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The Continuing Challenge of Agricultural Nitrogen Loss to the Environment in the Context of Global Change and Advancing Research

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ABSTRACT

Excess nitrogen in soil, aquatic and atmospheric environments is an escalating global problem as a result of technology and human actions increasingly dominating the nitrogen cycle at all environmental scales, which often leads to an accumulation of reactive nitrogen compounds in ecosystems. While sources of environmental nitrogen pollution are diverse and agriculture is not solely responsible, there is growing concern about the large number of identified impacts on water quality and greenhouse gas emissions, which originate from intensified agricultural management with its continually increasing nitrogen fertiliser consumption. Interactions of nitrogen in and with the environment are complex and our understanding of nitrogen cycling continues to be re-defined with the discovery of new nitrogen cycling processes and pathways. There is an increasingly urgent need for interdisciplinary, international studies that holistically investigate measures to control nitrogen losses and reduce agricultural costs while maintaining productivity. This is best achieved by joint actions among researchers, land managers and policy makers by assessing and implementing improved farm management practices that optimise agricultural production, minimise adverse effects on human and animal health and reduce environmental pollution. Similarly promising approaches to enhance environmental and economic sustainability of agricultural production are put forward by recent studies that take advantage of the improved understanding of soil nitrogen processes and plant uptake.

Keywords: anammox, climate change, global N cycle, nitrification and urease inhibitors, N use efficiency

Abbreviations: anammox, anaerobic ammonium oxidation; **DNRA**, dissimilatory nitrate reduction to ammonium; **NO_x**, nitrogen oxide ($NO + NO_2$); **NUE**, nitrogen use efficiency

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INTRODUCTION

In the late 18th century, the element nitrogen (N) was discovered almost concurrently by the Scottish medical student Daniel Rutherford, who first published his discovery in 1772, Joseph Priestley and Henry Cavendish in England and the chemist Carl Wilhelm Scheele in Sweden. The following years saw major scientific breakthroughs and discoveries, including the first observation of denitrification (Gayon and Dupetit in 1885), and biological N fixation in plants (Hellriege and Wilfarth in 1888) and cyanobacteria (Frank in 1889). The development of the theory on mineral nutrition of plants and the formulation of the Law of the Minimum by Justus von Liebig and Carl Sprengel in the early to mid 19th century mark the beginning of modern soil science and agricultural chemistry. The new understanding of the role of chemical elements in biological processes revolutionised the concept of plant nutrition. Eventually, the development of industrial fixation of N to produce ammonia through the Haber-Bosch process in 1913, led to the production of mineral fertilisers and formed the foundation of modern agriculture.

Nitrogen is the nutrient required in the largest quantities by plants. It typically comprises 1 to 5% of plant dry matter, is part of all vital cell constituents and the main component of most organic compounds in plants including amino and nucleic acids, enzymes, chlorophyll, ADP, ATP and proteins. Although N makes up about 78% percent (by volume) of the earth's atmosphere, it is often the major limiting factor for maximum plant growth, mainly because gaseous N can not be directly utilised by most organisms as only some are capable of efficiently cleaving the triple bond that links the two nitrogen atoms of the atmospheric di-nitrogen (N_2) molecule. They instead rely on using reactive nitrogen,

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Invited Review

Table 1 Worldwide fertiliser production and consumption (in ,000 t), food production index (in %; 1999/2000 = 100%) between 1961 and 2002.

	1961	**1970**	**1980**	**1990**	**2002**
Fertiliser production (,000 t)	33,511	72,935	124,752	148,286	147,932
Fertiliser consumption (,000 t)	31,182	69,308	116,720	137,829	141,571
Food production index (%)	39.3	49.8	62.3	79.7	103.5

Source: http://earthtrends.wri.org

Table 2 Changes in global fertiliser use intensity between 1980 and 2002 (in kg ha^{-1}).

	1980	**1990**	**2000**	**2001**	**2002**
Worldwide	80.6	90.9	88.2	89.5	91.9
Developed Countries	131.9	114.0	77.5	79.3	78.7
Developing Countries	51.5	78.7	96.7	97.9	102.3

Source: http://earthtrends.wri.org

which, based on the definition by Galloway *et al.* (2004), includes inorganic forms such as ammonia (NH_3), ammonium (NH_4^+), nitrate (NO_3^-), nitrogen oxides (NO_x) or nitric acid (HNO_3), and organic forms such as urea, amines, proteins and nucleic acids. As crop growth and physiological development depend on a readily available N supply, nitrogen fertilisation greatly increases yields and changes crop quality, with optimum nutrition resulting in, for example, higher plant protein content (Amberger 1996). This makes N the critical factor limiting crop production worldwide and lack of N the most common deficiency symptom observed in plants. Low N levels in agricultural soils reduce productivity and can lead to a decline in sustainability through physical soil degradation or accelerated nutrient depletion. It is thus unsurprising that greater availability of the nutrient through the manufacture of vast quantities of N fertilisers has resulted in a remarkable increase in agricultural productivity.

Global fertiliser production and consumption have risen dramatically over the last 60 years, which has allowed the world's population to expand considerably while continuing to meet its growing food requirements even when rising incomes increase per-capita consumption (**Table 1**). According to predictions by the Food and Agriculture Organisation of the United Nations (FAO), world crop production will grow by 57% until 2030, with a greater rate of increase experienced in developing than in industrialised countries. By that time, developing countries are expected to make up 72% of global crop production compared with 53% in 1961/63 (FAO 2002). Correspondingly, there has been a dramatic increase in fertiliser consumption in the developing countries over the last decades (**Table 2**). In comparison, in the industrialised nations, fertiliser use intensity (kg ha^{-1}) has declined in recent years and growth in fertiliser consumption (t yr^{-1}) has slowed down partly due to a reduction in over-application. In contrast to the predicted rise in crop production, fertiliser consumption is expected to increase by only 37% until 2030 (FAO 2002).

Agriculture has a major effect on the biosphere and human lives, environmentally, economically as well as socially. With the greater fertiliser N availability, agriculture has become more intensive and capable of producing higher yields per unit area. This has created new problems for the environment and society, ranging from soil degradation and erosion to loss of biodiversity, excess nutrients in the biosphere and contamination of drinking water. In particular, the effects of N on the environment are serious and long term (Jarvis *et al.* 1995). While agriculture is not solely responsible for the problems associated with excess N in the environment, the impacts of N loss through leaching and to the atmosphere are particularly severe under high-input management regimes, especially in the industrialised world where economically viable agricultural production often exclusively relies on the intensive use of synthetic fertilisers, high energy consumption, the use of non-renewable resources such as fossil fuels, and has a record of highly inappropriate manure handling (Oehlaf 1978; Lampkin 2002). Moreover, many developing countries have set food security, the elimination of food shortages and associated health problems, as their national priority rather than environmental protection. To meet the industrialised world's demand for food, fibre and fuel imports less developed countries aim to maximise their agricultural production, which also increasingly relies on the intensive use of N-based fertilisers. Along with the population growth in developing countries this is likely to cause a shift in the occurence of the N problem and, considering the far-reaching effect of nitrous oxide (N_2O) emissions on global warming, this is cause for worldwide concern.

