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Nitrogen cycling in a flooded-soil ecosystem planted to rice (*Oryza sativa* L.)*

Ciclo de nitrógeno en arroz (Oryza sativa) *cultivado bajo innundación*

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Abstract ^{15}N studies of various aspects of the nitrogen cycle in a flooded rice ecosystem on Crowley silt loam soil in Louisiana were reviewed to construct a mass balance model of the nitrogen cycle for this system. Nitrogen transformations modeled included 1) net ammonification (0.22 mg NH_4^+–N kg dry soil^{-1} day^{-1}), 2) net nitrification (2.07 mg NO_3^-–N kg^{-1} dry soil^{-1} day^{-1}), 3) denitrification (0.37 mg N kg dry soil^{-1} day^{-1}), and 4) biological N_2 fixation (0.16 mg N kg dry soil^{-1} day^{-1}). Nitrogen inputs included 1) application of fertilizers, 2) incorporation of crop residues, 3) biological N_2 fixation, and 4) deposition. Nitrogen outputs included 1) crop removal, 2) gaseous losses from NH_3 volatilization and simultaneous occurrence of nitrification-denitrification, and 3) leaching and runoff. Mass balance calculations indicated that 33% of the available inorganic nitrogen was recovered by rice, and the remaining nitrogen was lost from the system. Losses of N due to ammonia volatilization were minimal because fertilizer-N was incorporated into the soil. A significant portion of inorganic-N was lost by ammonium diffusion from the anaerobic layer to the aerobic layer in response to a concentration gradient and subsequent nitrification in the aerobic layer followed by nitrate diffusion into the anaerobic layer and denitrification into gaseous end products. Leaching and surface runoff losses were minimal.

Resumen Se revisaron varios aspectos del ciclo de nitrógeno estudiados con ^{15}N en un ecosistema de arroz de innundación en suelos franco limosos Crowley en Louisiana, USA, con el fin de construir un balance de masas para el nitrógeno.

Las tranformaciones que se incluyeron en el modelo fueron: 1) amonificación neta (0,22 mg NH_4–N kg^{-1} suelo seco dia^{-1}), 2) nitrificación neta (2,07 mg NO_3–N kg^{-1} suelo seco dia^{-1}), 3) desnitrificación (0,37 mg N kg^{-1} suelo seco dia^{-1}) y 4) fijación biológica de nitrógeno (0,16 mg N kg^{-1} suelo seco dia^{-1}). Las entradas de nitrógeno al sistema serían aquellas por aplicación de fertilizantes, incorporación de residuos de cosecha, fijación biológica de nitrógeno, deposición. Las salidas serían por cosecha, perdidas gaseosas por volatilización de NH_3 y la ocurrencia simultanea de nitrificación y desnitrificación, lixiviación y escorrentía. El balance de masas indicó que el 33% del nitrógeno inorgánico disponible fué recuperado por el arroz y el resto se perdió del sistema. Las pérdidas por volatilización de NH_3 fueron mínimas porque el fertilizante fué incorporado al suelo. Una proporción significativa del nitrógeno inorgánico se perdió por difusión de NH_4 de la capa anaeróbica a la aeróbica en respuesta al gradiente de concentraciones; luego ocurre nitrificación en la capa aeróbica, difusión y finalmente desnitrificación y pérdida en forma gaseosa. Las perdidas por lixiviación y escorrentía fueron mínimas.

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Introduction

Lowland rice is a major food for approximately 50% of the world's population. Throughout the rice-growing regions of the world, nitrogen is most commonly the nutrient limiting rice growth and yield.

Nitrogen in flooded-soil ecosystems occurs in inorganic and organic forms, with the latter form predominant. Organic-N includes compounds from amino acids, amines, proteins, and humic compounds with low N-content; inorganic forms include ammonium, nitrate, and nitrite. Ammonium dominates the inorganic-N pool at any given time; it comes from the mineralization of organic-N and the application of fertilizers. Gaseous forms of nitrogen that occur in this agro-ecosystem include NH_3, N_2 and N_2O.

