Nitrogen Cycle, Biological

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GLOSSARY

Ammonification Mineralization of organic compounds by microbes, formation of ammonium (NH_4^+).

Biogeochemical processes Chemical and physical reaction processes involving abiotic and biotic components of ecosystems.

Denitrification The reduction of oxidized nitrogen compounds (nitrate NO_3^-, nitrite NO_2^-) by denitrifying (anaerobic) bacteria. Nitrous oxide is an intermediate gaseous denitrification product. The final end product is molecular nitrogen (N_2). Gases are either consumed by organisms or emitted to the atmosphere.

Mineralization The conversion of organic nitrogen to its mineral forms (NH_4^+ or NO_3^-) during decomposition. Gross N mineralization is the gross rate of the process, which can be determined using ^{15}N dilution. Net N mineralization is gross N mineralization minus N immobilization or uptake by microbes.

Nitrification The oxidation of reduced nitrogen compounds (ammonia NH_3, NH_4^+) to NO_2^- and NO_3^- by nitrifying organisms. Nitrate is a plant available nitrogen form. By-products of nitrification are gaseous NO and N_2O. Gases are either consumed by organisms or emit to the atmosphere.

Nitrogen fixation (N-fixation) Conversion of nonreactive, atmospheric molecular nitrogen (N_2) into biochemically available forms, NH_4^+ and amino acids.

I. INTRODUCTION TO THE NITROGEN CYCLE

The *nitrogen cycle* refers to the internal cycling of N within an ecosystem, as well as the transformation of nitrogen at the planetary scale. The ecosystem may be terrestrial or hydrological (lakes, rivers, coastal, or open oceans). The biological processes which define the internal biological nitrogen cycle include the conversion of stable N_2 in the atmosphere to organic nitrogen, mineralization of nitrogen to ammonium, oxidation to nitrate, plant uptake of N, herbivore consumption of plants, volatilization of N through trace gas formation, and reduction of nitrogen back to gaseous N_2 (see bottom of Fig. 1). The *global nitrogen cycle* encompasses the N cycle of
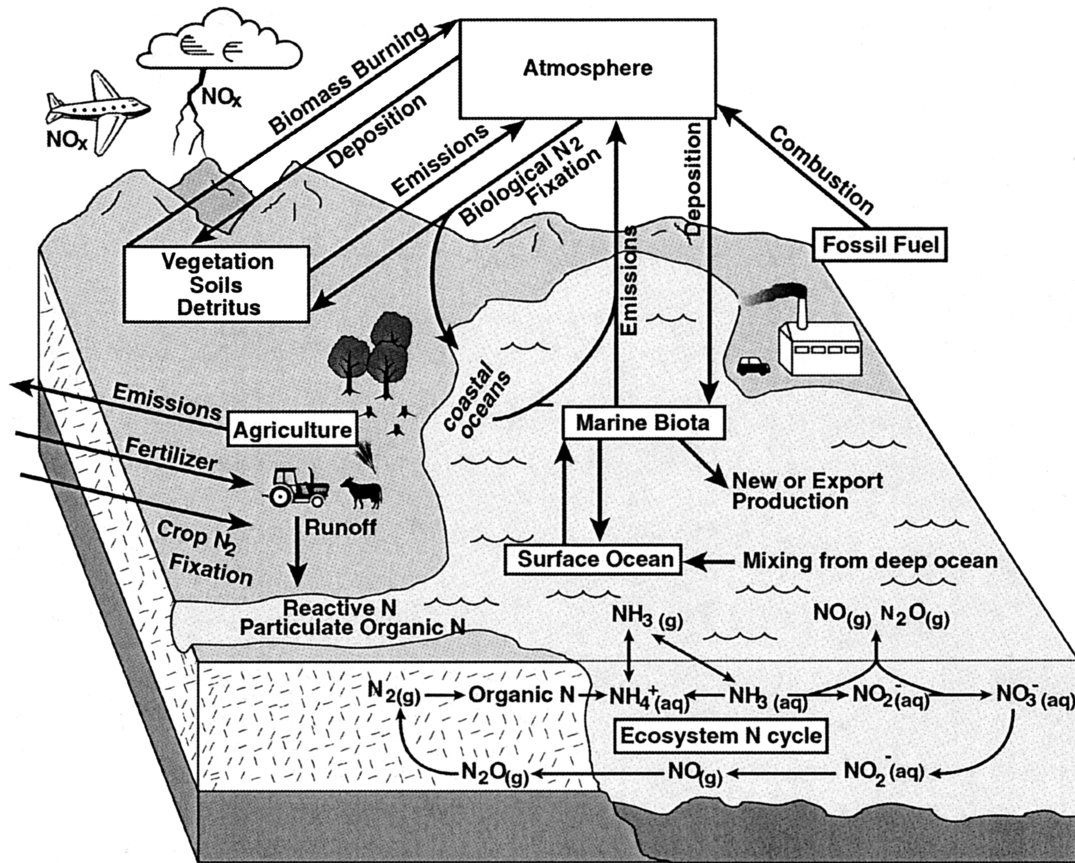
FIGURE 1 The global nitrogen cycle includes the internal transformations of nitrogen, mineralization, nitrification, denitrification, plant uptake, and N trace gas production which occur in soils and water. It also includes the inputs of nitrogen through nitrogen deposition, nitrogen fixation, and fertilizer application. The transformation of the modern global nitrogen cycle compared to the pre-industrial nitrogen cycle has been greater than for any other biogeochemical cycle. There are strong interactions with the carbon cycle, atmospheric chemistry, aerosol formation, and radiative forcing. The units most often used to describe the global nitrogen cycle are Tg = 10^{12} g.