In view of environmental challenges, especially climate change, increasing atmospheric N deposition to land and water and the increased pressure on agricultural productivity, excess N in the environment is an escalating global threat. Despite the critical importance of this issue, it is barely recognised or comprehended by politicians and policy makers resulting in a vast gulf between scientific understanding and public and political engagement. At the same time, there are major research advances continuously redefining our understanding of the soil N cycle (e.g. Schimel and Bennett 2004) and expanding our knowledge of nitrogen use efficiency and N uptake by plants (e.g. Good *et al.* 2007). In this two-part review, we discuss the, increasingly global, problem of N contamination in the context of agricultural, societal and environmental change. The article presented here focuses on the terrestrial N cycle and the effects of climate change, and highlights promising research findings as well as areas requiring further study, that will assist in improving agricultural sustainability and productivity while minimising environmental N pollution.

N TRANSFORMATION PROCESSES IN AGRICULTURAL SYSTEMS

The global N cycle plays a vital role in the functioning of all ecosystems and influences every aspect of the biosphere and the climate (**Fig. 1**). In the soil system, N fluxes can be divided into inputs and outputs (including losses), which can all be attributed to both natural soil processes and anthropogenic sources. Inputs into soils include application of commercial N fertilisers or organic wastes, atmospheric N deposition, biological N-fixation by symbiotic and non-symbiotic soil bacteria, incorporation of crop residues and other decomposable organic material that will release N into the soil by mineralisation. Outputs consist of harvested crops and animal feeds, export of agricultural produce such as milk or meat, and adsorption of ammonium to the soil matrix; losses from the soil system into the wider environment include nitrate leaching, ammonia volatilisation, emission of gaseous N compounds (nitrous oxide, nitric oxide [NO] or di-nitrogen) by nitrification and denitrification processes, and immobilisation, which refers to the uptake of nitrate and ammonium from the soil solution by soil microorganisms for metabolic maintenance, growth and reproduction, making it unavailable for other microorganisms or plants.

Plants and soil organisms mainly utilise the mineral

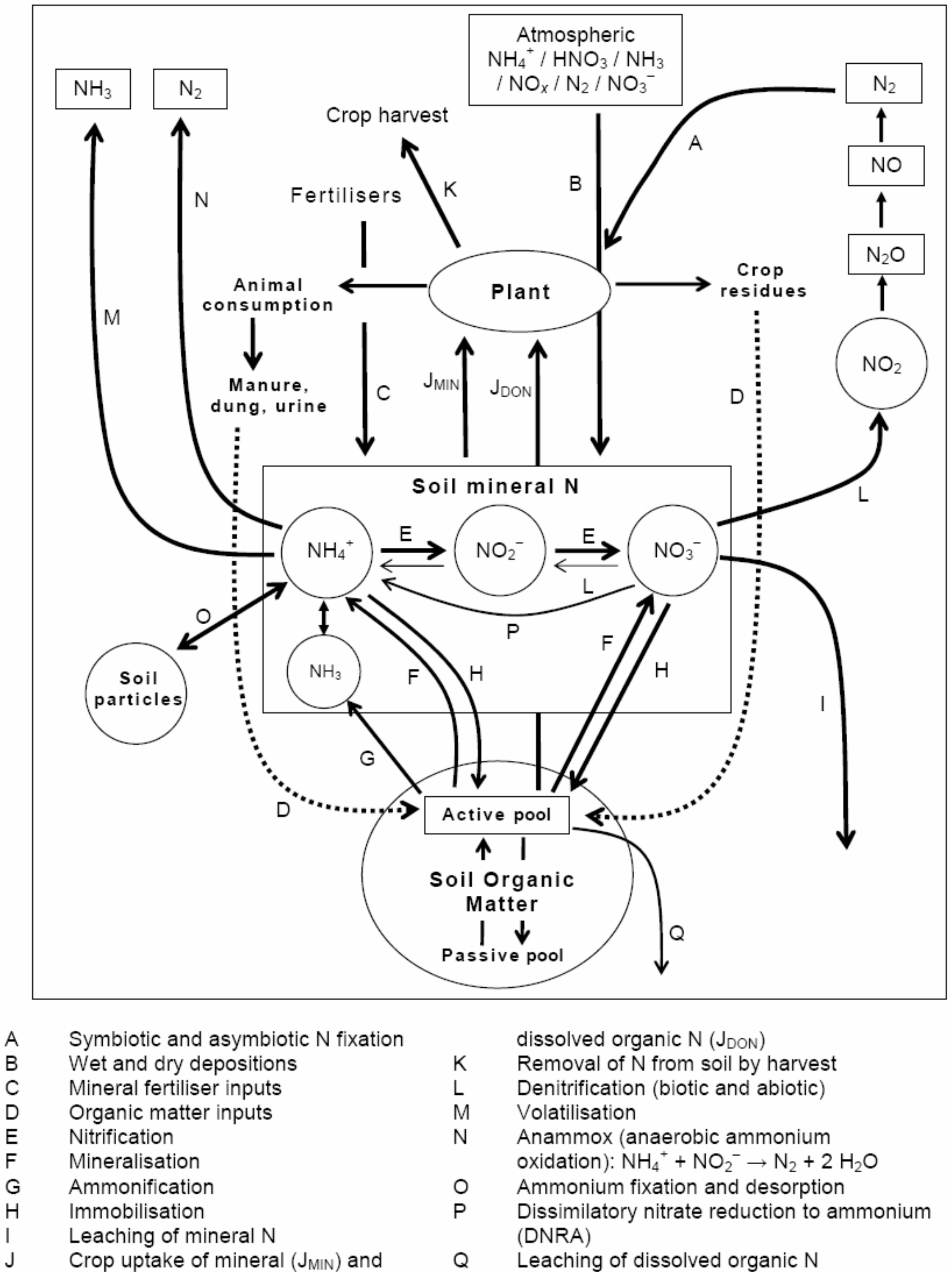

Fig. 1 Schematic representation of the soil nitrogen cycle.

forms of N (i.e. as ammonium or nitrate); while uptake of dissolved organic N has been observed (e.g. Schimel and Bennett 2004), it does not seem to be a major contributor to plant N acquisition (Hodge *et al.* 2000; Jones *et al.* 2005). Therefore, atmospheric N has to be made plant available by biological or industrial N fixation, and bound organic forms of N in the soil, such as amino acids, nucleic acids and proteins, have to be converted into mineral form via a process called mineralisation before they can be absorbed and assimilated by plants. Biological N fixation from the atmosphere is a specialised microbial ability that only a few bacterial species, some actinomycetes and blue-green algae can achieve. Some of these species live symbiotically, in association with plants of the family Fabaceae (legumes) [e.g. *Rhizobium* spp.] or with non-leguminous plants such as alder (*Alnus* spp. L.) [*Frankia* spp., *Azospirillum* spp.], while others are non-symbiotic, free living organisms (e.g. blue-green algae of the family *Nostocaceae*; various photosynthetic bacteria, e.g. *Rhodospirillium* spp.; several aerobic bacteria, e.g. *Azotobacter* spp., *Beijerinckia* spp., *Derxia* spp.; and some anaerobic bacteria, e.g. *Clostridium* spp.).