The gains and losses of nitrogen in the flooded-soil ecosystem are regulated by a series of biochemical and physicochemical processes that transform one form of nitrogen to another (Fig. 1). Nitrogen inputs (gains) to the systems come principally from 1) the application of fertilizers, 2) the incorporation of crop residues, 3) biological N_2 fixation, 4) interflow, runoff, and irrigation water, 5) atmospheric NH_3, N_2O, and NO absorption by soil and plants, and 6) dry deposition and rainfall. Nitrogen losses from the flooded soil system mainly result from 1) crop removal, 2) simultaneous occurrence of nitrification-denitrification reactions, 3) NH_3 volatilization, 4) non-reversible fixation of ammonium-N by clay minerals, and 5) leaching and surface runoff.

In this report I examine the agronomic and ecologic significance of the processes controlling nitrogen utilization by rice and the role of these processes in determining the N lost or gained by the ecosystem. In particular, I synthesize the considerable ^{15}N data that has recently accumulated for a flooded Crowley silt loam soil ecosystem in Louisiana. This soil type is typical of those used for rice cultivation in this region. Some characteristics of this ecosystem appear in Table 1.

Characteristics of flooded soil

Flooded soils are generally characterized by the absence of oxygen when compared to upland soils. In most rice fields, the dissolved oxygen content of the overlying water column remains relatively high due to a low density of oxygen-consuming organisms and photosynthetic oxygen production by algae. In contrast, oxygen is slowly renewed and the demand is usually high in the underlying soil, especially in those soils with high organic matter content. The greater potential consumption of oxygen at the soil-water interface compared to the renewal rate through the floodwater results in the development of two distinct soil layers: an oxidized or aerobic top layer and an underlying reduced or anaerobic layer. The thickness of the aerobic zone can vary considerably (Fig. 2).

Rice plants growing in anaerobic soil systems have a unique mechanism for

Table 1. Characteristics of flooded Crowley silt loam soil ecosystems

	Units
Climate	
Mean annual temperature	20°C
Mean temperature during growing season	27°C
Annual precipitation	1400 mm yr^{-1}
Precipitation during growing season	520 mm 4 $months^{-1}$
Growing season for rice	120 days yr^{-1}
Soil	
Carbon (dry weight)	0.70%
Nitrogen (dry weight)	0.08%
Soil organic N (30 cm depth)	2090 kg ha^{-1}
Soil inorganic N (30 cm depth)	68 kg ha^{-1}
Bulk density (upper 30 cm)	1.15 g cm^{-3}
Soil type	Typic albaqualfs
Texture	Silt loam
pH	5.6
Cation exchange capacity (meq 100 g dry $soil^{-1}$)	9.4
C:N ratio	8.75

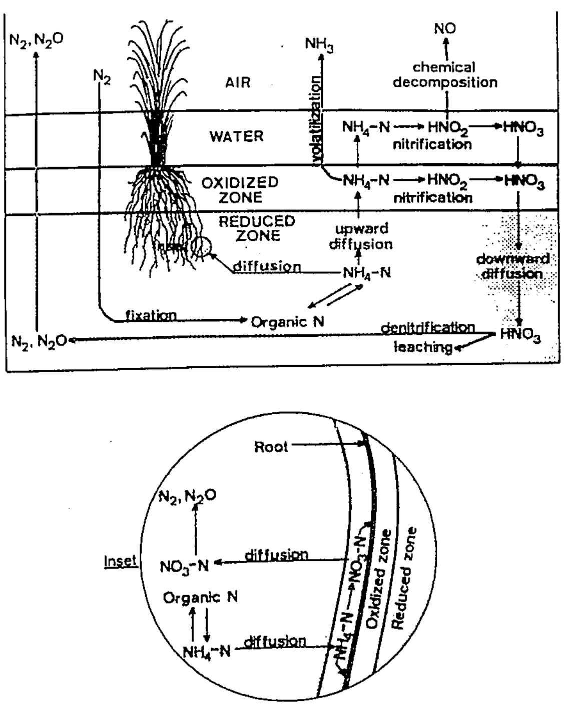

Fig. 1. Nitrogen cycle in a flooded soil ecosystem.