the earth and includes the transfer of mass among the earth's biogeochemical reservoirs: oceans, lakes, rivers, groundwater, the atmosphere, terrestrial biosphere, and geosphere (Fig. 1). Increases in the transfers of N among all of these compartments and the accompanying environmental changes have led to increasing concern about human alteration of the global N cycle for the following reasons:

- Pollution of streams, rivers, lakes, groundwater, and oceans with excess nitrogen
- Increased concentrations of nitrous oxide, a long-lived greenhouse gas involved in the destruction of the stratospheric ozone layer
- Increased concentrations of oxidized nitrogen that drive the formation of photochemical smog and tropospheric ozone in urban and rural areas
- Loss of base cations and soil nutrients such as calcium and potassium

- Acidification of soils, streams, and lakes through deposition of nitric acid
- Increased carbon uptake in terrestrial, aquatic, and marine ecosystems
- Accelerated losses of biological diversity
- Changes in the composition and functioning of estuarine and near-shore ecosystems that contribute to long-term declines in coastal marine fisheries

Both the global and internal nitrogen cycles are biologically regulated, but the transformations are the result of biotic and abiotic interactions. Electron transfers are at the center of the transformations which make the N cycle. Nitrogen loses and gains electrons during abiotic and biotic chemical transformation. The oxidation state of nitrogen can range from −3 to +5, an 8 electron difference. Knowing the oxidation state of nitrogen throughout its transformations helps to understand the role of the N-containing compounds in different environments.

Species	Oxidation state	Common name
NH_3	-3	Ammonia
NH_4^+	-3	Ammonium
NH_x	-3	$NH_3 + NH_4^+$
N_2	0	Molecular nitrogen
N_2O	$+1/2$	Nitrous oxide
NO	$+1$	Nitric oxide
NO_2^-	$+3$	Nitrogen dioxide
HNO_3^-	$+4$	Nitric acid
NO_3^-	$+5$	Nitrate

II. RESERVOIRS AND FLUXES OF THE BIOLOGICAL NITROGEN CYCLE

General cycle—The biological N cycle embraces reservoirs and fluxes of those nitrogen compounds in water, land, and atmosphere that are available to organisms. Since not all nitrogen is biologically available, only a part of the total N participates in the biological nitrogen cycle. Biologically available nitrogen is bound in living and dead organic matter, bound to mineral compounds, dissolved in solutions, or present as oxidized and reduced gaseous nitrogen species.

