

CHAPTER 2

The Biogeochemical Nitrogen Cycle

T. ROSSWALL

*SCOPE/UNEP International Nitrogen Unit,
Royal Swedish Academy of Sciences, Stockholm, Sweden*

ABSTRACT

The biogeochemical nitrogen cycle is complex with nitrogen occurring in valence states from -3 to $+5$. Although abundant on earth, 96 per cent is found in the lithosphere and does not take part in the biogeochemical cycle. In terrestrial systems, only four per cent of the nitrogen occurs in biomass, while 96 per cent is found mainly in soil organic matter.

Nitrogen is an essential nutrient but nitrogen compounds are also potential toxicants. The hazard of unwanted side effects is increasing, i.e. through the increased use of nitrogen fertilizers. By the end of this century, man made additions of combined nitrogen to terrestrial ecosystems will be as large as the amount added through biological nitrogen fixation.

An understanding of the individual processes of the nitrogen biogeochemical cycle is needed before attempts can be made to quantify the nitrogen cycle of ecosystems, regions, or the earth. The inorganic nitrogen cycle, which was earlier considered relatively simple, is becoming more complex as our knowledge increases.

To establish a quantitative nitrogen budget for a system, we need extrapolation in time and space. Extrapolation in space is difficult due to the patchy distribution of anaerobic microsites. Extrapolation in time calls for a thorough understanding of the factors affecting process rates in order to quantify yearly rates based on a few measurements only.

The nitrogen cycle in an ecosystem is an important characteristic. The pattern of nitrogen cycling changes as an ecosystem develops to its climax state, and it is also affected by disturbances such as management practices.

A quantification and understanding of the nitrogen cycle in various types of typical ecosystem of the world will offer us the jigsaw pieces needed to construct an authoritative picture of the global nitrogen cycle, intrinsically linked to other major elements such as carbon, phosphorus and sulphur.

2.1 INTRODUCTION

Few elements are as complex and interesting as nitrogen. Firstly, this complexity is reflected in the highly intricate biogeochemical cycle, where nitrogen occurs in valence states from -3 to $+5$ and where many of the transformations are carried out by a few organisms only, at normal temperatures and pressures.

Table 2.1. Distribution of Nitrogen on Earth. All values in Tg (10^{12} g). Data from Sweeney *et al.* (1978)

	Amount of nitrogen (Tg)	Proportion (%)
Lithosphere	574×10^8	93.8
Atmosphere	38×10^8	6.2
Hydrosphere	0.23×10^8	0.04
Biosphere	0.009×10^8	0.001

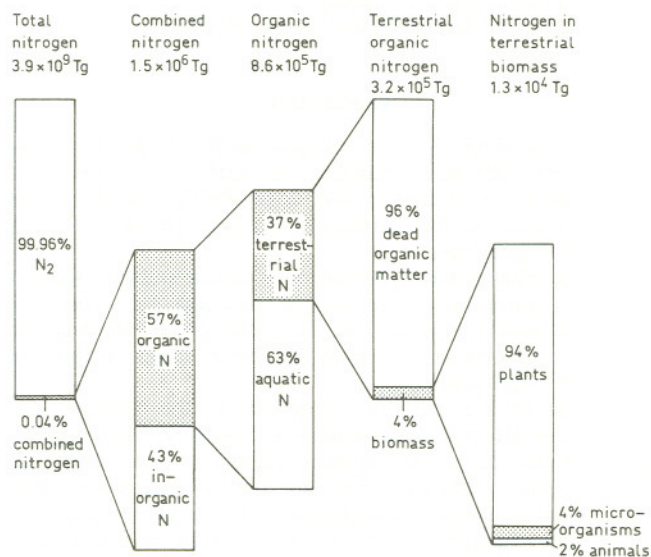


Figure 2.1 Distribution of nitrogen in the biosphere (Ross-wall, 1979a)

Secondly, nitrogen is an element which is abundant on earth, but only a very small proportion of it enters into the biogeochemical nitrogen cycle at significant rates. Of the nitrogen found on earth, only 0.001 per cent occurs in the biosphere (Table 2.1). Most of the nitrogen is thus found in the lithosphere (especially in primary rocks of the mantle; see Stevenson, 1972). The atmosphere, where nitrogen occurs abundantly in its molecular form, still only contains six per cent of all nitrogen on earth. Of all nitrogen taking part in the biogeochemical nitrogen cycle only 0.04 per cent occurs in compounds potentially available to living organisms (Figure 2.1). In the terrestrial system only four per cent occurs in biomass, the remainder forming a large reservoir as dead organic matter (96 per cent). The unavailability of the 99.96 per cent occurring as nitrogen gas, combined with the major role played

by nitrogen-containing substances in all forms of life, has caused nitrogen to be one of the key elements limiting the primary production on which man depends for his supply of food, fodder, fibre, and fuel.

Thirdly, the nitrogen cycle is easily manipulated by man, and it has been estimated that, by the end of this century, man-made additions of combined nitrogen will equal the amounts fixed annually through biological nitrogen fixation (Söderlund and Svensson, 1976). This increased addition from fertilizers, together with nitrogen oxides emitted into the atmosphere as a result of combustion, is undesirable since nitrogen compounds are a direct environmental hazard (Bolin and Arrhenius, 1977).

A SCOPE project on the global nitrogen cycle was started in 1974. It was terminated by the publication of a report quantifying the global cycle in detail not earlier attempted (Figure 2.2). The increased interest in the nitrogen cycle is reflected in the many global nitrogen budgets that have recently been published, e.g. Söderlund and Svensson (1976), Delwiche (1977), Hahn and Junge (1977), Sweeney *et al.* (1978), NAS (1978), and Bolin 1979. One of the main reasons behind this interest was the concern that nitrogen oxides may be acting as important catalytic agents regulating the thickness of the global stratospheric ozone shield. Our understanding of the nitrogen cycle is still, however, very rudimentary, and only by trying to understand the main factors regulating the many processes in the biogeochemical nitrogen cycle will it be possible to attain an improved quantitative picture of the global nitrogen cycle. An authoritative quantitative description is needed before we can quantify man's interventions in this cycle and their possible deleterious effects on the environment.

