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Rate-limiting Steps in Nitrogen-turnover: Ecosystems-based Nitrogen Needs and Actual Use

BIJAY SINGH and YADVINDER SINGH

Department of Soils, Punjab Agricultural University, Ludhiana 141 004

Nitrogen economy of any ecosystems is governed by the rates at which different N-turnover processes proceed. A host of soil, environmental and management factors influence overall rates of N transformations by retarding one or more steps often termed as rate-limiting steps. Rate of mineralization—immobilization turnover in the soil, the key process regulating the magnitude of N utilization by vegetation is controlled by conversion of organic N to NH_4^+. Balance between mineralization and immobilization is controlled by C/N ratio of the organic matter. In ecosystems with well aerated soils, nitrification proceeds very fast and supply of NH_4^+ appears to be the rate-limiting step. Nitrates can be lost via denitrification, controlled primarily by availability of carbon. In flooded rice ecosystems, denitrification rate is determined by NO_3^- supplying capacity of the system. Nitrate-N present in the soil will be lost via leaching if rainfall or irrigation event occurs when soil is at or approaching field capacity. In arid ecosystems, no leaching occurs and N is conserved in the profile. Before its conversion to NO_3^-, NH_4^+ whether originating from mineralization of organic matter or hydrolysis of urea can be lost to atmosphere via NH_3 volatilization -a process controlled by the rate of conversion of NH_3 (aqueous) to NH_3 (gas) in most ecosystems. In agroecosystems receiving heavy dressings of urea, conversion of NH_4^+ to NH_3 (aqueous) normally regulates potential loss of NH_3. Nitrogen uptake rates in intensively managed agroecosystems greatly exceed those in most natural ecosystems, but still more than 50% of the applied N is lost via different mechanisms. The N needs of agroecosystems whether met by addition of fertilizer or *Rhizobium*-legume symbiosis are much larger than those determined by yield and N content of crops.

Key Words: Nitrogen turnover, Rate-limiting steps, Ecosystems, N-needs, N-losses

Introduction

Soil is the focal point of N cycle processes. A host of chemical and biochemical processes are involved in the turnover of N in the soil. In the internal N cycle operating in the soil, immobilization and mineralization are continuously changing the mineral N reserves of the soil. In the external cycle operating between the soil and the atmosphere, gains in soil N occur through biological N_2 fixation, nitrogen deposition or N fertilization, while atmosphere depletes soil N via ammonia volatilization from soil or floodwater and denitrification. Mineral N in the soil is, of course, also removed by crop plants. Through non-har-

vested crop residues and organic manures, a part of the plant N is returned to the organic pool of the soil. Finally, mineral N may leach down beyond the reach of crop roots if excessive water percolation occurs.

In any given ecosystem, some N forms are readily transformed and flow rapidly through time and space whereas other forms remain relatively inactive over long time periods having little short term impact on the system. Some processes involve different amounts of various forms of N to form products that become substrates for other N transformations. Because N supplies, transformations and transfers are linked, understanding the N economy of a given ecosystem and its surroundings requires accurate understanding of rate limiting steps of different N turnover processes. Different N transformation processes are subject to constraints related to physical and biological environment and actual pathway followed and their rate-limiting steps vary with geographical location and season. Factors controlling rate-limiting steps in different processes can therefore be environmental conditions, inhibition of organisms by another, lack of substrate or lack of essential co-factors.

Mineralization-Immobilization Turnover (MIT) in Soils

The transformations that N undergo between entering and leaving the soil system can be adequately described through two individual processes—mineralization and immobilization. The continuous transfer of mineralized N into organic N and of immobilized N back into inorganic N-underlying the building up and dying away of heterotrophic biomass is defined as mineralization-immobilization turnover (MIT). As both mineralization and immobilization occur simultaneously in soil, the amount of mineral N found at any time represents the difference in the magnitude of the two opposing processes.

Since MIT is the result of complex interactions between microbial populations and activities, it is affected by many factors including composition of soil organic matter, environmental factors particularly moisture and temperature and soil factors. Variations in environmental parameters such as drying and rewetting (Agarwal et al. 1971), freezing and thawing (Campbell et al. 1971) or fluctuating temperatures appear to be particularly important. These phenomena often cause a flush in microbial activity and N mineralization. Fluctuations in environmental conditions can cause death of a significant proportion of the biomass and the dead biomass is readily mineralized by the surviving microflora. Alternatively, such phenomenon or even soil tillage can cause disruption of soil aggregates and the exposure of organic matter previously inaccessible to microbial attack.