Reservoir: atmosphere—Globally the atmosphere represents the largest nitrogen reservoir (3.9×10^{21} g N), with molecular nitrogen (N_2) accounting for about 79% of the air. N_2 molecules are, for the most part, excluded from the biological nitrogen cycle because of the stable triple bond between the atoms. A relatively small amount of N_2 undergoes N-fixation processes and enters the biological nitrogen cycle.

Reservoir: biosphere—The biosphere represents the second largest nitrogen reservoir after the atmosphere. Estimated global nitrogen content is 4100 Tg in vegetation, is 5000 Tg in detritus or dead organic matter, and is 95,000 Tg in soils. Oceans contain an estimated 2000×10^2 Tg of dissolved organic nitrogen. The nitrogen and carbon cycles are closely linked since N is essential for the functioning and growth of organisms. The transformation of N_2 into ammonium and amino acids via nitrogen fixation was one of the key building blocks for the development of life on earth. This nitrogen could then be further transformed by other paths and microbes. Ammonification and nitrification are the primary source for ammonium (NH_4^+) and nitrate (NO_3^-), which are both biologically available nitrogen species. Denitrification, however, represents a biological N-transformation process turning biologically available N oxides into unavailable N_2, providing closure of the entire N cycle. Biologically available nitrogen is a limiting factor for the productivity of terrestrial and aquatic ecosystems.

Reservoir: pedosphere (soils and rock)—Biologically available soil nitrogen is mainly stored in organic matter, bound reversibly to mineral soil particles, or dissolved in soil solution. The reservoir of soil inorganic nitrogen is relatively small compared to the amount of N cycling rapidly through the biosphere. Turnover times, and thus quantity and quality of soil organic matter, are major controls for the productivity of terrestrial ecosystems. The quality of organic material relates to its availability for biological processes upon decay, thus its aptness to decomposition and mineralization. The C to N ratio of organic material is the key regulator for mineralization and immobilization of organic compounds. Mineralized nitrogen compounds may undergo biological nitrogen transformation processes (ammonification, nitrification, denitrification) completing the biological N cycle or returning to the atmosphere as N_2. Some nitrogen is stored in geologic material, mainly in rocks derived from ocean sediments, restricted nitrate deposits, and hydrothermally altered basaltic rocks.

Reservoir: hydrosphere—The nitrogen load of rivers and groundwater results from leaching from soils. Coastal oceans receive nitrogen from river discharge, about 40 Tg N per year (Galloway *et al.*, 1995). Fixed nitrogen may enter the aquatic food chain. Dead organic material may sink to the deep sea and the ocean floor, the only mechanisms for nitrogen storage in marine systems. N_2 produced in anaerobic water or sludge through denitrification may emit to the atmosphere.

Abiotic and biotic N-fixation—In the atmosphere lightning and fire may trigger abiotic N-fixation reactions through temporarily very high pressure and temperature. Lightning is estimated to fix about 13 Tg N (Price, Penner, and Prather, 1997) per year into biologically available nitrogen forms. Biological nitrogen fixation occurs naturally in soils and oceans through biotic chemical reactions processes mediated by free and symbiotic living microbes. Estimations for biological N-fixation in aquatic ecosystems range from 30 to >300 Tg N (Galloway *et al.*, 1995) per year. Potential nitrogen fixation by natural ecosystems is 100–290 Tg N (Cleveland *et al.*, 1999). Human activity through agricultural practice increased the biological N-fixation. Cultivation of legumes enhanced N-fixation in terrestrial agriculture; in aquatic cultures (e.g., flooded rice fields) N availability increased through cultivation of N-fixing algae. Symbiotic N-fixation by crops is estimated to be 20 Tg N per year (Smil, 1999). Significant uncertainty surrounds all of these estimates.

Human-induced N-fixation—For about 60 years mankind has used industrial processes (Haber-Bosch) to form ammonia through the combination of hydrogen and atmospheric nitrogen under high pressure and temperature. Globally, industrial N-fixation through fertilizer

production amounts to about 80 Tg per year (Smil, 1999). Globally, nitrogen fixation by fossil fuel combustion is estimated to be more than 20–25 Tg N per year (Holland *et al.*, 1999).