The rate of N mineralisation in soils is driven by the amount of mineralisable N present in the soil organic matter as well as environmental factors (soil temperature, moisture), soil properties (soil type and texture, pH) and soil management (e.g. tillage type and frequency), which can affect aeration, organic matter quantity and quality and microbial activity (Stevenson and Cole 1999). Nitrification, the oxidation of ammonium to nitrate via nitrite, which follows initial mineralisation of organically bound N, is another key component of the soil N cycle and an important process in intensive agricultural systems. In most soils, the factors controlling nitrification are ammonium content and oxygen availability. The amount of ammonium is often low in soils as nitrification occurs rapidly under warm, moist conditions and most available ammonium ions are bound to the cation exchange complex of the negatively charged organic matter and clay particles. Nitrification is predominantly carried out by autotrophic bacterial species of the genera *Nitrosomonas* (oxidising ammonium to nitrite) and *Nitrobacter* (oxidising nitrite to nitrate), although more recently ammonia oxidation has been documented within the domain Archaea (Francis *et al*. 2007) (also cf. "Advances in understanding N cycling processes", p. 8). Together, mineralisation and nitrification increase the amount of plant available N in soils, which can lead to a surplus and loss of mineral N from soils, especially when plant requirements are low (Stevenson and Cole 1999). Nitrate ions in particular are freely mobile in the soil solution and thus prone to leaching or run-off and a possible contaminant in water. Factors that affect nitrate leaching include nitrate concentration, soil texture and structure, soil permeability, water holding capacity and degree of saturation.

Ammonia can be subject to volatilisation when it is in close contact with the atmosphere as is the case when ammonia- or ammonium-based fertilisers, manures or urea are surface applied to soils. The rate of ammonia volatilisation is affected by a wide range of factors, including fertiliser placement, soil temperature, soil moisture, cation exchange capacity, ground cover, wind speed, precipitation and soil pH, which make volatilisation variable and difficult to predict. Denitrification is the biological or chemical reduction of nitrite or nitrate, which takes place mainly under anaerobic conditions and results in the evolution of nitrogenous gases (N_2O, N_2 and NO). While nitrification is a relatively constant process across ecosystems, denitrification rates are temporally and spatially variable, and high denitrification activity can occur within anaerobic microsites created by water-filled pores, in the rhizosphere of crop plants, which supply organic matter and create anaerobic zones, or through decomposing plant material. As all microbially mediated N cycling processes are largely controlled and affected by soil mineral N concentration, soil moisture content, soil structure, temperature and available organic matter content, agricultural management techniques, such as fertilisation intensity and timing, irrigation, grazing intensity, crop type and management, have direct and indirect effects on N turnover rates and the release of readily available and mobile forms of N, that can be lost by leaching or as gaseous emissions adding to environmental pollution or N deficiencies in plants.

EFFECTS OF ENVIRONMENTAL CHANGE ON SOIL PROCESSES

Environmental changes on both local and global scales are likely to substantially affect the various components of terrestrial and aquatic ecosystems; however, very little is known about the nature of such changes and the extent to which they will impact on ecosystem processes and functioning. While the global N cycle is expected to be affected by the mounting pressures of anthropogenic disturbances and climate change (Gruber and Galloway 2008), predictions are mostly tentative. Ecosystem processes are the result of complex interactions, with each system component likely to respond differently to change and responses expected to vary in space and time. As emphasized by Rustad *et al*. (2001), 'scaling up' from the plot, site and farm level to regional or even global scales can lead to misinterpretation and should be approached with caution. Nonetheless, environmental changes such as rising temperature (0.5-1°C by 2030) and CO_2 levels (up to 550 ppm), more variable precipitation patterns causing more severe droughts and floods and accelerated rates of N deposition will have a growing impact on the productivity and functioning of agroecosystems worldwide by altering soil and growing conditions and plant productivity (IPCC 2007a). The unpredictable nature of these changes will put further pressure on farmers and the land they cultivate (Dueri *et al*. 2007; IPCC 2007b). The extent and actual effects will vary regionally subject to site-specific interactions of the various climatic factors as well as soil and crop type and soil nutrient status, which strongly depend on local conditions (Lynch and St. Clair 2004). Over recent years, a wealth of studies have addressed the issue of climate change effects (including global warming, drought, rising CO_2 levels and increased N deposition) on natural and agricultural ecosystems (Krupa 2003a, 2003b; van Meeteren *et al*. 2008) and on specific aspects relevant to farming, e.g. plant growth, agricultural productivity, C sequestration, biodiversity, water usage, socio-economics, soil fertility and nutrient uptake for a wide range of conditions and locations worldwide (e.g. Peñuelas *et al*. 2004; Rosenzweig *et al*. 2004; Lawlor 2005; Thomson *et al*. 2006; Tubiello and Fischer 2007).

Although regional impacts are difficult to predict, the changes in temperature will most likely result in a shift of optimal cropping zones and occurrence of pests and diseases (Fuhrer 2003). In the temperate climate zones, the suitable land area and cropping season are likely to expand while a shortening of the crop cycle is possible, resulting in higher yields. In other areas, fertile land might be lost to sea-level rise, flooding or extended droughts, which, in particular in combination with rising CO_2 concentrations, could reduce yields by advancing plant growth and maturation (Dueri *et al*. 2007). Elevated atmospheric CO_2 levels will stimulate plant biomass production and improve productivity through increased photosynthesis activity in some species, while it might have a negative effect on others. The narrowing of stomata under elevated CO_2 will lead to improved water use efficiency (Fosaa *et al*. 2004), while at the same time, increased evapotranspiration and lower soil moisture levels are anticipated, especially in the tropics, putting pressure on water resources (Sowerby *et al*. 2005). More unevenly distributed rainfall events might aggravate the negative impact of agriculture on the environment. Continuing increases in atmospheric N deposition will also have significant impacts on plant community composition and productivity of natural or semi-natural ecosystems as they have been found to have the potential to alter ecosystem nutrient balance and soil biogeochemistry, thus causing changes in species richness and composition. Other observed effects of N deposition include higher susceptibility of plants to pests, diseases and environmental stresses and increased inorganic and organic N losses to water and atmosphere (Krupa 2003a; Gidman *et al*. 2006; Brookshire *et al*. 2007).

The impacts of climate change on soil microbial processes are less well understood (Zak *et al*. 2000), especially for soil N dynamics, and actual effects on the soil microbial community at any specific site are variable and difficult to predict. With temperature, water, C and N content being the main drivers for biogeochemical processes in soils, environmental change will have direct and indirect effects on soil nutrient turnover processes, including C cycling, ammonification, nitrification and denitrification, by modifying soil microbial communities, plant nutrient uptake and root exudation (Phillips *et al*. 2006; Chung *et al*. 2007; Dijkstra and Cheng 2008). Increases in photosynthesis activity through rising atmospheric CO_2 levels will change the quality and quantity of root exudation by plants and consequently the nutritional status of the soil, probably inducing microbial growth and activity, increasing soil respiration and accelerating organic matter decomposition (Henry *et al*. 2005; van Meeteren *et al*. 2008), while extended droughts are likely to have the opposite effect, reducing nutrient turnover and retarding litter decomposition (van Meeteren *et al*. 2008). Barnard *et al*. (2005) reported that elevated CO_2 levels did not significantly influence nitrous oxide emissions, while enzyme activities associated with nitrification and denitrification decreased, which they attributed to a decrease in soil nitrate. In contrast, nitrification, denitrification and nitrous oxide emissions showed a strong positive correlation to soil N status as affected by N addition (Barnard *et al.* 2005). Similarly, Henry *et al.* (2005) found that selected extracellular enzyme activities increased significantly as a result of nitrate addition, while increasing soil moisture and atmospheric CO_2 levels had negative effects.