transporting atmospheric oxygen through the stems to the roots, and some of this oxygen diffuses into the adjacent root rhizosphere. This results in oxygen zonation in the soil around the root surface (Fig. 1). The aerobic soil layer supports the aerobic microflora and is the site for nitrogen processes that require oxygen, while the anaerobic soil layer supports anaerobic microflora and is the site for nitrogen processes that can occur in the absence of oxygen.

Lowland rice is normally grown under flooded soil conditions, but in certain situations these soils are subjected to alternate flooding and draining cycles. In the United States, most rice is grown only during the summer months (May through September) under flooded conditions, and for the remainder of the year these soils are drained. Under this type of management, anaerobic soil conditions predominate during flooding and aerobic conditions during the rest of the year.

Nitrogen-cycle processes

Nitrogen-cycle processes that control gains and losses of nitrogen in the flooded soil ecosystem include ammonification, NH_3 volatilization, nitrification, denitrification, assimilatory nitrate reduction, and N_2 fixation.

Ammonification

Ammonification (or N-mineralization) is the conversion of organic-N to ammonium-N. This process proceeds at a much slower rate in flooded-soil systems than in drained-soil systems. Ammonification supplies about 60% of the nitrogen requirement of rice crops grown on Crowley silt loam soils in Louisiana[11]. Dolmat *et al.*[2] observed that ammonium-N mineralized under anaerobic conditions was a good estimate of nitrogen available to rice during the growing season. Laboratory incubation studies showed that ammonium-N accumulation in flooded Crowley silt loam soil occurred at a rate of 0.22 mg NH_4–N kg dry soil^{-1} day^{-1} (0.575 kg N ha^{-1} day^{-1}), which is equivalent to approximately 3.4% of the total soil organic-N and crop residue organic-N over one cropping season.

Ammonia volatilization

Ammonia volatilization is a pH-dependent reaction. Alkaline pH favors the presence of aqueous forms of NH_3 in solution, while at acidic or neutral pH the NH_3 is predominately in the ionic NH_4^+ form. Losses of NH_3 through volatilization are insignificant if pH is below 7.5, and often losses are not serious if the pH is below 8.0. However, considerable NH_3 loss can occur if the pH of the system is in the range of 8 to 10, or above. In flooded soils planted to rice, NH_3 volatilization is not considered an important mechanism of nitrogen loss except in specialized cases where high ammonium-N concentrations exist in conjunction with high pH at the floodwater-soil interface. High pH conditions in floodwater can develop during sunlight hours as a result of an imbalance between photosynthesis and respiration of algae and submerged aquatic macrophytes. Under these conditions, the pH of the water column can increase by 2 to 3 units during mid-day when the photosynthetic process is actively with-drawing CO_2 from the system, and can fall at night when respiratory activities liberate free-CO_2 into water. When urea or ammoniacal fertilizers are applied to the surfaces of these systems, significant volatilization losses can be observed. However, these losses can be reduced by incorporating the fertilizers into soil[4,19].

Nitrification-denitrification

Nitrification and denitrification are known to occur simultaneously in flooded soil systems. Nitrification occurs in the aerobic zone while denitrification occurs predominantly in the underlying anaerobic zone. The magnitude of nitrification is controlled by oxygen diffusion rates, the thickness of the aerobic zone, the ammonium-N concentration, and levels of inorganic-C. Net nitrification rates in the surface aerobic soil layer of a flooded Crowley silt loam soil were found to be 2.07 mg NO_3–N kg dry soil^{-1} day^{-1} (ref.[18]). Nitrification is generally active during most of the day except under special conditions of high pH (>9.0) and free NH_3 at the floodwater-soil interface. In flooded Crowley silt loam soil, pH of the aerobic soil zone was in the range of 5 to 6.