Atmosphere–biosphere N-exchange—Direct exchange of N between the atmosphere and the biosphere occurs only through reactive nitrogen species [e.g., nitrogen dioxide (NO_2), ammonia (NH_3)]. The major exchange pathways are wet and dry deposition of atmospheric gaseous and particulate nitrogen compounds, diffusive gas exchange, and emission of biologically produced gaseous nitrogen species from soil and water surfaces.

Biosphere N-exchange to other reservoirs—Microbes are mediating biological nitrogen conversion processes in soils and water. These biological processes are controlled by N availability, temperature, moisture, redox, and pH conditions. Microbes produce ammonia (NH_3) and ammonium through ammonification of organic compounds. Volatile NH_3 may be emitted to the atmosphere, transformed and transported in the air, and deposited at any distance from the point of emission. NH_4^+ may become incorporated into organic compounds through ammonia assimilation and assimilatory nitrate reduction. Nitrifying bacteria oxidize reduced nitrogen (NH_3, NH_4^+) to nitrite (NO_2^-) and nitrate, which is available for plant uptake. Dissolved in soil pore water, nitrate and organic nitrogen (DON) are spatially mobile through passive transport (leaching) with draining soil water into groundwater, streams, rivers, and coastal oceans.

Anthropogenic effect on N fluxes—Naturally, atmospheric concentration and fluxes of reactive nitrogen species are subject to considerable diurnal, seasonal, and spatial variability. Human activity, mainly through fossil fuel combustion, increases the atmospheric reactive nitrogen reservoir and alters the natural concentrations and fluxes at both temporal and spatial scales. Wet and dry deposition of atmospheric reactive nitrogen may enhance ecosystem productivity. Excessive deposition may result in acidification and nitrogen saturation of ecosystems, introducing a negative feedback reaction on ecosystem productivity. Saturation effects are, e.g., reported for forest systems in Europe and the northeastern United States. Human land use practice increased nitrogen loads in rivers, estuaries, and coastal oceans. Land use changes mobilize nitrogen and increase the potential for nitrogen loss. About 20 Tg N per year N loss in terrestrial ecosystems is attributed to forest conversion, and about 10 Tg N per year is attributed to wetland drainage.

Fertilization increased agricultural productivity (green revolution) through enhanced biomass production, though commonly only part of the added fertilizer N gets incorporated into the cultivated crop. Fertilizer is partly consumed by soil microbes and partly stays in the soil available N-pool and may be transferred from the rooting zone to groundwater and rivers by leaching with draining soil water. At the community scale, plant species shifts may be induced by N additions, leading to species distribution changes which often favor weeds over native plants, which may reduce species diversity and later ecosystem function (Vitousek *et al.*, 1997). In oceans, external nutrient sources may reduce nitrogen fixation because of competition with other phyotplankton (Karl *et al.*, 1997). In more nutrient-rich coastal regions, nutrient eutrophication has been linked to the rise in harmful algal blooms, hypoxia, and shifts at higher trophic levels away from more traditional crustacean-dominated food webs that support many fisheries (Carpenter *et al.*, 1998).

N fluxes to the atmosphere—By-products of nitrification processes are nitric oxide (NO) and nitrous oxide (N_2O) gas which may emit to the atmosphere. With progressing oxygen depletion in the anaerobic environment, denitrifying microbes transform NO_3^- into N_2O (incomplete denitrification) or N_2 (complete denitrification). Thus, in the anaerobic environment, complete denitrification removes nitrogen from the biological cycle. Organically bound nitrogen may be converted to N_2 by fire (pyrodenitrification). Biomass burning is estimated to return about 5–33 Tg N per year to the atmosphere by volatizing fixed nitrogen.

III. NITROGEN TRANSFORMATION PROCESSES

A. Fixation of Atmospheric N_2

Molecular nitrogen (N_2) is a relatively inert gas due to the strong triple bond between the two nitrogen atoms. The biological N cycle is largely restricted to molecules in which nitrogen is bound less strongly to elements other than nitrogen. Atmospheric N_2 may enter the biological nitrogen cycle through biotic or abiotic nitrogen fixation processes.