Coupled with the expected rise in air temperature is an increase in soil temperature (Parton *et al.* 1987). Over the last 100 years, the surface temperature has increased by approximately 0.6°C globally due to the atmospheric increase in greenhouse gas concentrations linked to human activity. If the concentration of greenhouse gases continues to rise, it is predicted that the global average surface temperature will increase by between 1.4 and 5.8°C until 2100 (IPCC 2007a). Elevated temperature levels and changing rainfall patterns are expected to stimulate microbial activity and increase microbially mediated soil processes. This could change relative N loss from soil systems by stimulating mineralisation, which increases soil nitrate availability, or by promoting plant growth and N uptake as well as microbial N immobilisation (Smith *et al.* 1997; Fuhrer 2003; Beier *et al.* 2004). Hart (2006) reported increases in active microbial biomass, net N mineralisation and nitrification (over 80%), net CO_2 efflux and net methane consumption as a consequence of elevated temperature, while Barnard *et al.* (2005) concluded from a meta-analysis of published experimental data that elevated temperature had no significant effects on enzyme activities and net nitrification. Raising soil temperatures by 0.5°C increased N mineralisation resulting in higher concentrations and subsequent losses of nitrate and dissolved organic N at a heathland site in the Netherlands (Schmidt *et al.* 2004). While warming increased N mineralisation also at UK and Danish sites, it did not have a significant effect on mineral N concentration in leachates at these sites. The authors argued that this was due to a higher N retention potential of the vegetation or the soil (Schmidt *et al.* 2004).

In one of the few publications discussing the effects of climate change on nitrate leaching from agricultural land, Ducharne *et al.* (2007) analysed three possible forcing scenarios by numerical modelling. Their outcomes show that the impacts of temperature and CO_2 increases on N dynamics and hydrology are also highly variable and difficult to predict. Combined with variable effects on productivity, climate change might result in higher N loss relative to the amount of N being removed by harvest. This implies that the effects of climate change on the environment are far reaching and will have major implications on future land management practices, including N fertilisation. Because of the vast uncertainties associated with predicting and modelling future developments, all present findings and suggestions have to be taken into consideration when devising research strategies and allocating funds, if we are to limit the deleterious impacts of N on the environment. It is also essential to appreciate the relative importance of single factors that affect ecosystem processes and plant productivity (e.g. temperature, soil moisture, crop type, land-use history, etc.) at different spatial and temporal scales (Rustad *et al.* 2001), in order to be able to fully understand the impacts of environmental changes on natural and agricultural ecosystems, to be able to make valid predictions for the future, and to identify practical and sustainable mitigation and adaptation strategies.

RESEARCH DEVELOPMENTS AND NEEDS

Nitrogen use efficiency

According to Good *et al.* (2004), the term nitrogen use efficiency (NUE) has a wide range of definitions and, as a conservative measure for ecosystem productivity, is commonly used to express nutrient utilisation efficiency in plants, in which case NUE is defined as the ratio of crop yield produced per unit N assimilated by the plant. However, a more accurate description for the term might be the ratio of yield to fertiliser N applied (also known as N uptake efficiency), which implies a close link between NUE and enhanced crop yields and improved N recovery (Subbarao *et al.* 2006). Good *et al.* (2004) also argued that as NUE is closely linked to plant physiology, crop type and harvestable product, so should the ways of estimating it. In this regard, NUE and the process of N uptake from soils through the roots are more complex concepts than originally believed.

Intensively managed agroecosystems in developed and developing countries often show poor NUE with high levels of surplus N and low N recovery rates, which can be as low as 30% or less of fertiliser N applied (Raun and Johnson 1999). In 1997, the average annual N surplus – i.e. the discrepancy between inputs and outputs – for 15 EU member states amounted to 74.5 kg N ha^{-1} (**Table 3**), much of which would have been lost to the wider environment. And in the United States, the economic cost of fertiliser N loss from soils by leaching or denitrification has been estimated at 15 billion US$ annually (Raun and Johnson 1999; Subbarao *et al.* 2006). In agronomic farm nutrient balances, a large percentage of N is often unaccounted for as a result of difficulties to accurately quantify the various soil N fluxes (Gruber and Galloway 2008). In a long-term study, Watson *et al.* (2007) attributed a large fraction of unaccounted N to gaseous emissions in the form of ammonia, di-nitrogen and nitrous oxide, and to assimilation into the soil organic matter. In addition, it has been found that in animal-based production systems, such as beef and dairy farming, feed N is often used inefficiently by the animals. Only 20% of N ingested are converted into milk or meat, while the remaining 80% are excreted by ruminant animals in the form of urine (high in labile, inorganic N) and dung (high in organic N) (Jarvis *et al.* 1995). This indicates that animal-based agricultural systems have the potential to be leaky with regard to N, and high losses are often associated with intensive grazing or land application of agricultural wastes in excess of plant needs due to inappropriate rates or timing. The limitation of other plant nutrients, such as phosphorus and sulphur, can be a major contributor to poor NUE (Murphy and Quirke 1997). Declining atmospheric sulphur depositions due to improved air quality in Europe, for example, have highlighted the need for land managers to assess avail-

Table 3 Agricultural N fluxes and N use efficiency (NUE = Surplus N as % of total N inputs) in selected European countries and European average (in kg ha^{-1}).

	BE[**]	**DK**	**DE**	**F**	**IE**	**NL**	**UK**	**EU**
Depositions[*]	33	18	29	16	10	36	15	16.1
Mineral fertilisers	114	106	104	89	91	184	77	87.3
Fixation by legumes	3	8	3	5	1	1	3	2.9
Organic manures	220	114	65	46	123	265	67	86.4
Harvest or grazing	225	135	109	116	162	230	125	118.3
Surplus N	145	111	92	41	63	256	37	74.5
NUE (%)	39.2	45.1	45.8	26.3	28.0	52.7	22.8	38.7

[*] Depositions = wet and dry depositions; [**] BE, Belgium; DK, Denmark; DE, Germany; F, France; IE, Ireland; NL, The Netherlands; UK, United Kingdom; EU, European Union (EU-15, 1997). Source: http://epp.eurostat.ec.europa.eu.

ability of all essential plant nutrients in soils to ensure optimum plant growth.

A high NUE indicates optimum nutrient utilisation by plants and lower losses of N to the environment. Uptake of N by plants from the soil is dependent on a number of environmental factors, such as soil type, climate conditions, microbial competition and type of N source (Kaye and Hart 1997; Hodge *et al.* 2000; Abassi *et al.* 2005). This indicates a close link between the agroecosystem's NUE and the soil's potential for N loss by leaching and denitrification, which in turn depends on temperature, timing and amount of rainfall and soil type. High levels of soil N and subsequent losses are generally the result of excess fertilisation or conditions that favour mineralisation and nitrification (Dueri *et al.* 2007). While global fertiliser consumption is expected to grow at a slower rate than in the past (FAO 2002), the generally poor NUE indicates that reduced fertiliser usage alone will not alleviate environmental problems associated with N loss in years to come. Moreover, the relatively low cost of fertiliser and pressure to maximise yields often result in over- rather than undersupply (Glass 2003). It becomes apparent that N uptake by plants is influenced by a wide range of interactions of different factors that lead to inefficient N use and cause uptake rates well below the full potential.