2.2 NITROGEN METABOLISM IN ECOLOGICAL TERMS

2.2.1 Nitrogen Assimilation

Plants and most microorganisms are dependent on ammonium or nitrate salts for growth, though they seem generally to prefer ammonium as a nitrogen source. Ammonium nitrogen can be metabolized by two different pathways—either through glutamate dehydrogenase (GDH) or through glutamine synthetase/glutamate synthase (GS/GOGAT) (Figure 2.3). Although GDH was previously considered the major enzyme involved in ammonium assimilation, it now seems clear that, especially at low ammonium concentrations, GS/GOGAT is the major enzyme system involved both in microorganisms and in plants (Mifflin and Lea, 1977; Brown and Johnson, 1977); Lee and Stewart, 1978). This latter system has a much higher affinity for the substrate (K_m for GS: $1-2 \times 10^{-5}$ M; Lee and Stewart, 1978) than glutamate dehydrogenase ($K_m = 4 \times 10^{-3}$ M; Mifflin and Lea, 1977). It should be noted that glutamine synthetase is ATP-dependent, whereas glutamate dehydrogenase is not. This system is thus probably the rate-limiting step, since ammonia uptake seems to be a passive process (Higinbotham, 1973).

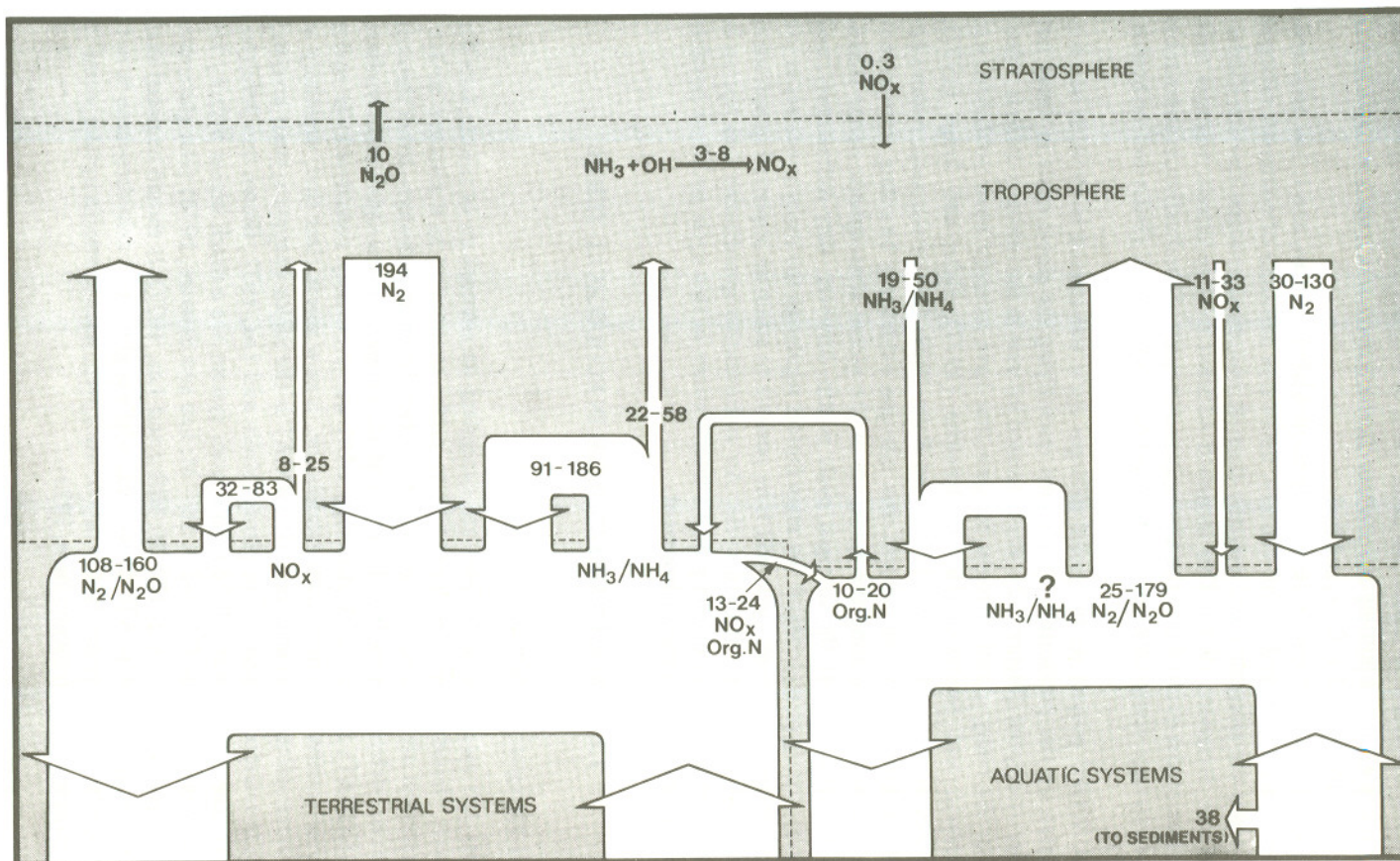


Figure 2.2 The global nitrogen cycle. Flows in Tg yr^{-1} are valid for 1970 (Söderlund and Svensson, 1976)

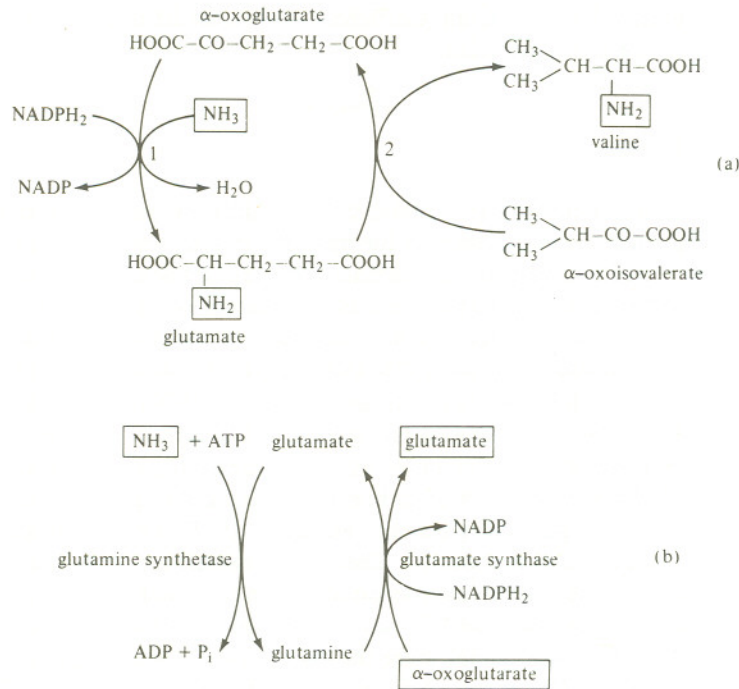


Figure 2.3 Assimilation of ammonia (a) by glutamate dehydrogenase (1) and subsequent transfer of the amino group by a transaminase (2); (b) by glutamine synthetase/glutamate synthase (GS/GOGAT). From Gottschalk (1979)