Microbial (biotic) fixation of atmospheric N_2 is the most important natural nitrogen source for the biosphere. Nitrogen-fixing microorganisms in terrestrial and oceanic ecosystems produce ammonia following the basic reaction:

$$N_2 + 5\,H_2O \rightarrow 2\,NH_4^+ + 2\,OH^- + 1.5\,O_2. \quad (1)$$
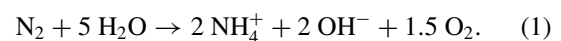
Nitrogenase is the key enzyme for biotic nitrogen fixation, acting as the catalyst in the biochemical break up of the N_2 triple bond. Free-living autotroph bacteria in soils (e.g., *Acotobacter* in aerobic soils, *Clostridium* in anaerobic environments), blue-green algae (*Cyanobacteria*), and

bacteria living in a symbiosis with plants (e.g., *Rhizobium* with legumes) are able to fix atmospheric N_2 and incorporate N into bacterial biomass. Fixed nitrogen becomes available for other organisms after the death and decomposition of microbes. In symbiotic relations, the host plant may take advantage of the nitrogen fixed by the bacteria, while the microbes benefit from the nutrients assimilated by plant roots.

Abiotic fixation of molecular nitrogen requires a very high energy input to split the triple bond of N_2. In the presence of extremely high temperatures (e.g., during lightning strikes), N_2 molecules dissociate. A fraction of the dissociated nitrogen gets oxidized to form nitric oxide (NO) gas:

$$N_2 + O_2 + energy \rightarrow 2\,NO. \tag{2}$$
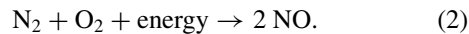
The primary mankind-induced abiotic nitrogen fixation processes are fossil fuel burning and fertilizer production (Haber-Bosch process). Industrial activity throughout the past 150 years affected the global biological nitrogen cycle noticeably. Human activity significantly altered reservoir sizes (e.g., atmospheric nitrogen oxide concentrations, soil nitrogen loads) and nitrogen fluxes (e.g., emission of nitrogen oxides from soils) of the global nitrogen cycle.

B. Atmospheric Deposition of Reactive Nitrogen Gases

What is reactive nitrogen deposition? The definition is most easily split into its wet and dry components (http://nadp.sws.uiuc.edu/; http://www.epa.gov/castnet/;). Wet deposition of nitrogen includes deposition of ammonia, ammonium, nitrate, and nitric acid and a range of organic reduced and oxidized compounds in precipitation. The timing of nitrogen deposition events is driven by the episodic nature of precipitation and is likely important for coastal and open ocean ecosystems (Paerl, 1997). Dry deposition of nitrogen is the removal of N-containing gases by deposition onto a surface, e.g., leaves, soil, and open water. The N compounds which are exchanged via dry deposition include NH_3 (g), NO_2 (g), HNO_3 (g), particulate NH_4^+ and NO_3^-, and organic compounds including PAN, organic acids, nitrogen-containing aerosols, and simple amino acids. Much of our understanding of the spatial patterns and magnitude of N deposition is restricted to the well-sampled areas of the United States and Europe (http://nadp.sws.uiuc.edu/; http://www.epa.gov/castnet/; http://www.emep.int/). Both the measurements and the models are incomplete. The uncertainty associated with wet deposition measurements is much less than the substantial uncertainty associated with measurements/estimates of dry deposition.

C. Ammonia Assimilation and Plant Nitrogen Uptake

Autotroph organisms assimilate inorganic nitrate (NO_3^-) ions into their body substances after conversion of NO_3^- into ammonium. The combined process of nitrate reduction and ammonia assimilation is referred to as the assimilatory nitrate reduction. Immoblization of nitrogen into organic N reduces the probability of nitrogen loss from the ecosystem.