At the agroecosystem and production level, NUE is tightly linked with the reduction of N loss, which is also apparent from the nature of strategies that have been proposed and examined for their potential to reduce N losses and increase the efficiency of N fertiliser utilisation in arable and pasture production systems. In parts, these techniques have an applied soil and crop management focus by directly targeting N loss from the soil system with an emphasis of maintaining high nutrient levels available for plant uptake in the soil. Often agronomic optimisation and identifying nutrient surpluses on farms will lead to reduced fertiliser use. Other approaches include implementation of low-input systems; improved mode of fertiliser application (e.g. reduced and/or split application to apply smaller dosages at any one time); better timing of fertilisation to more precisely meet crop requirements; use of different types of fertilisers (e.g. slow-release fertilisers); avoiding runoff; mitigation of losses from soil and plants; improved irrigation management based on soil moisture deficits, soil and crop type; and retarding ammonification and nitrification through the use of biological or chemical nitrification inhibitors (Raun and Johnson 1999; Atkinson *et al.* 2005; Alva *et al.* 2006; Subbarao *et al.* 2006; Cui *et al.* 2008; Dawson *et al.* 2008). When comparing N use of winter and spring wheat under conventional and organic management regimes, findings showed that for winter wheat, organic practices resulted in a more efficient use of resources than conventional management (L-Baeckström *et al.* 2006). Montemurro and De Giorgio (2005) showed that NUE was not statistically correlated to N fertilisation levels especially when climate conditions were not limiting plant growth. Overall, their results indicate that environmental variables had a greater effect on sunflower yields, total N uptake and NUE than genotype or fertilisation intensity. In contrast, Janat (2007) reported a positive correlation between N uptake and N fertilisation rate in potatoes, while a reduction of N inputs resulted in better N recovery rates under two irrigation regimes. Research on NUE in grassland systems showed linkages of N utilisation with soil moisture status and N source, with application of ammonium resulting in higher dry matter yields (DM), higher N recovery efficiency (in %) and physiological efficiency (in kg DM kg^{-1} N) (Abassi *et al.* 2005), which is in accordance with Glass (2003), who reported inhibition of nitrate uptake in the presence of high ammonium concentrations in the soil solution. Cui *et al.* (2008) described the successful application of a fertilisation strategy for winter wheat (*Triticum aestivum* L.) under experimental conditions in China, which was based on in-season soil mineral N testing. The improved N management resulted in substantial savings of fertiliser N (128 compared to 325 kg N ha^{-1} as commonly applied by farmers) without experiencing losses in grain yields, thus increasing economic gains and reducing residual nitrate-N in the top soil and consequential N losses. This emphasizes the financial and environmental importance of successful N management, which reduces losses and maintains high yields. Due to the high environmental cost of N fertiliser production and the environmental impact that excess N can have, better synchronisation is necessary between crop demand and nutrient supply throughout the growing season (Atkinson *et al.* 2005).

While inherent soil properties, environmental factors and management techniques can have a significant influence on N uptake and NUE, the capacity of plants to assimilate N from soils is to a large degree influenced by the health and physiological state of the crop and driven by molecular controls within the plant (Glass 2003; Abassi *et al.* 2005). Other strategies to improve NUE are therefore more plant-centred and aim at improving the use of available soil resources and nutrient uptake by plant roots through, for example, crop and cultivar selection, breeding, implementation of crop rotations to influence the soil microbial community and forms of N present, including the use of green manures and legumes, use of arbuscular mycorrhizae to optimise N uptake potential of the root system and through genetic manipulation of uptake, assimilation and translocation of N within plants (Abrol *et al.* 1999; Raun and Johnson 1999; Glass 2003; Good *et al.* 2004; Atkinson *et al.* 2005; Hirel *et al.* 2007; Dawson *et al.* 2008). Two approaches have been identified to address the issue of improving NUE at the plant level: The first consists of a combination of traditional breeding and marker-assisted selection in an attempt to identify the genes involved in N uptake (Good *et al.* 2004). Over recent years, significant progress has been made to isolate and characterise genes, and identify processes and molecular regulators involved in the N uptake by and assimilation within plants. Efforts have been made to breed for cultivars that express improved NUE, and overexpression of a variety of genes in plants has been considered in order to increase NUE (Lea and Azevedo 2006; Hirel *et al.* 2007).

The second approach capitalises on research advances made in connection with genetic modifications of crop plants as newly designed transgenes are used to improve specific aspects of NUE (Lea and Azevedo 2006; Good *et al.* 2007; Strange *et al.* 2008). In contrast to previous experiments, which studied the initial steps of primary N uptake and metabolism (e.g. nitrate transporters such as nitrate reductase and glutamine synthetase), Good *et al.* (2007) focussed on the manipulation of metabolic pathways further downstream of N transport by genetically modifying plants to overexpress alanine aminotransferase, which resulted in an increase in nitrate influx and higher dry matter and seed yields under low N conditions. As emphasised by Good *et al.* (2004), transgenic approaches will need to be closely combined with more traditional methods, such as plant breeding and marker-assisted selection, in order to be successful and obtain the greatest possible benefits from the introduced genes.

Due to the economic costs of excessive use of N fertilisers and the environmental risks posed by surplus nutrients in soils, air and water, there is a continued interest among farmers, policy makers and researchers alike, to improve soil nutrient retention and crop NUE. In recent years, studies have increasingly focussed on assessing the possibilities to manipulate NUE at the plant level by employing and integrating novel molecular and genetic techniques. The extent of interest and the progress that has been made suggest that these approaches have a lot of promising potential. However, results generally indicate that the evidently straightforward process of N uptake from soil by plant roots is more complex than originally believed and that there is still a lot to learn. Soil and crop management based techniques to improve NUE can often be implemented with relative ease and at low costs, while introduction of genetically modified plants is likely to incur further costs and might meet with opposition from both farmers and the general public. Nonetheless, any approach requires the appreciation that low NUE is an important issue that needs addressing and the willingness to change and adopt new ideas on part of the land manager.