All plants, except certain bog species, are able to utilize nitrate as well as ammonium. If no other factors limit microbial growth, microorganisms will efficiently scavenge the surroundings for available ammonium nitrogen. Since ammonium oxidation through nitrification proceeds rapidly in most soils, nitrate is probably the most important nitrogen source for most plants. In contrast to ammonium uptake, plant root uptake of nitrate is dependent on a permease system (Lee and Stewart, 1978). The occurrence of nitrate reductase in the plant seems to give an indication of the rate of nitrate supply in the plant (Lee and Stewart, 1978). A comparison of net assimilation or net growth with nitrate reductase activity at different points in time could give an indication of the relative importance of ammonium and nitrate as the nitrogen source for plants at different times during the growing season.

Microorganisms generally prefer ammonium as a nitrogen source, and their ability to use nitrate is restricted. Of the 2500 genera of fungi described, only 20 have been reported to assimilate nitrate (Payne, 1973; Downey, 1978). The occurrence of nitrate assimilation in bacteria seems to be more common than in fungi, although it is in no way ubiquitous (Hall, 1978). Since the assimilatory nitrate re-

ductase is repressed by ammonium (Gottschalk, 1979), the latter is the preferential nitrogen source for microorganisms.

2.2.2 Mineralization

Ammonium is liberated through mineralization, mainly by microorganisms, from organic compounds. Immobilization is the opposite process, whereby inorganic nitrogen is assimilated and built up into organic compounds. For soil microorganisms, the balance between mineralization and immobilization of ammonium nitrogen, i.e. positive or negative nitrogen net mineralization, is regulated primarily by the C/N ratio of the substrate (Parnas, 1975, 1976). Microbial biomass in soil has been estimated to contain four per cent nitrogen (Rosswall, 1976), and if the carbon content is 50 per cent, the microbial biomass has a C/N ratio of 12.5. When an organic substrate is broken down by microorganisms, the quality of the substrate will determine the relative proportion of carbon assimilated and respired. If the assimilatory efficiency is 40 per cent (Heal and MacLean, 1975), no net mineralization will occur if the C/N ratio is above 31. There are, however, very few data available on the assimilatory efficiency of microorganisms growing in soil, and this efficiency is very critical in determining the C/N ratio below which net mineralization occurs (Figure 2.4). However, one cannot judge the mineralization capacities of soils from their C/N ratios alone. In systems which accumulated organic matter, the C/N ratio is generally about 30 (Parsons and Tinsley, 1975). In tundra peat it has been observed to be as high as 48 in the top 10 cm (Rosswall *et al.*, 1975), where most of the net mineralization occurs. Scots pine needle litter from a coniferous forest on glacial sediment in central Sweden originally had a C/N ratio as high as 120, whereas at the time when net mineralization started it was 80 (Staaf and Berg, 1977). If microbial biomass contains four per cent N, carbon/nitrogen ratios of 48 and 120 would require assimilatory efficiencies as low as 23 and 10 per cent respectively for net mineralization to occur (Figure 2.4).

One of the main difficulties in using such a crude concept as the C/N ratio of the substrate for determining whether mineralization or immobilization occurs relates to the forms of nitrogen in organic matter. Part of the nitrogen, especially that bound in proteins, is often easily mineralized, but another part, bound to the lignin fraction, is very resistant to mineralization. Such differences must be kept in mind in any attempt to describe net nitrogen mineralization.

Soil animals may play an important role in regulating nitrogen mineralization in at least two ways. The effect of faunal grazing on microorganisms may increase mineralization rates (Rosswall *et al.*, 1977; Coleman *et al.*, 1977). It also seems that soil invertebrates may play an important role through their excretion of significant amounts of simple nitrogenous substances, such as uric acids, urea, and also ammonia (Table 2.2). They may thus play a more important role in nitrogen mineralization than hitherto assumed.

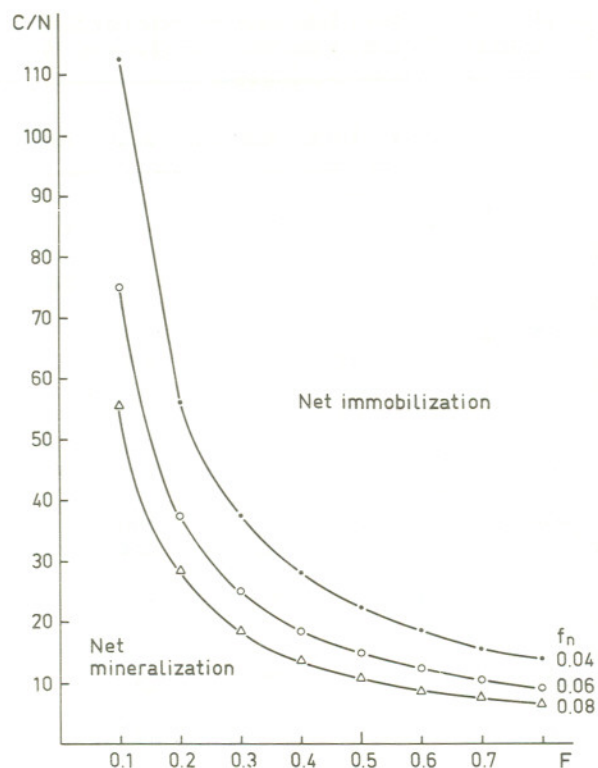


Figure 2.4 The dependence of net mineralization versus immobilization on the carbon/nitrogen ratio of the substrate, the assimilatory efficiency of the decomposers (F), and the nitrogen content of microbial biomass (f_n)

2.2.3 Nitrification-Denitrification

Nitrogen also plays an important role in generating energy in certain groups of microorganisms. Autotrophic nitrifying bacteria obtain energy from the oxidation of ammonium or nitrite, while denitrifying bacteria use nitrate, nitrite, or nitrous oxide as terminal electron acceptors during the oxidation of organic substrates. Nitrate can also be used in a fermentative process by *Clostridium perfringens* (Hasan and Hall, 1975), although since the process uses an inorganic electron acceptor, it is by definition a respiratory process. The amounts of energy obtained by these processes are listed in Table 2.3.