C/N Ratio and Substrate Quality

Regulation of the magnitude of the two opposing processes in MIT and the resulting net effect usually depends on the ratio between the carbonaceous material (energy source) and the N in the organic matter. Well balanced nutritional conditions of the soil biomass in a normal arable soil are represented by a C/N ratio of 25 when immobilization and mineralization are about in equilibrium (Vlek et al. 1981). Therefore, organic materials having C/N ratio greater than 30 result in net immobilization by microorganisms. On the other hand, organic materials with C/N ratios below 20 lead to increased mineral N levels through mineralization. When rapid decomposition occurs under conditions favourable for microbial activity, mineral-N is consumed by microorganisms resulting in net immobilization of N. However, when C/N ratio of the decompos-

ing material gets lowered to about 20, there occurs a net mineralization.

Substrate quality is the critical factor determining the rate of mineralization and release of mineral N. Although N content of organic matter corresponding to critical C/N ratio of 20 to 30 is 1.5 to 2.5%, it is by no means the only factor regulating MIT. Apart from N content, other important indices of substrate quality include concentration of polyphenols and particularly lignin. Work of Upadhyay and Singh (1985) shows that rate of mineralization (indicated by a rise in % N) of leaves of four evergreen species in Himalayas with similar C/N ratios were inversely related to the lignin content of the leaves (figure 1).

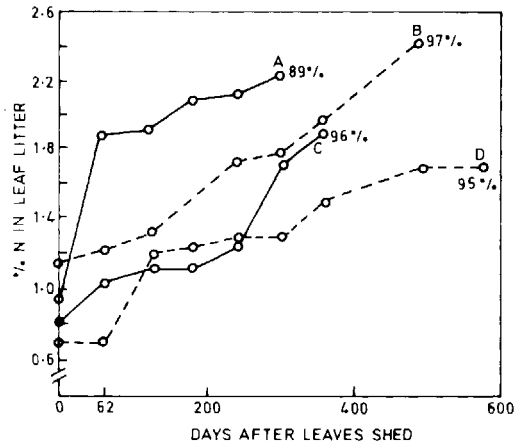

Figure 1 Effect of lignin content on rate of breakdown of leaves of four evergreen species (*from* Upadhyay & Singh 1985). The percentage values given are the fresh weight losses after the appropriate time. The species and lignin content of leaves (% dry weight) are: **A**, *Quercus glauca* (10.8%); **B**, *Q. leucotrichophera* (16.7%); **C**, *Lyonia ovalifolia* (15.8%); **D**, *Rhododendron arboretum* (17.9%)

Nitrification

Ammonium N mineralized from organic matter or gained by soil through N_2 fixation and additions of fertilizers and manures, is either assimilated by microorganisms or plants or oxidized to NO_3^- by process called nitrification. In the context of MIT, it is interesting to note that although heterotrophic microorganisms prefer NH_4^+ over NO_3^- during immobilization, yet when NO_3^- is available but NH_4^+ missing, the former is utilized (Jansson 1958).

The rate limiting step of N mineralization at *p*H 7 is the conversion of organic N to NH_4^+. The two subsequent steps—conversion of NH_4^+ to NO_2^- by *Nitrosomonas* and NO_2^- to NO_3^- by *Nitrobacter* comprising the process of nitrification are faster and rarely limit the rate of production of nitrate (Smith 1982). Only at low and high *p*H or at water potentials below 1.5 MPa (Justine & Smith 1962) NH_4^+ or NO_2^- might accumulate. Under most soil conditions, oxidations of NO_2^- proceeds at more rapid rate than oxidation of NH_4^+. Saturation constants for oxygen-uptake are in the range 0.3 to 1.0 mg O_2/l with *Nitrobacter* slightly more sensitive to oxygen limitation than *Nitrosomonas*. Thus conditions favouring accumulation of NH_4^+ also result in temporary accumulation of NO_2^-. Nitrifiers have been found to adapt to soil climatic conditions, particularly temperature. In western Canada (mean annual temperature 2.5°C), optimum temperature for nitrification was found at 20°C and nitrifier activity almost ceased at 30°C (Malhi & McGill 1982). On the other hand, in north-western India (Singh et al. 1993) and in northern Territory of Australia (Myers 1975) mean annual temperature is about 25°C so that optimum temperature for nitrification was found to be at 35°C and nitrification rate at 20°C was reduced to <0.1 of that observed at optimum temperature.