Rates of denitrification are influenced by readily oxidizable-C, temperature, pH, denitrifying populations, and nitrate-N concentrations. In a flooded Crowley silt loam, denitrification rates of 0.37 mg N kg dry soil^{-1} day^{-1} in the anaerobic soil layer have been measured[17]. These reactions involve both oxidation (nitrification) and reduction (denitrification), with corresponding N valence changes of from -3 (for NH_4–N) to $+5$ (for NO_3–N), followed by reductions to $+1$ (for N_2O) or to zero (for N_2). Four moles of oxygen are required to produce one mole of N_2 gas. A combined nitrification-denitrification reaction can be written as:

$$24\,NH_4^+ + 48\,O_2 \rightarrow 24\,NO_3^- + 24\,H_2O + 48\,H^+$$
$$24\,NO_3 + 5\,C_6H_{12}O_6 + 24\,H^+ \rightarrow 12\,N_2 + 30\,CO_2 + 42\,H_2O$$

$$24\,NH_4^+ + 5\,C_6H_{12}O_6 + 48\,O_2 \rightarrow 12\,N_2 + 30\,CO_2 + 66\,H_2O + 24\,H^+$$

In this reaction nitrate-N is an intermediate product and does not appear in the final reaction. Laboratory and field investigations using ^{15}N have indicated very little or no nitrate-N accumulation in these systems. The major source of ammonium-N to the aerobic zone comes from fertilizers, mineralization of organic-N in the aerobic zone, and diffusion of ammonium-N from the underlying anaerobic zone. The nitrate-N formed in the aerobic layer is the only nitrogen that is constantly supplied to the anaerobic zone. Nitrate-N moves to the anaerobic zone by diffusion, and is subsequently removed by denitrification (Fig. 3)[6]. In lowland rice fields nitrate-N is not used as a fertilizer N-source. In a