There seem to be very close couplings between nitrification and denitrification (Figure 2.5). It has been postulated that the nitroxyl radical HNO is a possible intermediate in the oxidation of hydroxylamine to nitrite by *Nitrosomonas* (Lees,

Table 2.2 Examples of Nitrogenous Substances Excreted by Soil Animals. The Figures are Percentages of Total Nitrogen Excretion (Persson, 1980)

	NH ₃	Urea	Allantoin	Uric acid	Amino-N	Other
PROTOZOA						
Ciliates	++				+	
NEMATODES						
<i>Ditylenchus</i>	39				28	
EARTHWORMS						
<i>Lumbricus terrestris</i> (well fed)	56	42		1.5		
<i>L. terrestris</i> (starving)	19	81				
WOODLICE						
<i>Oniscus asellus</i>	47			5	6	38
INSECTS						
<i>Forficula</i> (earwigs)				100		
Heteroptera			60-100	0-40		
<i>Lucilia</i> -larvae (blowfly)	93		2	5		
<i>Bibio marci</i> (terrestrial diptera larvae)			55	25		
SNAILS						
<i>Helix pomatia</i>				43		Xanthin 38 Guanin 18

1954). There is still no direct evidence for this, however (Nicholas, 1978). The presence of the nitroxyl radical would also explain the possibilities for N₂O production during nitrification, since, especially under anaerobic conditions, there would be a spontaneous (chemical) decomposition of [HNO] to N₂O (Anderson, 1964).

Nitroxyl also has been suggested by Kluyver and Verhoeven (1954) to be an intermediate in nitrite reduction by denitrifying bacteria, and since a dimerization step is entailed, this radical would seem to be a probable intermediate (Delwiche and Bryan, 1976).

Nitrosomonas also appears to reduce nitrite under anaerobic conditions (Ritchie and Nicholas, 1972). From an ecological viewpoint, there may be several advantages (Rosswall, 1980):

- (i) nitrite may be used as a terminal electron acceptor during brief periods of anaerobiosis;
- (ii) nitrite reduction may offer a detoxifying mechanism if nitrite concentrations become too high; and
- (iii) under certain circumstances nitrite reduction may minimize possible competition from *Nitrobacter* which is dependent on nitrite for growth.

Table 2.3 Free Energy Changes (kJ mol^{-1}) in Inorganic Nitrogen Metabolism Reactions (from Zumft and Cárdenas, 1979; Delwiche, 1977)

	$\Delta G'_0$ (kJ/mol)
Nitrate respiration <i>Escherichia coli</i> $\text{NO}_3^- + \text{H}_2 \rightarrow \text{NO}_2^- + \text{H}_2\text{O}$	-161
Denitrification <i>Pseudomonas aeruginosa</i> $2 \text{NO}_3^- + 2 \text{H}^+ + 5 \text{H}_2 \rightarrow \text{N}_2(\text{g}) + 6\text{H}_2\text{O}$	-1121
Other possible reactions $\text{N}_2\text{O}(\text{g}) + \text{H}_2 \rightarrow \text{N}_2(\text{g}) + \text{H}_2\text{O}$	-340
$\text{NO}_2^- + \frac{1}{2} \text{H}_2 + \text{H}^+ \rightarrow \text{NO}(\text{g}) + \text{H}_2\text{O}$	-76
$2 \text{NO}(\text{g}) + \text{H}_2 \rightarrow \text{N}_2\text{O}(\text{g}) + \text{H}_2\text{O}$	-306
$2 \text{NO}_2^- + 2 \text{H}^+ + 2 \text{H}_2 \rightarrow \text{N}_2\text{O}(\text{g}) + 3 \text{H}_2\text{O}$	-459
Nitrate reduction $\text{NO}_3^- + 2 \text{H}^+ + \text{H}_2\text{O} \rightarrow \text{NH}_4^+ + 2\text{O}_2$	+348
Nitrate fermentation <i>Clostridium perfringens</i> $\text{NO}_3^- + 2 \text{H}^+ + 4 \text{H}_2 \rightarrow \text{NH}_4^+ + 3 \text{H}_2\text{O}$	-591
Nitrification <i>Nitrosomonas</i> $\text{NH}_4^+ + \frac{1}{2} \text{O}_2 \rightarrow \text{NH}_2\text{OH} + \text{H}^+$	+15
$\text{NH}_2\text{OH} + \text{O}_2 \rightarrow \text{NO}_2^- + \text{H}_2\text{O} + \text{H}^+$	-289
<i>Nitrobacter</i> $\text{NO}_2^- + \frac{1}{2} \text{O}_2 \rightarrow \text{NO}_3^-$	-77

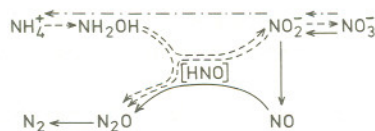


Figure 2.5 The inorganic nitrogen cycle in soil

Certain heterotrophic microorganisms may also oxidize ammonium to nitrate (Focht and Verstraete, 1977). Heterotrophic nitrification may be important in view of the possible ecological significance of some of the products identified. Hydroxamic acids may be important growth factors, possibly linked to iron uptake, and several of the identified metabolic products from heterotrophic nitrification are biocidal (Focht and Verstraete, 1977).

Another interesting feature in the metabolism of inorganic nitrogen relates to the inhibitory effect of acetylene on several of the enzyme systems involved, viz.

nitrogenase (Dilworth, 1966), ammonium oxidase (Suzuki, 1978; Hynes and Knowles, 1978), and nitrous oxide reductase (Balderston *et al.*, 1976; Yoshinari and Knowles, 1976). The effect on nitrification may complicate the use of the acetylene inhibition technique for determining denitrification in systems that are dependent on nitrate production by nitrifying bacteria (Hynes and Knowles, 1978).

2.2.4 Nitrogen Fixation

Interest in nitrogen fixation has increased in recent years for several reasons. From a practical viewpoint, it was largely triggered by the tripling in the price of nitrogen fertilizers after 1974, and by the difficulties—especially for farmers in the less developed countries—of supplying nitrogen to the soil in sufficient amounts to increase crop production. Much attention was accordingly given to optimizing the use of biological nitrogen fixation.