There is considerable evidence that a limiting supply of NH_4^+ regulates nitrification in many ecosystems (Ardakani et al. 1974, Singh et al. 1993). Under submerged soil conditions, limited nitrification takes

place in aerobic zones which exist in close proximity to anaerobic zone and also due to presence of O_2 in the aerobic root rhizosphere of aquatic plants. In desert ecosystems, nitrification can lead to accumulation of nitrates.

Addition of N to Ecosystems

For sustained productivity, modern high yielding agricultural ecosystems depend on large fertilizer inputs. Current estimates are that global inputs of fertilizer N are of the order of 30-60% of those supplied by biological N_2 fixation. Reduction of N_2 to NH_3, the basic chemical process in N_2 fixation by nitrogenase system requires an O_2 pressure which is much below the partial pressure prevailing in the atmosphere. Thus, average rates of biological N_2 fixation in flooded rice soils are in a range of 50 kg N/ha/year and are much higher than the rates encountered in arable soils (12 kg N/ha/year) (Hauck 1971). In flooded rice soils, besides aerobic N_2-fixing bacteria (*Beijerinckia* and *Azotobacter*) and autotrophic bacteria like *Clostridium* and *Desulfovibrio*, the cyanobacterium *Anabaena azollae* living in symbiosis with *Azolla pinnata* in the surface water may assimilate as much as 800 kg N/ha/year under favourable conditions (Singh 1979).

In the transfer of N from the atmosphere to the soil, the symbiotic living bacteria of the genus *Rhizobium* is of particular importance. The symbiosis of *Rhizobium* with higher plants ensures permanent supply of digestible organic C, a controlled O_2 supply brought about by leghaemoglobin and rapid translocation of NH_3 out of bacteroid to avoid accumulation of NH_3, glutamate or glutamine (Antoniw & Sprent 1978) which block the Nif genes responsible for the synthesis of nitrogenase. Plants with a high photosynthetic activity translocate the photosynthates into the roots at high rates thus supplying the *Rhizobium* bacteroides with plenty of energy which has a favourable impact on the rate of N_2 fixation. Quantity of N_2 fixed by *Rhizobium* decreases as the ability of the soil to provide mineral N particularly NO_3^- increases. Hauck (1971) observed that highest N_2-fixation rates existed in leguminous pastures (table 1). In forests too, high N_2-fixation rates are observed due to *Rhizobium* and *Actinomyces* living in symbiosis with several trees species. In many arid ecosystems, legumes are rare or absent and the major source of N_2 fixation is cyanobacteria. Skujins (1981) has estimated average N input from this source to range from 0.5 to 13 kg N/ha/year.

Table 1 *Range in nitrogen fixation rates in various ecosystems.*

Ecosystem	kg/N/ha/year
Arable land	7-28
Pasture (non-legume)	7-114
Pasture (grass-legume)	73-865
Forest	58-594
Paddy	13-99
Waters	70-250

Losses of Nitrogen from Ecosystem

Even under the best circumstances, no more than two-thirds of the N added as fertilizer or biological N_2 fixation can be accounted for by utilization by vegetation or in the soil. Losses as much as one half of the amount of N applied are commonly observed. Nitrogen from cropped ecosystems can more oftenly be lost via ammonia volatilization, denitrification and leaching; although erosion can also result in substantial losses under some circumstances.