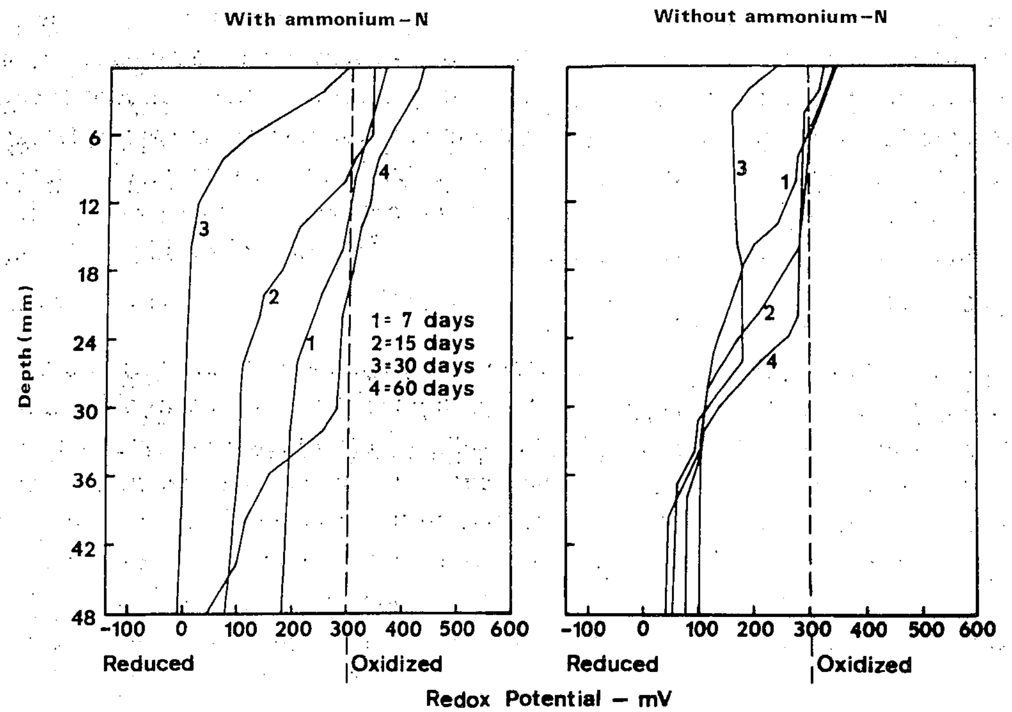

Fig. 2. Depth of aerobic layer in a flooded soil after different periods of incubations with and without added ammonium nitrogen.

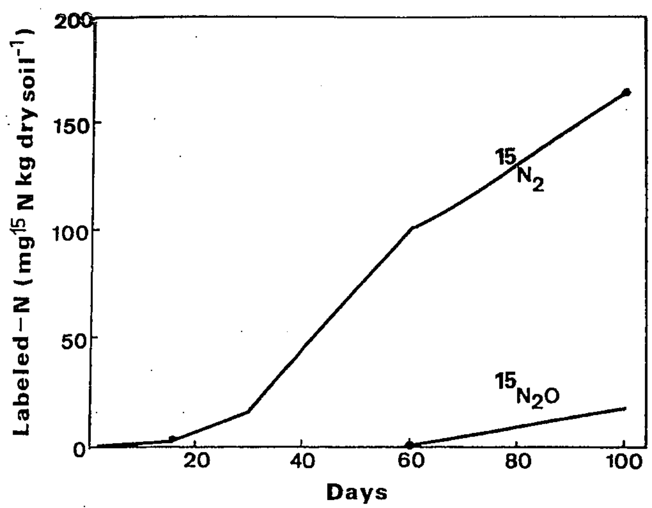

Fig. 3. Gaseous losses of added ammonium-N in an incubated and flooded Crowley silt loam treated with $^{15}(NH_4)_2SO_4$.

flooded field subjected to alternate flooding and draining, nitrification can occur when soil is drained and then the accumulated nitrate be denitrified upon reflooding. In Louisiana and other rice growing areas of the United States, this practice is not followed during the growing season. However, nitrate-N accumulates in these systems when flooded fields are drained after the rice harvest and this nitrate-N is readily denitrified upon reflooding for the next rice crop.

Nitrogen fixation

Atmospheric N_2 fixation in flooded rice fields occurs in the floodwater and aerobic soil layer, in the anaerobic soil layer, and in the root rhizosphere. Laboratory studies[14] with ^{15}N showed that in a flooded Crowley silt loam soil containing no plants, N_2 fixation occurred at 0.16 mg N kg dry soil^{-1} day^{-1} (0.78 μg N cm^{-2} day^{-1}), and that most of this fixation was by algae in the surface 0.5 cm of the aerobic soil layer. The amount of N_2 fixed by intact soil cores obtained from a rice field was in the range of 0.12–0.15 mg N kg dry soil^{-1} day^{-1} (0.58–0.75 μg N cm^{-2} day^{-1}). In this study, N_2 fixation occurred primarily in the surface 0.5 cm soil layer. However, a field experiment using the acetylene reduction method showed a higher fixation rate of 0.41–0.74 mg N kg dry soil^{-1} day^{-1} (2–3.6 μg cm^{-2} day^{-1}). The amount of N_2 fixed in this system is low and not enough to support high yields of rice, but may be an important contribution to the nitrogen economy of the soil.

Nitrogen movement

Nitrogen transport in flooded soil systems can occur by 1) ion diffusion, 2) leaching and interflow, and 3) surface runoff.