N cycle inhibition

Ammonification or hydrolysis of urea (the conversion of N bound in the organic compound urea to ammonia and ammonium) and nitrification (the oxidation of ammonium to nitrate via nitrite) are key components of the soil N cycle and are both considered important processes in most intensive agricultural systems. Both processes are driven by soil microbial activity and increase the amount of plant available N in soils. Urea is hydrolysed by the enzyme urease leading to the formation of CO_2 and ammonia, which under most soil conditions is rapidly converted into ammonium. However, in the soil solution, ammonium is in equilibrium with ammonia, which can volatilise easily and, upon reaching the atmosphere, contributes to N deposition and indirectly to global warming (IPCC 2007a). Ammonium, on the other hand, can be bound to negative exchange sites of soil organic matter or clay particles or is fixed in clay molecules. Nitrification results in the formation of highly mobile nitrate, which is susceptible to loss from the root zone by leaching and/or gaseous emissions of di-nitrogen or nitrous oxide through denitrification. As the loss of soil N in solution or gaseous form can cause pollution as well as N deficiencies in crops and pasture, the prospect of actively regulating these soil processes has major implications not only for environmental quality but also for plant productivity. The application of compounds that retard nitrification or urease activity is used to improve N recovery and N use efficiency in agricultural soils, while at the same time limiting the environmental impacts of N loss and thus improving sustainability (Amberger 1989; Jarvis 1996; Fillery 2007). (For a more detailed overview of processes and principles involved in urease and nitrification inhibition refer to Watson (2000) and Subbarao *et al.* (2006), respectively.) Nitrification inhibitors have been successfully employed to reduce nitrate leaching (Di and Cameron 2006) and mitigate nitrous oxide and methane emissions from, for example, animal urine patches and rice-wheat systems (e.g. Malla *et al.* 2005; Clough *et al.* 2007), while urease inhibitors have been used to decrease ammonia volatilisation not only from soils but from animal manure storage facilities. Varel (2007) reported a delay in urea hydrolysis by 4-11 days after a one-off treatment of manure with the urease inhibitor N-(n-butyl) thiophosphoric triamide (nBTPT). When nBTPT was repeatedly applied every 8 days at rates of 1 and 2 kg ha^{-1}, ammonia volatilisation was reduced by 49 and 69%, respectively, under simulated animal feed lot conditions (Parker *et al.* 2005). When nBTPT was applied to cattle manures simultaneously with the antimicrobial agent thymol in order to reduce the microbial degradation of the urease inhibitor, the inhibition efficiency was further improved. Over 56 days, urea concentrations decreased by 43% in the manure amended with nBTPT and thymol compared to 89% in the manure with nBTPT alone (Varel *et al.* 2007). However, McCrory and Hobbs (2001) concluded that the use of urease inhibitors to reduce ammonia losses from animal manures was not economically feasible as they are too expensive and easily broken down or inactivated in soils and thus do not provide any financial or practical benefit to the farmer.

Most nitrification inhibitors target the ammonia monooxygenase enzyme specific to ammonia-oxidising bacteria that convert ammonium to nitrite, the first step in nitrification, and reduce nitrification rates in soils. Compounds with known nitrification inhibiting qualities include synthetic chemicals such as nitrapyrin (marketed under the trade name N-Serve®) (2 chloro-6-(trichloromethyl) pyridine) (e.g. Wolt 2000), DCD (dicyandiamide) (e.g. Di and Cameron 2002), ammonium thiosulfate, thiourea (e.g. Malla *et al.* 2005) and DMPP (3,4-dimethylpyrazole phosphate) (e.g. Zerulla *et al.* 2001) as well as biological nitrification inhibitors (BNI), which are plant-derived substrates such as neem (*Azadirachta indica* Juss) (Subbarao *et al.* 2006; Fillery 2007). Neem products, e.g. neem cake, neem oil and neem seed- or oil-extracts, are recognised as an effective plant-derived nitrification inhibitor and have shown promising results. Moreover, research by Subbarao *et al.* (2007) indicates that molecular techniques might serve to introduce and manage the trait of biological nitrification inhibition into plant species that show a potential for BNI.

The application of nitrification inhibitors can affect crop yield, N retention in the root zone, microbial biomass and activity in the rhizosphere, nitrate leaching into ground water and nitrous oxide emissions to the atmosphere (Wolt 2004; Mahmood *et al.* 2005). Their effectiveness strongly depends on environmental factors such as soil temperature, application rate and method and is variable especially under field conditions (Wolt 2000; Vallejo *et al.* 2005). Most nitrification inhibitors have shown good potential under laboratory conditions, while their assessment *in situ* often showed little promise and has in most cases proven not to be cost effective. Nitrification inhibitors can be subject to volatilisation (esp. nitrapyrin), microbial decomposition, especially when soil temperatures are above 10-15°C leading to their removal from the active zone of nitrification (Vallejo *et al.* 2005), and leaching. This is particularly an issue for DCD (Meijide *et al.* 2007), which might, however, be overcome by using a fine particle suspension as recently described by Moir *et al.* (2007).

Thus far, the potential side effects of nitrification inhibitors on the soil ecosystem have not been established in detail. The existing literature suggests that their use does not negatively affect the soil microbial community, and there is evidence that nitrification inhibitors have no effects on microbial biomass, respiration and enzymatic activities (Müller *et al.* 2002; Di and Cameron 2004; Mahmood *et al.* 2005). In agreement with these findings, Egamberdiyeva *et al.* (2001) reported increased numbers of oligonitrophilic bacteria and cellulose degradation activity and a decrease in the number of nitrifying and denitrifying bacteria after application of potassium oxalate as nitrification inhibitor, while at the same time availability of fertiliser N to plants was increased. They concluded that the combination of potassium oxalate and mineral fertilisation showed promising potential concerning nitrification inhibition. While their study did not assess the specific effects of synthetic nitrification inhibitors on soil microbial populations, Austin *et al.* (2006) showed that reduced nitrification can have significant impacts on the soil carbon cycle and, for example, decrease organic matter decomposition, when applying nitrapyrin to an undisturbed semi-arid steppe. Their results indicated that N species (i.e. ammonium vs. nitrate) may be a more important driver of carbon cycling and ecosystem functioning than the quantity of N present in the system. This underlines the significance of different forms of N in terms of carbon turnover in soils and highlights the need for further studies into the effects of chemical nitrification inhibitors on all nutrient turnover processes and their interactions in soil ecosystems.

Urea hydrolysis is a ubiquitous process, and a wide range of microorganisms including bacteria, yeasts, filamentous fungi, actinomycetes and algae possess the enzyme urease (Mobley and Hausinger 1989). While urease activity occurs at temperatures as high as 37°C and as low as 2°C, the optimum environment are warm, moist soils with soil moisture contents favourable for plants. Under optimum conditions, most of the urea is transformed to ammonium in several days. The optimum pH varies depending on urea concentrations and can range from pH 6.5-7 to pH 8-9 (Mulvaney and Bremner 1981). Urease activity can be restricted at pH levels above 7, when high ammonia concentrations occur in the soil solution. Ammonia emissions from urea application can thus be reduced by maintaining a low pH near the urea prill through the addition of acidifying compounds, such as potassium chloride (KCl), phosphoric acid (H_3PO_4) and monocalcium phosphate ($Ca(H_2PO_4)_2$) (Ouyang *et al*. 1998). Urease activity also decreases with increasing urea prill size due to a hotspot effect, which locally increases the concentrations of urea, ammonium and nitrite and consequently soil pH in the immediate vicinity of urea application (Khalil *et al*. 2006).