Ammonia Volatilization

Rapid changes in NH_4^+ level in soil can be observed due to chemical volatilization of

NH_3. Overall rate of ammonia volatilization can be controlled by any one step in the chain represented by:

$$NH_4^+ \rightarrow NH_3(aq) \rightarrow NH_3(g) \rightarrow NH_3(atm)$$

In this chain, NH_3(aq) is mainly controlled by cation exchange reactions, soil moisture and of course amount of NH_4^+ present in the soil. Conversion of NH_4^+ in soil solution to NH_3(aq) is an extremely rapid first order process (rate constant 24.6/sec) (Emerson et al. 1960) and is, therefore, rarely a rate limiting step in the overall process. NH_3(aq) changes linearly with temperature and increases about 10-fold with every unit increase in *p*H up to *p*H 9 (Vlek & Stumpe 1978).

Reaction $NH_3(aq) \rightarrow NH_3(g)$ is governed by Henry's law and is a function of temperature. Equilibrium between NH_3(aq) and NH_3(g) depends on rate of NH_3(g) transfer away from source sink surface. Temperature gradient and wind accelerate the transfer and can increase the dispersion coefficient 10 to 600 times higher than the diffusion coefficient in still air (Inoue et al. 1975). The flux (F) of NH_3 out of the soil surface may thus be represented by

$$F = k[NH_3(g) - NH_3(atm)] \quad \ldots(1)$$

where k is an exchange coefficient whose value may vary with wind speed (Vlek & Craswell 1981, Freney et al. 1983).

There is no evidence that NH_3(atm) concentration in well aerated soils may limit the NH_3 volatilization rate in the field (Vlek & Craswell 1981, Freney et al. 1983). According to calculations made by Vlek and Craswell (1981), NH_3(aq) concentration of 0.5 ppm or greater can result in NH_3(g) levels in soils which greatly exceed commonly observed NH_3(atm) levels of 2-6 μg NH_4-N/m^3 and equation (1) can be simplified to

$$F = k[NH_3(g)]$$

Thus, actual rate of ammonia loss from soil is likely to be limited primarily by NH_3(g) at the soil-air interface which in turn depends on the total ammonical N concentration, *p*H, temperature and moisture content of soil. Equation (1) is equally valid in flooded and non-flooded soils (Freney et al. 1983). In fact, it is relatively easy to measure $NH_4^+ - N$ concentration, *p*H and temperature within the water overlying a flooded soil and also to obtain values for the exchange coefficient k for the transport of NH_3 away from the flood water surface. Leuning et al. (1984), however, found that because of temperature gradients within the water, the NH_3 concentration at the water-air interface was not generally characteristics of that in equilibrium with the bulk of the floodwater. Thus, rate of NH_3 volatilization in flooded soil is critically influenced by transport processes in both the air and water. Wind also affects NH_3 volatilization losses through mechanical mixing of the surface water.

For unfertilized flooded soils, ammonia volatilization losses could be negligible because NH_3 is the most soluble gas known. However, for flooded soils, fertilized particularly with urea, as much as 50% of surface applied urea was lost as NH_3 within 2-3 weeks (Vlek & Craswell 1979). Urea-N applied either as animal urine or as fertilizer undergoes hydrolysis catalyzed by the enzyme urease to form $(NH_4)_2CO_3$ and the reaction causes localised area of high *p*H close to the site of hydrolysis. This high *p*H greatly favours ammonia volatilization losses. Ammonium ions produced from urea hydrolysis interact with soil cation exchange complex or may get fixed in clay lattice, but also enter into equilbrium reactions with NH_3(aq). According to Hayens and Sherlock (1986) it is the conversion of NH_4^+ to NH_3(aq) that normally regulates potential loss of NH_3

through volatilization when N in the form of urea is applied to the soil.

Denitrification

Nitrate-N is lost rapidly from soil via denitrification when (i) bacteria possessing the metabolic capability for denitrification are present, (ii) suitable electron donors such as organic C compounds, reduced S compounds or molecular hydrogen are available, (iii) conditions are anaerobic or O_2 availability is restricted, and (iv) there is a supply of NO_3^- to serve as terminal electron acceptor. The occurrence of denitrification in various environments depends on the interaction of many limiting factors. As a result, high rates of denitrification from soil are frequently observed as 'short pulses' which occur when soil conditions become congenial (Aulakh et al. 1992).