The use of *Rhizobium* for inoculating legume crops constitutes the most promising approach and has been widely used for many years. Significant research projects are being carried out in a large number of countries to optimize biological nitrogen-fixation using *Rhizobium*. In tropical ecosystems the contribution of indigenous legumes is often more important than that of cultivated species, such as soy bean, peanut, cowpea and chick-pea (A. Foury, 1950; cited by Franco, 1978). Specialized regional microbiological resource centres (MIRCENs) devoted to the use of biological nitrogen fixation have been set up in Kenya and Brazil under the sponsorship of UNEP and Unesco (Rosswall, 1979b). Important research efforts also are being made by the international agricultural research institutes, e.g. International Institute for Tropical Agriculture (IITA) in Nigeria and the International Crop Research Institute for the Semi-arid Tropics (ICRISAT) in India. Strain selection from native legumes will be important, especially the isolation of *Rhizobium* strains with an efficient hydrogenase, since strains which can recycle the hydrogen formed during nitrogen fixation have been shown to be more efficient in fixing nitrogen (Albrecht *et al.*, 1979).

Attention has also been focused recently on the possibilities of associative symbioses between microorganisms and plant roots, the most important of which seems to be the association of *Azospirillum* with sorghum, maize (von Bülow and Döbereiner, 1975), and sugar cane (Ruschel *et al.*, 1978). The association of *Azotobacter paspali* and *Paspalum notatum* is another such association that has received increased attention (Döbereiner, 1970, 1977). The possibility that *Azospirillum* may denitrify and thus fix nitrogen under anaerobic conditions, with nitrate as a terminal electron acceptor, is another interesting recent finding (Neyra and Van Berkum, 1977), which is a further important link in the coupling of inorganic nitrogen metabolism in bacteria, as discussed above.

The aquatic water fern *Azolla*, together with the blue-green alga *Anabaena azollae*, provides another example of a nitrogen-fixing association that can fix substantial amounts of nitrogen and be of agronomic significance (Moore, 1969). It is

especially important in rice fields (Talley *et al.*, 1977). The recent isolation of the cyanobacterium responsible for the nitrogen fixation (Newton and Herman, 1979) will be important in further attempts to investigate—and ultimately select—strains which are efficient in the symbiosis. An *Azolla* species which excretes ammonium during the entire growing season seems to be especially promising for agronomic use (R. C. Vallentine, personal communication).

Non-legume symbiosis with actinomycetes of the genus *Frankia* occurs in several temperate species, such as *Alnus glutinosa*, *Hippophaë rhamnoides* and *Myrica gale* (see Bond, 1967, for a review). *Alnus* species, for example, may become important in short-term, rotation forestry for energy production (Zavitkovski *et al.*, 1979). *Myrica gale* is a common bog species in Europe and N. America and could be important in the nitrogen economy of such bog ecosystems (Sprent *et al.*, 1978). *Myrica* can perhaps be used in the early stages of forest plantation after drainage. Recent reports of the successful isolation of *Frankia* from *Alnus* nodules and its growth in pure culture in laboratory media (Baker and Torrey, 1979) constitute an important breakthrough in the attempts to understand this symbiosis.

Other nitrogen-fixing associations include leaf nodules of the angiosperm *Gunnera*, cycad-bluegreen algae root-nodule symbiosis, liverworts and lichens (see Stewart, 1977, for review). New nitrogen-fixing species are, however, still being discovered, such as the *Rhizobium* symbiosis with the legume *Aeschynomena indica*, forming large numbers of stem nodules fixing nitrogen (Yatazawa and Yoshida, 1979), and the herb *Datisca cannabina*, which has been shown to form root nodules of the *Alnus* type (Chaudhary, 1979). It is likely that a large number of nitrogen-fixing species is as yet unidentified, some of which may prove useful in agriculture and forestry. For tropical ecosystems, it seems especially important to consider the use of legume trees in crop-rotation practices and multiple cropping systems, and their importance in savanna ecosystems has been stressed (Rosswall and Vitousek, in press).

Interest has also been shown in the interaction between nitrogen-fixing bacteria and animals, one example being nitrogen fixation in the gut of termites (Breznak *et al.*, 1973). The bacterium responsible, *Citrobacter freundii*, has been isolated from termites, and it may be important in supplying combined nitrogen to the animals, which feed mainly on carbohydrate-rich material with a low nitrogen content (French *et al.*, 1976).

In the more distant future, the possibilities of introducing the genes (*nif* genes) for nitrogen fixation into new hosts that can be used for practical purposes is a fascinating prospect (see, for example, Postgate, 1977; Klingmüller, 1979), even if there are still very large difficulties.

2.3 A MICRONICHE CONCEPT OF NITROGEN CYCLING

Most biological nitrogen transformations are brought about by microorganisms, these processes being regulated both qualitatively and quantitatively by a large

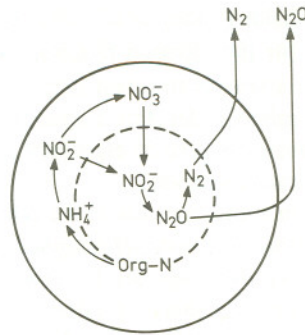


Figure 2.6 A schematic soil crumb with an aerobic outer sector in which nitrification can take place and an inner anaerobic centre from which nitrogen may be lost through denitrification (Knowles, 1978)

number of factors. The qualitative aspects are primarily regulated by oxygen and energy sources, while the quantitative aspects are regulated mainly by temperature and moisture. For example, soil water has a dual function. Moisture is a rate-limiting factor for all biological processes. At moisture contents below 20 per cent, activity is generally low, while at higher moisture contents there is a rapid increase in activity; the process often reaches a maximal rate at about 80 per cent, after which it starts to decline (e.g. Bunnell and Tait, 1974). Soil moisture regulates process rates and is thus an important quantitative factor. However, the often observed decreased rate at very high moisture contents reflects a qualitative change rather than a direct quantitative change. At increased water contents, oxygen diffusion becomes limiting and the microbial metabolism switches from aerobic to anaerobic. Water then acts as a regulator of the quality and only secondarily of the quantity, since anaerobic processes are generally slower than aerobic.