Another way to reduce the rate of urea hydrolysis and the subsequent formation of volatile ammonia is the application of chemical urease inhibitors (Bremner 1995; Watson 2000). A wide range of compounds have been tested as urease inhibitors, such as hydroquinone, hydroxyurea, hydroxamic acids, phosphoramides, thiourea, boron containing compounds (e.g. boric acid), and halogens (e.g. fluoride), or urease inactivators, such as alkylating agents and disulphide (Mobley and Hausinger 1989; Watson 2000). Of the commercially available inhibitors tested, the phosphoryl di- and triamides nBTPT and PPD (phenylphosphorodiamidate) were the most promising with varying degrees of efficacy depending on environmental conditions and management (Gioacchini *et al*. 2002). As described for nitrification inhibitors above, the efficiency of urease inhibitors also depends on climate and soil conditions during and following application. For example, application was particularly efficient in reducing ammonia emissions following rainfall, i.e. under environmental conditions favouring urea hydrolysis (Sommer *et al*. 2004). Inhibitor efficiency is, however, strongly compound specific. For example, the most widely commercially available urease inhibitor, nBTPT, must be converted to the oxygen analogue N-(n-butyl)phosphorictriamide for optimum efficiency, while PPD is immediately effective but is known to decompose rapidly (Bremner 1995). Hydroquinone, which is commercially available in China in a formulation with urea fertiliser, is a less effective urease inhibitor than the phosphoramides but has been found to have physiological benefits for plants as it minimises the adverse effects of urea on seed germination and seedling growth by reducing the concentrations of ammonia released during urea hydrolysis (Bremner 1995). As a result of the often high costs of commercially available urease inhibitors and the desire to reduce the use of chemicals in agricultural systems, researchers have been trying to identify an effective, biologically benign inhibitor. Corresponding to their use as biological nitrification inhibitors, neem compounds have been the subject of extensive research in recent years with regards to their urease inhibition properties. Neem seed kernel powder has been found to reduce urease activity in an acid soil and sustained higher soil urea concentrations for two weeks after application compared to samples treated with urea alone (Mohanty *et al*. 2008).

Synthetic nitrification or urease inhibitors are not seen to be financially viable as they are often too expensive for broadscale application and the additional cost is not offset by savings in fertiliser N or increases in crop yield (Subbarao *et al*. 2006; Fillery 2007). However, as the price of fertiliser N increases, the cost/benefit of urease and nitrification inhibitors might improve and make their application more commercially viable. Moreover, when assessing the financial cost of inhibitor use, we need to bear in mind that these calculations are primarily based on agronomic considerations and rarely take into account the economic and ecological cost of excess N in the environment. Management based approaches to reduce N losses, such as tailoring N fertiliser inputs to crop needs, might result in higher costs for fuel and labour and amplify gaseous emissions due to the increased frequency of fertiliser application. Application of nitrification and urease inhibitors may allow agricultural systems to better match N availability and crop needs without such unwanted side effects.

Unfortunately, to date, there is no evidence of the long-term impacts of nitrification inhibitors on the soil micro- and macrofauna, as well as on soil microbial community composition, microbial diversity and function in general and on non-target organisms in particular. While questioning the effectiveness of synthetic nitrification inhibitors under field conditions, recent reviews do not address the issue of the possibly harmful environmental impacts of long-term application of these compounds (Subbarao *et al*. 2006; Fillery 2007). Experiences with the introduction of chemical substances into the environment indicate that a cautionary approach is desirable as often problems were recognised too late. One example is the excessive use of synthetic N fertilisers, which has resulted in the vast and unexpected negative effects on the global environment that we are dealing with now. It is essential to avoid the same mistakes with regard to synthetic inhibitors. To ensure their use is environmentally sound and does not negatively affect soil micro- and macro biota as well as microbially mediated soil processes, it is vital to conduct detailed laboratory and long-term field studies taking into account external factors, such as local climate, soil and plant type.

Advances in understanding N cycling processes

Recent advances in our understanding of N cycling processes and the discovery of new N transformation pathways have fundamentally altered the way we view this vital biogeochemical cycle. The observed increase in freshwater, estuarine and coastal eutrophication, along with the associated legislative pressure, and the environmental and agronomical challenges posed by changing climate, increasing fossil fuel costs and growing populations have led to a large volume of research being conducted to investigate the underlying mechanisms and processes determining nitrogen availability and emissions. This increase occurred in conjunction with substantial developments in the areas of environmental and molecular microbiology. Modern molecular based techniques have facilitated the discovery of novel N processes, such as anaerobic ammonium oxidation (anammox) and aerobic ammonia oxidation within the domain Archaea (Francis *et al*. 2007), dissimilatory nitrate reduction to ammonium (DNRA) (Gardner *et al*. 2006), chemotrophic iron and sulphur denitrification (Burgin and Hamilton 2007), and denitrification associated with methane oxidation (Raghoebarsing *et al*. 2006).

Until recently, oxidation of ammonia to nitrite (i.e. the first step of nitrification) was thought to be carried out by only a small number of bacterial genera (*Nitrosomonas* ssp., *Nitrosospira* ssp. and *Nitrosococcus* ssp.). However, this view changed with the discovery that ammonia oxidation is carried out by Crenarchaeota of the domain Archaea (Francis *et al*. 2005). Based on the number of copies of the *amoA* gene, which codes for the enzyme ammonia monooxygenase, Crenarchaeota have been found to be significantly more abundant than bacterial ammonia oxidisers in the wider environment, such as soils (Leininger *et al*. 2006) and marine environments (Wuchter *et al*. 2006). Leininger *et al.* (2006) found that ammonia oxidation genes were equally active as numerically abundant in Archaea. However, gene presence, abundance and activity alone does not give any indication if and under what environmental conditions archaeal ammonia oxidisers dominate the nitrification process in soils. This indicates the need to further study environmental factors influencing population growth and activity of bacterial and archaeal ammonia oxidisers in soils in greater detail.

Anammox has been proposed to occur in most natural ecosystems under anaerobic conditions and is attributed to currently four recognized bacterial genera (Francis *et al.* 2007). Through this biological process, nitrate is partially reduced to nitrite, which is used as an electron acceptor for the oxidation of ammonium to N_2, which is environmentally benign. The microbial process of dissimilatory nitrate reduction to ammonium (DNRA) couples electron flow from organic matter to the reduction of nitrate via fermentation reactions and is thought to be prevalent in nitrate-limited environments, which are rich in labile carbon (Burgin and Hamilton 2007). A second pathway for DNRA is chemolithoautotrophic, which couples the reduction of nitrate to the oxidation of reduced sulphur forms, including free sulphide and elemental sulphur. The fate of the reduced nitrate may be determined by the ambient concentration of free sulphide (Burgin and Hamilton 2007). DNRA is thought to be responsible for providing ammonium-ions for the anammox process. When anammox and DNRA occur concurrently, the resulting N_2 is indistinguishable from that produced by denitrification (Francis *et al*. 2007). It is important to discriminate between the various products formed during these nitrate removal processes, as only the completely reduced N_2 (formed by anammox) is environmentally acceptable. The conversion of nitrate to ammonium (as in DNRA), on the other hand, yields more biologically available N, even though ammonium tends to be less mobile due to adsorption to organic matter and clay particles. It has become increasingly clear that the microbial N cycle in aquatic and soil environments is considerably more complex than previously thought. Losses of nitrate from suboxic systems are no longer synonymous with denitrification; many other processes are potentially responsible for nitrate removal. Moreover, it has been recognised that denitrification is not only a heterotrophic process but also occurs in abiotic reactions (chemo-denitrification), which may be of importance in suboxic environments. During chemo-denitrification, nitrate is reduced to nitrite and nitric oxide by reacting with ferrous iron (Fe^{2+}) or reduced manganese (Mn^{2+}), which is followed by a rapid conversion of nitrogen dioxide to N_2. Alternatively, it has been hypothesised that these abiotic processes maybe linked to N immobilisation in forest soils, where nitrate is reduced to nitrite, which then reacts with dissolved organic matter to produce dissolved organic N (Davidson *et al*. 2003). Although the existence of abiotic pathways of reduction in soils has been reported for a long time in the literature (Carsley 1930), the importance and occurrence of these processes still warrants and requires further investigation in a range of ecosystems and environmental conditions. Another critical component of the soil N cycle might be the uptake of dissolved organic N by plants and microorganisms (Schimel and Bennett 2004; Jones *et al*. 2005; Boyle *et al*. 2008). In this context, fungi, including mycorrhizae, may be crucial in influencing N turnover in soils due to their hyphal networks connecting microsites and producing extracellular enzymes that promote the depolymerisation of N compounds (Schimel and Bennett 2004).