Ammonium-N diffusion

Ammonium-N diffusion from the anaerobic soil layer to the aerobic soil layer provides ammonium-N to the nitrifying organisms. The rate of this movement is governed by 1) the concentration gradient established as a result of ammonium-N consumption in the aerobic zone, 2) the ammonium-N regeneration rate in the anaerobic zone, 3) the ammonium-N concentration in the pore water, 4) other cations on the soil exchange complex, 5) the cation exchange capacity of the soil, and 6) the relative volume of pore space which is a function of the soil's bulk density. The quantity of ammonium-N transferred by diffusion per unit area per unit time is proportional to the diffusion coefficient and the concentration gradient. Studies on flooded Crowley silt loam soil[16] showed that ammonium-N flux was about 10.4 μg NH_4–N cm^{-2} day^{-1}, and diffusion of ammonium-N from the anaerobic soil layer accounted for more than 50% of this (5.97 μg cm^2 day^{-1}); the ammonium-N diffusion coefficient was 0.216 cm^2 day[18].

Nitrate-N diffusion

In a flooded rice field, nitrate-N in the floodwater and aerobic soil layer readily diffuses into the anaerobic soil layer in response to the downward concentration gradient. The flux of nitrate-N from the floodwater and the aerobic soil layer to the anaerobic soil layer is controlled by 1) the oxidizable-C supply in the anaerobic zone, 2) the thickness of the aerobic zone, 3) floodwater depth, 4) the nitrate-N concentration in the floodwater and in the aerobic zone, 5) temperature, and 6) mixing and aeration in the floodwater. For flooded Crowley silt loam soil, the measured diffusion coefficient for nitrate-N's moving from the floodwater and aerobic zone to the anaerobic zone[18] was 1.33 cm^2 day^{-1}. This value is about six times higher than the diffusion coefficient value for ammonium-N diffusion.

Leaching, interflow, and runoff

In flooded rice fields of Louisiana, losses of nitrogen through leaching, interflow and runoff are insignificant compared to other sources of loss. In ^{15}N field studies[7] very little or no fertilizer-N moved deeper than 20 cm in a flooded Crowley silt loam. In drained fields, nitrate-N accumulates and subsequently a significant portion can be lost through leaching. Very little quantitative information is available on the importance of leaching, interflow, and runoff to the nitrogen balance of rice paddies.

Plant uptake

Rice is noted for its poor utilization of fertilizer-N. Several ^{15}N field studies of Crowley silt loam rice systems[9,11,13] have shown that *ca.* 63% of total nitrogen uptake by rice is derived from native soil-N and fixed N_2, with the remainder derived from fertilizer-N.

Another study using ^{15}N[7,13] revealed that over one cropping cycle approximately one-third of the fertilizer-N applied to the rice was recovered in the grain, approximately one-fifth to one-fourth was recovered in the straw, approximately one-fourth remained in the soil and roots, and the remaining one-fifth to one-fourth was lost from the system. Incorporation of crop residues resulted in less than 10% of the added-N released during the second year. These studies also showed that during early growth, the rice plant largely utilized fertilizer-N rather than native soil-N, while during later growth native soil-N was the major source of nitrogen for the plant. ^{15}N studies conducted in several other countries have also showed poor recoveries (12 to 41%) of fertilizer-N by rice[3]. DeDatta *et al.*[1], using ^{15}N-labelled ammonium sulfate, observed recoveries of 15 to 71% of the added-N by rice. In another field study, Reddy and Patrick[15] found that about 26 and 31% of added-N was removed by rice from plots receiving surface applications of ^{15}N-labelled urea and ammonium sulfate, respectively, while only 10% of the added-N was recovered from plots treated with ^{15}N-labelled rice straw.