Water has a profound effect in the soil and makes generalizations of process rates (expressed as grams of nitrogen transformed per square metre) very difficult. As an example, let us consider the inorganic nitrogen metabolism of microorganisms. A schematic representation of a soil crumb is shown in Figure 2.6, in which organic nitrogen is mineralized most rapidly in the aerobic zone; after nitrification, nitrate can diffuse into the anaerobic centre, where it can be denitrified, and gaseous nitrogen products are lost to the system. It has been estimated that most soil crumbs with a diameter of more than 3 mm have anaerobic centres (Currie, 1961; Greenwood, 1969). It is also possible that *Nitrosomonas* bacteria can briefly switch to anaerobic metabolism, using nitrite as an electron acceptor, as previously discussed. Nitrogen-fixing aerobic bacteria may be able to use nitrate as a terminal electron acceptor and continue to fix nitrogen under anaerobic conditions, since it has been

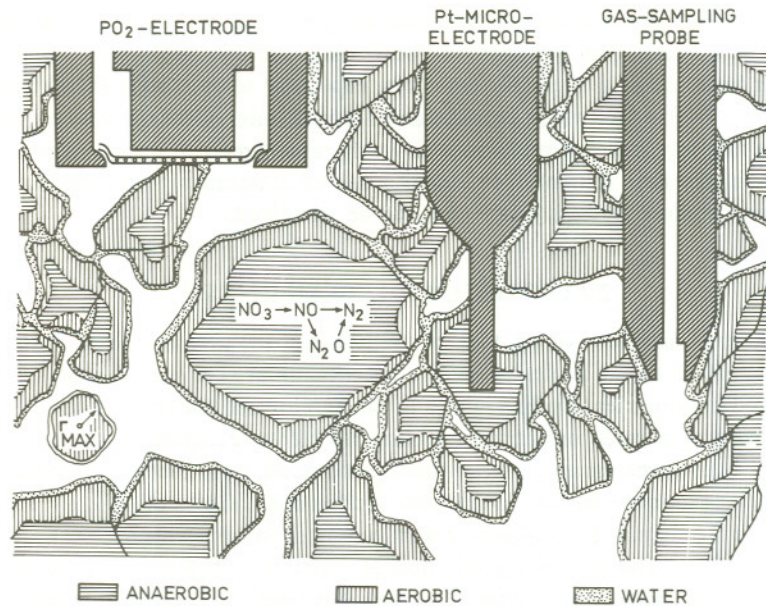


Figure 2.7 Schematic drawing showing the various sensors used to assess the extent of anaerobiosis in soil in relation to soil structural elements (Flühler *et al.*, 1976)

shown that *Rhizobium* (Zablotowicz *et al.*, 1978) and *Azospirillum* (Eskew *et al.*, 1977; Neyra and Van Berkum, 1977) can denitrify. It is possible that the nitrous oxide production observed from the nitrogen-fixing *Klebsiella pneumoniae* (Yoshida and Alexander, 1970) will be shown to be an end-product of denitrification (Rosswall, 1978), since it does not seem as if N₂O can be produced during assimilatory nitrite reduction (Losada, 1975/76).

The occurrence of anaerobic microsites is probably also the reason for the observed denitrification rates in pelagic invertebrate fecal pellets (Söderlund and Svensson, 1976; Wilson, 1978).

The difficulties of determining the aerobic versus anaerobic activities in soils are linked to the difficulty of determining the extent of anaerobiosis. A schematic representation of a soil system with the various sensors which can be used for determining the aeration status of a soil, viz., an oxygen electrode, a redox electrode and a gas sampling probe, is shown in Figure 2.7. Pt-microelectrodes with a diameter of less than one micron have been developed for use in live tissues (Lübbbers, 1969), but a very large number of determinations must be made to determine the extent of anaerobiosis if such microsites are few (Flüher *et al.*, 1976).

The difficulties of determining the different processes in the biogeochemical nitrogen cycle even on a square-metre basis are obvious. The difficulty of extrapolation, however, not only relates to space but also to time. Single or even repeated

measurements of, nitrogen fixation, for example, are very difficult to extrapolate to a yearly basis (Burris, in press). Soil bacteria show very rapid fluctuations in numbers just over a few days, especially after rainfall (Clarholm and Rosswall, 1980), a fact which provides another indication of the difficulty of extrapolating monthly rate determinations to yearly rates. Frequent measurements must be made at the time of rainfall or irrigation as well as during high and low temperature regimes before realistic yearly rates can be calculated.

2.4 ECOSYSTEM NITROGEN CYCLES

The pattern of nitrogen cycling, together with that of the cycling of other nutrients, is an important factor in describing the functioning of ecosystems. Odum (1969) postulated how nutrient cycling relates to the development of ecosystems. Detailed studies have been made on nitrogen cycling in different ecosystems, but these have generally been made assuming steady-state conditions. Only recently has attention been given to non-steady-state conditions such as comparisons of different successional stages, and impact of disturbances on ecosystem nitrogen cycles.

The concept of an increasing retention of available nitrogen during the successional development of a terrestrial ecosystem has been interpreted in a number of ways. Haines (1977) suggested the following possible hypotheses:

- (i) roots in succeeding stages become more efficient in the uptake of dissolved and exchangeable nutrients;
- (ii) increased soil organic matter in succeeding stages retains an increasing proportion of dissolved and exchangeable nutrients;
- (iii) a smaller proportion of the total nutrient pool of succeeding stages is lost from the system; and
- (iv) in succeeding stages, a smaller proportion of the nutrient pool of the system is in flux at any given time.

It seems as if nitrate uptake decreases while ammonia uptake increases with succession (Haines, 1977). The possibility of an allelopathic effect of root exudates of climax species has been advanced as a possible explanation for the observed decrease in nitrate uptake (Rice and Pancholy, 1972, 1973), but there is only circumstantial evidence that this is the case. Only by understanding what factors affect the various processes in the nitrogen cycle will it be possible to evaluate the merits of such an assumption.