Inorganic nitrogen (NO_2^- and NO_3^-) molecules may enter the biological N cycle through plant uptake via roots or leaves. Plants assimilate inorganic nitrate dissolved in soil pore water or bound exchangeably to soil particles with the water sucked through the root tissue into the plant internal transport flow. Stomata dynamics control the transpiration flow and, thus indirectly, the root nutrient uptake. Agronomists use the NO_3^- concentration of the plant sap flow to evaluate the plant nitrogen supply. Stomata conductivity controls the uptake of gaseous nitrogen (NO_2) from the atmosphere into leaves through passive diffusive transport. Atmospheric NO_2 together with carbon dioxide (CO_2) diffuses through the stomata opening. Inside the leaf, NO_2 dissolves into the intercellular water of the stomata tissue and gets transformed to NO_2^- or NO_3^-. In plant cells, inorganic nitrogen may be assimilated into the biological nitrogen cycle through direct incorporation into organic compounds or after reduction by the enzyme nitrate reductase. Isotope studies suggest that assimilated atmospheric nitrogen may be allocated in any growing part of the plant. Direct uptake of nitrogen deposited from the atmosphere onto above-ground plant surfaces (cuticula, bark) is of minor importance for the nitrogen supply of plants.

Until recently, it was thought that all N taken up by plants was taken up as a mineral form (NH_4^+ and NO_3^-) through their roots or as a gas through leaves and stomata (NH_3, NO, NO_2, or HNO_3). There is an accumulating body of evidence to suggest that plant roots are capable of taking up relatively simply amino acids directly, thus bypassing N mineralization (Näsholm *et al.*, 1999; Schimel and Chapin, 1996). This pathway is particularly important for boreal and tundra plants. Plant associations with mycorrhizal fungi may also play an inportant role in the nitrogen nutrition of plants through increasing surface area available for absorption and the production of proteases.

D. Mineralization of Nitrogen

Nitrogen is incorporated into organic substances or is available as inorganic NH_4^+ and NO_3^- molecules. Decomposition and mineralization mobilizes nitrogen that is fixed in organic matter; the produced nitrogen species

may complete the biological N cycle or return to the atmospheric N_2 pool. Microbial communities perform mineralization processes in both terrestrial and aquatic ecosystems.

Decomposition is primarily a biological process. In terrestrial ecosystems, it may be supported by physical processes, e.g., freezing breaks structural elements in dead organic matter. Organisms consume and transform organic material to gain energy and substance, with N mineralization and immobilization processes occurring simultaneously. Consequently, gross mineralization exceeds net mineralization due to immobilization of mineralized nitrogen into newly formed organic substances. The carbon to nitrogen (C:N) ratio of the decomposing organic matter largely determines transformation processes. Net immobilization occurs at C:N ratios >25, and net mineralization occurs at C:N ratios <25. High carbon content is related to structural, supportive elements in organic matter, which leads to higher resistance against decomposition and mineralization. Organic matter with a low C:N ratio decomposes easily. For example, microbial biomass with a C:N ratio of about 4–5 is rapidly mineralized given appropriate environmental conditions. Biological processes follow optimum functions for temperature and moisture and thus are subject to seasonal and general climatic influences, e.g., mineralization is slow in cold and dry environments and high in warm and moist climates. Net mineralization is the result of many interacting factors, mainly microbial biomass, C:N ratio, and the environmental conditions through mineralization processes.

A variety of soil microbial species are able to mineralize organic nitrogen through ammonification:

$$R\text{---}NH_2 + H_2O \rightarrow NH_3 + R\text{---}OH. \qquad (3)$$

Ammonia dissolves rapidly in water, forming the easily bioavailable ammonium (NH_4^+) molecules

$$NH_3 + H_2O \rightarrow NH_4^+ + OH^-. \qquad (4)$$
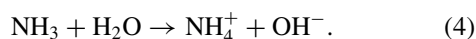
Biologically available inorganic nitrogen (NH_4^+, NO_3^-) in soils is either dissolved in pore water or adsorbed reversibly to charged locations on surfaces of mineral particles. Commonly low anion exchange capacity of soils leaves NO_3^- molecules in solution. Leaching with draining soil water may deprive the soil nitrogen reservoir. Leaching loss is correlated to the seasonal dynamics of nitrogen mineralization, soil water content, soil properties, and agricultural management. Nitrate loss is generally smaller from heavier textured soils (loam and clay) with higher cation exchange capacity compared to light textured sandy soils. Natural ecosystems show low leaching losses since growing vegetation utilizes soil available nitrate. High leaching loss rates are known, especially from fertilized agricultural soils. Appropriate agricul-

tural management practice controls leaching loss from soils.