Functional genes within microorganisms encode the enzymes that initiate and regulate most steps of the global nutrient cycles. To study the presence, abundance and activity of these genes and the microorganisms, in which they are present, and to determine the driving environmental factors will lead to more detailed knowledge of nutrient cycling processes in soils and aquatic systems. Examples of recent advances are the development and application of PCR-DGGE (Polymerase Chain Reaction followed by Denaturing Gradient Gel Electrophoresis) based techniques and the use of microarrays, which facilitate the assessment of functional genes within the N cycle, such as *nxrA* (coding for nitrite oxidoreductase), *nirS* and *nirK* (nitrite reductases), and *amoA* (ammonia oxidase) as well as the application of these methods on environmental samples to study natural and agricultural ecosystems (Rotthauwe *et al.* 1997; Braker *et al.* 1998; Taroncher-Oldenburg *et al.* 2003; Poly *et al.* 2008; Wertz *et al.* 2008). Any new approach represents an important and necessary step towards more comprehensive studies of N turnover in terrestrial and marine ecosystems. Continuing advances in the development of molecular techniques and their more routine application in the field of biogeochemistry will help us to better understand microbially mediated nutrient cycles, potentially opening ways to actively and precisely manage microbial communities and the associated processes, which in turn would improve our ability to manipulate nutrient cycling processes and N retention more successfully *in situ*. While many of these newly discovered processes and pathways have been studied extensively in oceans, we have little knowledge and understanding of their importance and extent in soils, rivers, lakes and groundwater systems (Burgin and Hamilton 2007). Anammox, for example, has been identified as an important and widespread process in marine environments and current findings suggest that it is a ubiquitous process that is likely to occur in all N-containing ecosystems with suboxic conditions (Francis *et al.* 2007), however, the magnitude of contribution of the process to the terrestrial N cycle is still unclear and few measurements have been made in soil systems.

These new insights into aerobic and anaerobic ammonia oxidation have further highlighted the complexity of the global N cycle. The recently discovered pathways and modes of transformations within the global N cycle have led to new challenges for researchers who aim to estimate and model these transformation processes at regional and global scales, while currently only limited data are available on the actual extent of fluxes and processes. It will be an important task to further identify, isolate and enumerate the microbial communities contributing to N cycling in soils and determine the role of environmental parameters in influencing microbial community dynamics and activities, such as the N mineralisation rates.

SYNOPSIS

Until recently, many farmers have been unaware of the environmental and financial costs associated with N pollution and have often not recognised the environmental and socio-economic benefits they could provide to the wider society by implementing best management practices. To date, agricultural research has provided farmers with a range of tools and best management practices that aim to optimise production whilst reducing fertiliser costs and minimising adverse environmental impacts, for example, by tailoring fertiliser inputs to crop requirements, selecting species for improved nutrient use efficiency, applying N cycle inhibitors or using leguminous species, e.g. clover (*Trifolium* spp. L.) and other Fabaceae, in mixed pastures, or as green manures as part of arable crop rotations (e.g. lupin, *Lupinus* spp. L.). Implementation and adoption of these measures and practices have mostly been hampered by the relatively low price of easily available N fertilisers, which often made it more cost effective to apply fertilisers in excess than implement best management practices. Theoretically, an economic substitution will occur when it is cheaper for farmers to use new techniques or apply recommended best management practices (e.g. replace synthetically with biologically fixed N). This economic ‘tipping point’ is not fixed but will depend on the relationship between input and output costs and overall profit margins. While the growing worldwide demand for food and fibre is likely to require the continued use of synthetic N fertilisers, this situation may change dramatically in the coming decades if fossil fuel prices continue to increase beyond their current (May 2008) high of US\$128 barrel^{-1} (158.98 litres), which will result in commensurate increases in the cost of fertiliser N. The long-term effects of globalisation and the removal of importation tariffs on agricultural cost structures and profit is difficult to predict and beyond the aim of this paper, but it is considered unlikely for the *status quo* to remain. Farmers will need to alter their production systems, possibly radically, in order to both maintain profitability and ensure environmental protection.

The predicted increases in agricultural productivity, farming intensity and fertiliser consumption will intensify the negative effects of agriculture on the environment, of which N loss to atmosphere and water are critically underestimated problems. Environmental changes are also likely to have a large, but difficult to predict, impact on agricultural production, which in turn could further exacerbate climate change in a self-reinforcing positive feed back loop. Although, or even because, the potential effects of global change on N emissions to air and water are so difficult to predict, they constitute a growing threat to environmental quality and bring about new challenges with regard to managing N loss. International research has lead to the discovery of new processes in the global N cycle, advances in understanding pathways of N uptake as well as developments in agronomy, soil and plant science. Yet, managing N loss from agricultural systems still constitutes an ongoing challenge and the development of sustainable, i.e. environmentally sound, profitable and socially acceptable, production systems appears likely to remain a critically important task for policymakers, scientists and land managers for the foreseeable future. If they are to be successful, it is imperative that research is more integrative and interdisciplinary, and that there is continual and open dialogue between the science community and those that work in policy and manage land. The issues surrounding N in the environment are as much social and political as technical, and solutions have to be sought within all arenas. Farmers are unlikely to be able to implement changes on their own: There is little point identifying environmentally damaging agricultural practices unless related agricultural research provides feasible and economic viable alternatives that farmers can implement. Without the active involvement of all participants in the entire process, from problem identification through to solution, there will not be any long-term resolution.

The large number of long-standing and new problems regarding N in the environment, as well as the recent research developments emphasize the continuing importance of managing N loss from agricultural systems and industry in industrialised as well as developing nations. Environmentally sound, economically viable and productive agroecosystems are required to meet the growing worldwide need for agricultural produce, while at the same time reducing environmental pollution. Supported by research and innovation, modern agriculture can continue to maximise N use efficiency, reduce emissions to meet environmental targets and contribute to the enhancement of the global environment. Advancing our knowledge of N cycling processes and pathways in soil, water and plants will allow the development of customised and integrated mitigation strategies for N loss to air and water, while novel research methods, innovative application of techniques and interdisciplinary approaches will help to achieve these tasks. However, no meaningful scientific research is possible without sufficient resources. Confronting the continuing challenge of N loss to the environment and solving the N problem not only requires for the issues at hand to be recognised and appreciated, it also demands ongoing policy commitment and financial investment by governments and corporate funding bodies into long-term, integrated, science programs and projects. In the second part of this review, we will discuss the integrity of the N cycle in more detail, outline problems arising from environmental N loss, e.g. effects on climate change and human health, and examine mitigation strategies including policy-based approaches targeted at controlling and limiting environmental N emissions at national and international levels.

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