The fact that nitrate production can be accelerated in ecosystems subject to destructive disturbance was noted early on by Hesselman (1917), and a number of studies on the magnitude of nitrogen losses following disturbance have been made; one of the major studies being carried out is that in the Hubbard Brook Experimental Forest (Likens *et al.*, 1977; Bormann and Likens, 1979). The leaching of nitrogen from ecosystems following disturbance was recently investigated in a number of forest ecosystems in the USA (Vitousek *et al.*, 1979). It has been suggested that the concepts of resistance and resilience could be used in describing the

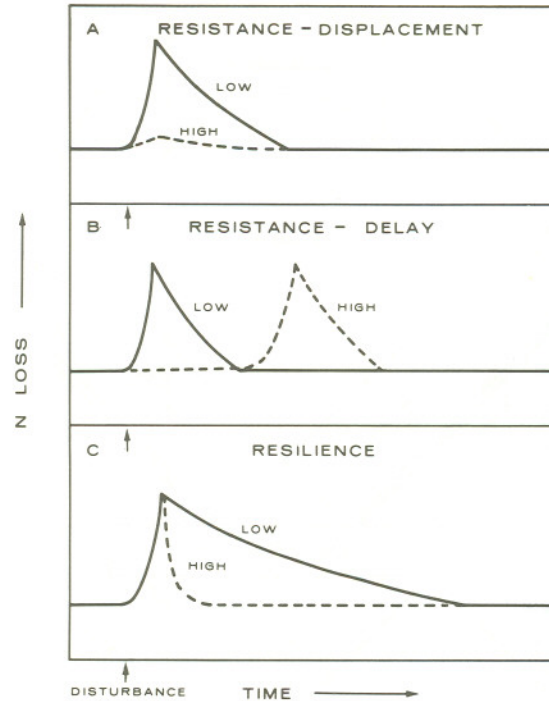


Figure 2.8 Relations between resistance and resilience of ecosystems to disturbance and subsequent nitrogen losses (Vitousek, 1980)

effects on nitrogen leaching from ecosystems after disturbance. Resistance is the ability of an ecosystem to withstand perturbations, while resilience concerns the speed with which the system returns to its original condition. With regard to the resistance of ecosystems to nitrogen losses by leaching, Vitousek (1980) suggested that these are of two types, one related to the total amount of nitrogen leached (displacement) and the other the resistance in time (delay). Using these terms, Vitousek proposed the following factors to be related to the mentioned group of responses (Figure 2.8):

- (i) resistance to displacement, which is related to rates of nitrogen cycling before perturbation;
- (ii) delay, which is caused by nitrogen immobilization; and
- (iii) resilience, which is related to the rate of re-establishment of plant nitrogen uptake.

Most attention has been given the quantification of inputs and outputs of nitrogen in studies of the biogeochemical nitrogen cycle. It should be noted,

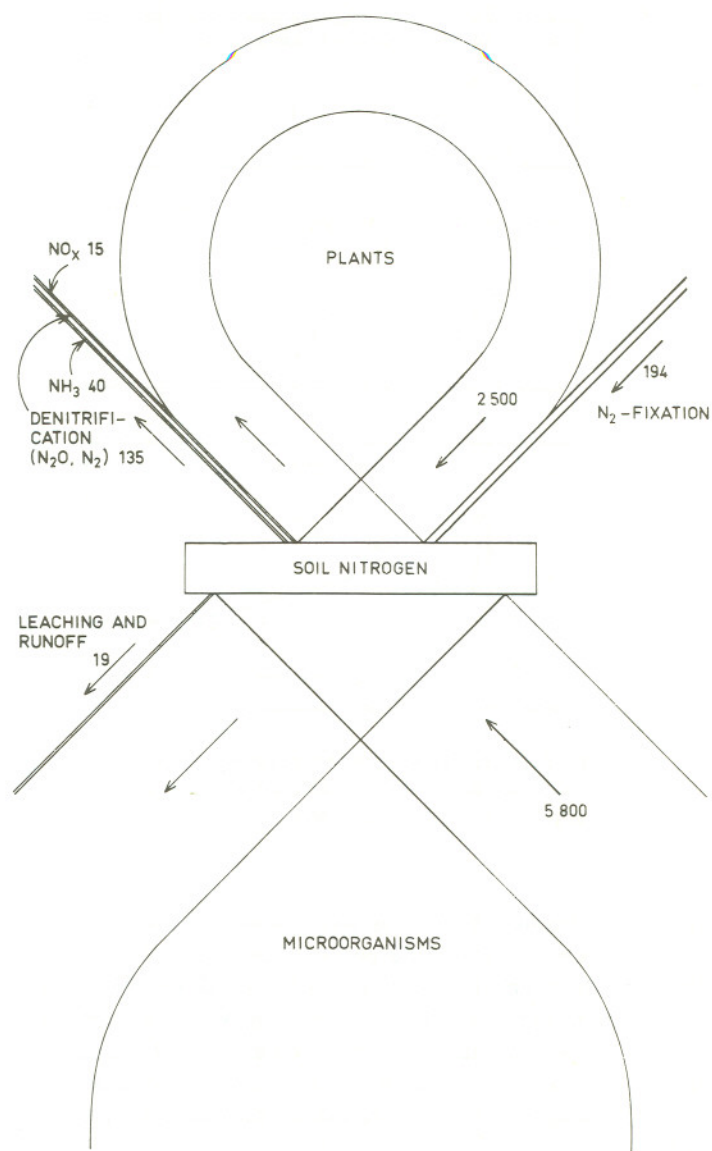


Figure 2.9 Annual transfers of nitrogen on a global basis between primary producers and microorganisms as compared to flows to and from the terrestrial system. All flows in Tg yr⁻¹ and storages in Tg (Rosswall, 1976)

however, that the inputs and outputs of the nitrogen circulating in the vegetation-microorganism-soil system annually (Figure 2.9). To understand what factors regulate transfers of nitrogen to and from ecosystems, further detailed

knowledge of the processes involved in nitrogen transformations within the system is essential.

Data on ecosystem nitrogen budgets and an evaluation of the functional characteristics of the cycles are needed as important jigsaw pieces in the efforts to produce an authoritative and quantitative description of the global nitrogen cycle. Such an understanding is vital if we are to evaluate man's impact on the nitrogen cycle and the consequences that any disturbance might have.

2.5 THE GLOBAL NITROGEN CYCLE

Some recent global nitrogen budgets are summarized in Table 2.4 and it is evident that large uncertainties exist (see also Chapter 6). For example, to what extent does nitrification contribute to the global production of nitrous oxides, and do the oceans and terrestrial systems act both as a sink and source for nitrous oxide? We are slowly developing an ecological theory regarding nitrogen cycling in ecosystems and, based on an understanding of the individual processes, efforts are being made to generalize the observed strategies that ecosystems have developed. Knowledge of the theory of microbiological nitrogen transformations and ecosystem theory will be indispensable when attempts are made to forecast the effect of management practices on the biogeochemical nitrogen cycle.