High concentration of dissolved NH_4^+ and OH^- ions in recently fertilized or limed soils may cause the formation of gaseous ammonia (NH_3):

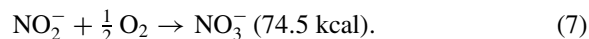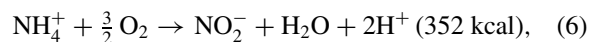$$NH_4^+ + OH^- \rightarrow NH_{3\text{-gas}} + H_2O. \qquad (5)$$
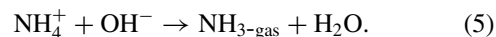
Ammonia molecules diffuse to the atmosphere (ammonia volatilization), get transported with wind, and, finally, deposit as NH_3 or NH_4^+. Volatilized NH_3 is lost for the biological nitrogen cycle at the emission location, though considering larger scales it re-enters the biological N cycle after a time lag due to migration.

Ammonium molecules may be bound nonexchangeably into the mineral structure of silica, substituting similar sized potassium atoms. The amount of fixed nitrogen in the lithosphere is estimated to be about 50 times the amount of nitrogen in the atmosphere. However, this reservoir is not effective for the biological nitrogen cycle since nitrogen release by weathering is a negligently slow process.
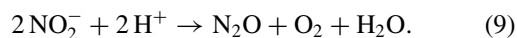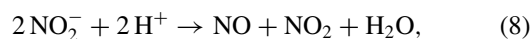
E. Nitrification and Denitrification

In aerobic soils, autotroph nitrifying bacteria gain energy for their metabolic processes by catalyzing the exotherm oxidation reaction of NH_4^+ to NO_2^- (*Nitrosomas*) and of NO_2^- to NO_3^- (*Nitrobacter*):

$$NH_4^+ + \tfrac{3}{2} O_2 \rightarrow NO_2^- + H_2O + 2H^+ \ (352 \text{ kcal}), \quad (6)$$

$$NO_2^- + \tfrac{1}{2} O_2 \rightarrow NO_3^- \ (74.5 \text{ kcal}). \qquad (7)$$

The nitrification reactions change the nitrogen oxidation state from -3 in the reduced form (NH_4^+) to $+5$ in the most oxidized form (NO_3^-). Nitrifying bacteria are ubiquitous in soils. Some heterotrophic organisms are also capable of nitrification. Nitrification rates are controlled by nitrogen availability, temperature, moisture, pH, and redox state (oxygen availability). Temporal dynamics (diurnal and seasonal) of these variables affect nitrification. For example, in temperate zone soils nitrification rates are smaller during winter compared to summer (temperature is the major control), and in semi-arid areas rates slow down with start of the dry season (soil moisture is the major control). Nitrate availability is the major control in humid tropical soils.

A fraction of the nitrate entering the nitrification process gets oxidized to gaseous forms (NO and N_2O):

$$2\,NO_2^- + 2\,H^+ \rightarrow NO + NO_2 + H_2O, \qquad (8)$$

$$2\,NO_2^- + 2\,H^+ \rightarrow N_2O + O_2 + H_2O. \qquad (9)$$

Nitrogen availability, temperature, and soil moisture are the key controls for gaseous loss. Oxygen availability in soils controls the partitioning between the nitrification

by-products NO, NO_2, and N_2O. In the aerobic environment microbes predominantly produce NO. With increasing soil moisture content, the oxygen availability decreases and gaseous nitrogen production shifts towards N_2O. Increasing water content affects soil trace gas fluxes, because gas molecules diffuse through the air-filled pore space in soils. In structured, aggregated soils, aerobic and anaerobic microspots may occur in direct vicinity, resulting in simultaneous production of NO and N_2O gas.