Several studies have reported that increases in C content of the system increases the denitrification potential of the soil, provided other factors are favourable. Significant correlations have been observed between denitrification and the content in the soil of 'available' C (Stanford et al. 1975), water-soluble C, mineralizable C assessed under anaerobic conditions (Singh et al. 1988) and total C (Beauchamp et al. 1980). Further evidence that carbon supply may limit denitrification in soils comes from work with added carbon sources such as glucose and straw but with excess nitrate added (Stanford et al. 1975). In the rhizosphere, denitrification may be related to plant photosynthesis in a way it varies with plant species. Beans (*Phaseolus vulgaris*) support more dentrification than maize (*Zea mays*) (Scaglia et al. 1985) probably because legume exudates have lower C/N ratio than those of cereals.

Rate of denitrification increased 1.7 to 2.0 fold with 10°C rise in temperature from 25 to 35°C (Mangaraja & Misra 1978). The effect of moisture on denitrification is largely due to its effect on aeration but as temperature decreased, the minimum soil water content for denitrification to occur increased (Singh et al. 1989).

In flooded soils, denitrification rate is regulated by the NO_3^- supplying capacity of the system. On the other hand, flux of NO_3^- is governed by the denitrification rate in the reduced soil layer, thickness of the oxidized soil layer, flood water depth and NH_3^- concentration in the flood water and oxidized soil layer. Denitrification in the flood water has been found to increase with increased availability of available C in the underlying anaerobic soil layer (Engler & Patrick 1974). Denitrification losses have been found to be reduced in the presence of rice plants than in systems without plants (Reddy & Patrick 1980). The controlling factor of N loss from the rhizosphere is the competition for NO_3^- uptake between denitrifying bacteria and rice roots.

The organic C and/or NO_3^- content of soil may more often limit activity of denitrification in well aerated/desert soils than presence of specific bacteria. Although, it is common notion that anaerobiosis is rarely achieved in well aerated soils in arid regions, substantial losses in denitrification occur because nitrification and denitrification can occur concurrently in close proximity due to the presence of anaerobic microsites in small water filled pores as determined by size and geometry.

Leaching

According to Vlek et al. (1981) total leaching losses of N is equivalent to the sum of the fluxes of the individual N compounds at the root zone: substratum interface, i.e.

$$J_{NT} = \Sigma J_w C_n + \Sigma J_D$$

Where J_{NT} is the total N flux; J_w, the flux of water into the subsoil; C_N, the concentration of the individual N solutes in the percolating

water and J_D represents diffusion. In well drained soils, N is generally leached as NO_3^-, with only a small fraction in the form of NH_4^+ (Myers 1975).

Two major factors controlling leaching losses of NO_3^- are concentration of NO_3^- in the soil profile at the time of leaching and quantity of water passing through the soil profile. High soil NO_3^- levels and sufficient downward movement of water to move NO_3^- below the rooting depth are oftenly encountered in soil of the humid and subhumid zones, to a lesser extent in soils of the semi-arid zone and quite infrequently if at all in arid zone soils. In agroecosystems, NO_3^- originates from mineralization of soil organic matter and crop and animal residues, fertilizer N not used by crops and to a lesser extent rainfall inputs. Fertilizer N application generally increases leaching losses. When high fertilizer rates are combined with heavy irrigation regimes on light textured soils, leaching losses of NO_3^- can be substantial (Singh & Sekhon 1976).

Voluminous data regarding leaching losses of N from agricultural soils have accumulated but due to differences in method, crop, soil management, fertilizer, soil type and climate it is difficult to make comparisons. Some generalization from cropped ecosystem are listed below. Substantial leaching losses occur if rainfall is received when soils are at or approaching field capacity. Both intensity and amount of rainfall or irrigation are important in determining the rate and extent of leaching. Where summer fallow is followed by a monsoon type heavy rainfall, leaching can occur to a serious extent. Optimum irrigation water supplies can improve crop N uptake and reduce leaching losses, but excessive irrigation oftenly increases NO_3^- leaching. Factors that increase fertilizer use efficiency by the crop generally decrease. leaching losses.

N Needs and Actual Use in Different Ecosystems

Natural ecosystems differ from agroecosystems in the level of synchronization between demand for nutrients and supply through mineralization processes. In natural systems, the nutrient cycles are usually tight and the system has a high degree of sustainability, whereas in agroecosystems the reverse could be true. In crop ecosystems, the demand for N may occur when its release from soil organic matter or plant residues may not be matched either in amount or in timing. At certain periods (such as maturity phase of crops) demand for N may be very small and it is subjected to losses from the system. Thus in agroecosystems, N is applied as fertilizers, manures or *Rhizobium*-legume symbiosis to reduce disparity between demand and supply of N.