The scale on which qualitative data on nitrogen cycles is needed depends on the question under consideration. An interpretation of nitrogen retention must relate to the competition between microorganisms and plant roots to utilize ammonium-N or nitrate-N. A microniche concept is then needed. Developing an optimal agroecosystem management practice with regard to crop uptake of added nitrogen fertilizers calls for an understanding of the biogeochemical nitrogen cycle at the ecosystem level. An evaluation of the possible effect of nitrogen oxides on the stratospheric ozone layer requires a quantification of the global nitrogen budget.

Only by combining basic laboratory studies with observations of nitrogen cycling dynamics in representative ecosystems—for example, as parts of the MAB programme—and by trying to integrate these data into a global quantitative model, will it be possible to meet the challenge for supplying the data badly needed for a cost-benefit analysis of fertilizer use and environmental risk assessments related to the increasing occurrence of nitrogen compounds as pollutants.

2.6 INTERACTIONS BETWEEN NITROGEN AND OTHER BIOGEOCHEMICAL CYCLES

The interactions between biogeochemical cycles are covered by other papers in this volume. It should be stressed that the biogeochemical nitrogen cycle should not be viewed in isolation, as there are close couplings with cycles of, for example, water, carbon, phosphorus, and sulphur.

As mentioned above, the water cycle is instrumental in determining the fate of

Table 2.4 Estimates of Global Nitrogen Transfers

	Eriksson (1959)	Robinson and Robbins (1970)	Delwiche (1970)	Burns and Hardy (1975)	Söderlund and Svensson (1976)	McElroy <i>et al.</i> (1976)	CAST (1976)
Biological fixation: land	104	118	44	139	139	170	149
ocean	n.d.	12	10	36	30-130	10	1
Atmospheric fixation (lightning)	n.d.	n.d.	8	10	?	10	10
Industrial fixation	n.d.	20	30	30	36 ¹	40	57 ²
Combustion	15	19	n.d.	20	19 ¹	40	20
Fires	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
Biogenic NO _x production	n.d.	234	n.d.	n.d.	21-89	n.d.	n.d.
Denitrification: land	65	n.d.	43	140	107-161	243	70-100
oceans	87	n.d.	40	70	25-179	106	70-100
Ammonia volatilization	99	957	n.d.	165	113-244	150	n.d.
Dry deposition NH ₃ /NH ₄ ⁺	n.d.	175	} n.d.	n.d.	72-151	} 220	} n.d.
Wet	99	796		140	38-85		
Dry deposition NO _x	n.d.	22		n.d.	25-70		
Wet	48	83	} n.d.	60	18-46	} 220	} n.d.
Dry deposition Org. -N	n.d.	n.d.		n.d.	?		
Wet	36	n.d.	} 30	n.d.	10-100	} 20	} n.d.
River runoff NH ₄ ⁺	-	} 13		} 15	<1		
NO ₃ ⁻	21				5-11		
Org. -N	-			8-13			
N ₂ O sink: land	n.d.	353	n.d.	n.d.	n.d.	0	n.d.
oceans	n.d.					50	

Table 2.4 (Continued)

	Delwiche and Likens (1977) and Delwiche (1977)	Liu <i>et al.</i> (1977)	Hahn and Junge (1975)	Sweeney <i>et al.</i> (1978)	NAS (1978)	Bolin (1979)
Biological fixation: land	99	200	180	100	139	140
ocean	30	40	85	15-90	100	20-120
Atmospheric fixation (lightning)	7	10	n.d.	0.5-3	30	?
Industrial fixation	40	40	40	35	70 ³	40
Combustion	18	20	n.d.	15	21	20
Fires	50	n.d.	n.d.	n.d.	10-200	n.d.
Biogenic NO _x production	—	n.d.	?	n.d.	22-66	20-90
Denitrification: land	120	140	150	90	197-390	63-245
oceans	40	130	165	50-125	0-120	35-330
Ammonia volatilization	75	190	170	15 ⁵	36-90	110-250
Dry deposition NH ₃ /NH ₄ ⁺	} 79	} 220 ⁴	} 200	} n.d.	} 83-242	} 110-240
Wet						
Dry deposition NO _x	} 34	} 220 ⁴	} 200	} n.d.	} 83-242	} 40-110
Wet						
Dry deposition Org. -N	} n.d.	} 220 ⁴	} 200	} n.d.	} 83-242	} n.d.
Wet						
River runoff NH ₄ ⁺	} 35	} 30	} 40	} 30	} 18	} 25-35
NO ₃						
Org. -N						
N ₂ O sink: land	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.
oceans	n.d.	n.d.	n.d.	n.d.	n.d.	n.d.

n.d. = no data given; ¹ data for 1970; ² data for 1974; ³ data for 1976; ⁴ precipitation only; ⁵ net transfer from land to oceans.

nitrogen in an ecosystem. Water regulates the rates of the processes involved in nitrogen transformations, it acts as a diffusion barrier for oxygen creating anaerobic conditions and it transports nitrogen to and from the ecosystem.

The bulk of soil nitrogen occurs in organic matter and mineralization of organic carbon leads to a release of ammonia nitrogen, although the relative proportions of carbon and nitrogen play an important regulatory role in net nitrogen mineralization as discussed above. When nitrogen fertilizers are added to a crop, photosynthesis and carbon immobilization usually increase, but fertilization could also lead to increased soil organic matter decomposition with subsequent release of carbon dioxide.

Specific examples of the effect of phosphorus on nitrogen transformations are many. Nitrogen fixation and nitrification seem to be particularly sensitive to the availability of soil phosphorus. In P deficient soils, nitrogen fixation by legumes is increased considerably if the legume has an efficient VA-mycorrhizal symbiont, through which P uptake can improve. (e.g. Crush, 1974; Daft and El-Giahmi, 1974; Sanni, 1976). In addition to the discussion above on the regulation of nitrification rates, Pancholy suggested that phosphorus deficiency was the main reason for restricted nitrification rates observed in phosphorus-poor savanna soils.

Both nitrogen and sulphur compounds can acidify the environment and such changes in pH will affect nitrogen cycling processes (Helyar, 1976). It is important to quantify the relative contributions of nitrogen and sulphur compounds to the possible acidification of soils and the fate of the acidifying compounds as they relate to the acid-base status. Nitrogen fixation and nitrification are particularly sensitive to reduced pH in soils.

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