In the aerobic soil environment facultative anaerobic bacteria (e.g., *Pseudomonas*) gain energy through heterotrophic respiration. However, in wet, oxygen limited soils, the same bacteria perform denitrification reactions to gain energy, using oxygen bound in NO_3^- and NO_2^- as electron acceptors:

$$2\,NO_2^- + 2\,H^+ \rightarrow N_2O + O_2 + H_2O, \qquad (10)$$

$$2\,NO_2^- + 4\,H^+ \rightarrow N_2 + O_2 + 2H_2O. \qquad (11)$$
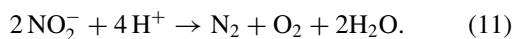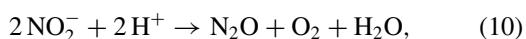
A major control for the occurrence of either reaction is the oxygen availability or redox condition in soils. Nitrogen reduction increases with increasing oxygen limitation. Thus, with decreasing aeration, denitrification shifts more and more towards N_2 as the final product. Globally, denitrification returns 54–115 Tg N to the atmosphere as $NO + N_2O + N_2$.

Nitrogen emitted from soils in gaseous form is largely lost to the biosphere. Fertilizer nitrogen lost from soils in gaseous form (NO and N_2O) reduces the fertilizer efficiency. Effects of agricultural management and fertilization on soil trace gas fluxes also became important research questions in the context of global atmospheric warming and pollution.

IV. LINKS BETWEEN THE NITROGEN AND CARBON CYCLES

Biota and biogeochemical processes closely link the nitrogen and the carbon cycles. The ecosystem losses of nitrogen are determined by the coupling of N release and uptake. Because biospheric carbon uptake is N limited, the addition of nitrogen through nitrogen deposition (or fertilization) can stimulate carbon uptake and storage. The deposited nitrogen, which is immobilized by microbes to form soil organic matter, is stored at a C:N ratio close to that of microbial biomass, between 4 and 15. Nitrogen assimilated by plants is stored at a much wider C:N ratio between 30 and 90 for leaves and a C:N ratio of 150–300 for wood (Townsend *et al.*, 1996). Microbial N has a residence time of less than a year compared to the nitrogen in wood, which can have a residence time of decades to centuries. Decomposition of organic material which starts at a C:N ratio of $\sim$25 requires immoblization of N by mi-

crobes. The quantity of nitrogen required depends on the microbial growth efficiency. Microbial N immobilization is the mechanism by which microbes compete with plants for available nitrogen. Below a C:N ratio of $\sim$25, there is net nitrogen mineralization, releasing nitrogen into the "bioavailable" nitrogen pool for plant or further microbial uptake. Gross nitrogen mineralization rates in soils are controlled by the physical structure and chemical quality of decomposing organic material, soil temperature, moisture, pH, and redox conditions. As with most biological reactions, there is a temperature optimum for mineralization. Soil moisture also regulates mineralization. In dry soils mineralization increases with increasing moisture content. Above field capacity, reduced oxygen availability in increasingly wet soils slows mineralization rates down.

In marine ecosystems, bioavailable nitrogen is one of the key limiting nutrients in the upper ocean along with phosphorus, silicon, and iron. As with terrestrial ecosystems, atmospheric nitrogen deposition serves as a "new" nutrient source to the ecosystem, and increased inputs typically lead to enhanced primary production and net community export of organic matter either through sinking particles or through advection of dissolved organic matter. There are parallells between the carbon and nitrogen links in terrestrial and marine ecosystems. The vertical partition of carbon in the ocean and net air–sea CO_2 flux are, in turn, strongly modulated by the export flux, highlighting the close linkage of the marine nitrogen and carbon cycles. However, the C:N ratio is operated in a much more restricted range, much closer to that of microbial biomass. Atmospheric N deposition decouples the macronutrient input from ocean physics (which also tends to supply high metabolic CO_2 water to the surface layer) and therefore can alter marine biogeochemistry disproportionately.

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