The rate of N uptake by vegetation in different ecosystems varies with ecosystem conditions. In general, plants with low production rate usually have a low N uptake demand. But it is not yet clear whether low production rate or a low uptake limits N uptake (Cole 1981). However, plants in N-deficient ecosystems make more efficient use of the N utilized by them. The rate of N uptake by vegetation per unit area in ecosystems not very favourable for plant growth (such as desert ecosystems) are considerably lower than that of temperate forests and grasslands. The N uptake rates in intensively managed agroecosystems greatly exceed those in most natural ecosystems.

Most modern high yielding agricultural systems depend on the addition of fertilizer N or an efficient *Rhizobium*-legume symbiosis for their N supply. N needs of ecosystems based on high yielding agricultural crops are oftenly determined by yield and N content, the effectiveness of a crop to recover mineral N from soil profile and

availability of fertilizer N as influenced by immobilization, leaching and gaseous losses. In agroecosystems located in arid regions, due to minimal leaching of NO_3^-, fertilizer needs are often based on expected yields, estimates of amount of N required for different yield levels and the amount of residual NO_3^- in the soil. Feigenbaum et al. (1984) observed that at the end of dry year, about 45% of the fertilizer N applied to wheat in arid climate was found as mineral N in the soil and much of this was used in the following growing season. In humid regions or in wetland rice ecosystems, soils are less likely to contain or retain residual NO_3^- and fertilizer N needs can be calculated by multiplying the expected yield by a factor that can be adjusted to take into account the economic optimum as well as such factors as expected mineralization and use of manures and legumes.

Amount of N utilized by different crops differ greatly. For high yield of grain crops such as rice and wheat, more than 200 kg N/ha must be absorbed in tops plus roots. In warmer climates, potential yield and consequently N uptake is higher. For high yielding C4 crops such as sugarcane, uptake in excess of 300 kg N/ha may be required. Nitrogen budgets constructed for many different agricultural systems utilizing both conventional and ^{15}N tracer techniques provide an idea of the actual amount of N used by the crops. The recovery of applied N by difference method in field experiments conducted in India has been found to vary from 28 to 34% for rice and from 40 to 60% for other cereals (Prasad et al. 1971). Obviously a substantial portion of N applied to rice is lost via ammonia volatilization, leaching and/or denitrification. A number of N balances for various cropping systems are shown in table 2. Utilization of applied N varies greatly (21-68%) and losses by different mechanisms can be large (upto 50%). High N recoveries by rice reported by Koyama et al. (1977) and Reddy and Patrick (1978) can be attributed to continuous flooding, split application of N, NH_4^+ fertilizer N source and N rates that could be easily assimilated.

The actual N used by a crop and the final N balance sheet is the product of many physical, chemical and biological processes interacting with one another over time. Changes in one process are reflected by change in other processes including N

Table 2 *Some estimates of plant recovery, soil recovery and losses in different agroecosystems*

Cropping system	Percentage of applied N			Reference
	Plant recovery	Soil recovery	Losses	
Rice	24	27	49	Krishnappa and Shinde 1980
Maize-wheat-mungbean	23-37	55-65	0-13	Subbiah and Sachdeva 1981
Rice	21-31	24	46-50	Katyal et al. 1985
Wheat	32-52	32-35	16-42	Katyal et al. 1987
"	22-29	34-65	6-16	Feigenbaum et al. 1983
Maize	30-68	33-62	16-25	Broadbent and Carlton 1978
Rice	47	26	27	Koyama et al. 1977
"	51-61	24-27	15-22	Reddy and Patrick 1978
Maize (fodder)-rice	29	—	—	George and Prasad 1989
Cowpea (fodder)-rice	27	—	—	George and Prasad 1978

utilization. Efficient management of N needs of any ecosystem based on knowledge of rate limiting steps of various N transformations is the key to efficient N utilization and is the solution of problem concerned with high crop production, minimal pollution and energy conservation.

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