% $\mathrm{yr^{-1}}$ (see recent review of Khalil and Rasmussen [1983]). The origins for this increase are various (industrial combustion, biomass burning, agricultural fertilizer use) but it is possible that increased nitrogen gas emissions from disturbance of natural lands could be a factor.

Conclusions and recommendations

It is apparent from this review that nitrogen gas emission rates from non-agricultural ecosystems are probably much lower that their potential rates, except perhaps in coastal wetlands. As a consequence, losses of gaseous nitrogen from natural ecosystems are not large compared to other local nitrogen flux rates. Over long periods, the mass of nitrogen lost by hydrologic plus gaseous export can be balanced by atmospheric inputs, especially if dry deposition of nitrogen is considered. However, losses of nitrogen gases from natural lands may be stimulated by natural and anthropogenic disturbances. Nitrogen gas emissions from natural areas are an important portion of the estimated global nitrogen source and sink strengths, especially of N_2O and NO_x.

This review suggests that there are several central issues that deserve high priority for research:

1. Why are nitrogen gas losses from natural lands so small when conditions appear to favor larger losses? What factors control the natural emission rates?
2. How do gaseous exchanges (e.g. soils emissions and dry deposition) interact with hydrologic exchanges (e.g. streamwater and bulk precipitation) to affect the long-term nitrogen balance in natural ecosystems?
3. Will large-scale disturbance (especially in the tropics) accelerate nitrogen gas loss and so alter the nitrogen balance in highly managed ecosystems?

4. How can we improve current estimates of the spatial and temporal variability of local nitrogen gas emissions to more accurately and precisely scale these estimates for comparison to total industrial and agricultural emissions and, ultimately, to global atmospheric budgets?

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