Nitrogen losses

Studies conducted with paddy soils in different parts of the world have indicated that the low recovery of ammoniacal fertilizers by rice is largely due to losses of nitrogen through nitrification and subsequent denitrification. Laboratory studies using ^{15}N on a flooded Crowley silt loam indicated that substantial nitrogen losses occurred following ammonium-N application[6,8,12,15]. The studies demonstrated that nitrification-denitrification reactions were controlling nitrogen loss, and also showed that more ammonium-N was lost from a flooded soil than was actually present in the aerobic soil layer at any one time. Apparently, ammonium-N diffused from the anaerobic zone to the aerobic zone where it underwent nitrification, and nitrate-N thus formed diffused into the anaerobic zone where it underwent denitrification[6,16]. Losses in the laboratory studies amounted to as much as 80% of the added-N. In a field study about 25% of the applied ammonium-N was unaccounted for[11], even when the fertilizer was applied at 7.5 cm depth. This indicates that a significant portion of the nitrogen lost was probably *via* this nitrification-diffusion-denitrification pathway.

Severe N losses were also shown to occur in a Crowley silt loam soil subjected to alternate draining and flooding. Organic-N is converted to ammonium-N in both aerobic and anaerobic soils, with the ammonium-N thus formed oxidized to nitrate-N under aerobic conditions and the nitrate-N then denitrified under anaerobic conditions. Such losses can be high in soils planted to lowland rice where management practices require draining and flooding. Patrick and Wyatt[5] observed a large nitrogen loss (up to 20% of total N) following repeated cycles of flooding and drying to field moisture. Reddy and Patrick[10] observed a loss of 24% of total-N in a Crowley silt loam soil which underwent incubation for 2 days under aerobic conditions followed by 2 days under anaerobic conditions for 4 months.

The agronomic significance of the high pH that develops in the floodwater of rice fields has largely been neglected as a factor favouring direct volatilization loss of NH_3. Losses due to volatilization can be serious when fertilizers are broadcast into floodwater rather than incorporated into soil. Volatilization losses of surface-applied urea have ranged from 8 to 50%, while losses from surface applied ammonium sulfate have ranged from 4 to 15 percent[4,19,20]. Losses of ammonium-N through volatilization were less than 1% when fertilizers were incorporated into the soil. In flooded soil ecosystems of Louisiana (Crowley silt loam), losses of added-N through volatilization were observed to be less than 3% (unpublished results, W. H. Patrick, Louisiana State University, Baton Rouge, LA).

Table 2. Nitrogen budget for a flooded Crowley silt loam soil planted to rice. The growing season is 4 months (May–August) and the effective soil profile depth is 30 cm. Asterisks (*) indicate estimated values. Potential mineralizable-N = the maximum amount of soil organic N available for plant uptake. Fertilizer N was incorporated into the soil.

	kg N ha^{-1} $season^{-1}$
Inputs	
Potential mineralizable-N*	69
Inorganic N in the soil profile	68
Crop residue N	35
Fertilizer N added	100
Rainfall	2
Biological N_2 fixation	10
Total IN	284
Outputs	
Crop removal	93
Biological immobilization	30
Ammonia volatilization	5*
Nitrification-denitrification	102*
Inorganic N in the soil profile	26
Leaching	<1*
Interflow	<1*
Surface runoff	<1*
Total OUT	259

Nitrogen budget

A list of input and output values obtained from ^{15}N studies on various components of the nitrogen cycle are shown in Fig. 4 and Table 2 for a flooded Crowley silt loam soil planted to rice. The major nitrogen inputs are ammonification of soil organic-N, fertilizer-N, and biological N_2 fixation. Ca. 49% of the added fertilizer-N is recovered by rice during the cropping season. The remainder of the plant-N was derived from native soil organic-N. A large portion of the fertilizer-N did not appear in any of the plant or soil components. Possible loss mechanisms include NH_3 volatilization, nitrification followed immediately by denitrification, and leaching and surface runoff. Fertilizer-N was incorporated into the soil, thus decreasing the possibility of NH_3 volatilization losses. Some of the nitrogen was probably lost in leaching or surface runoff, although ^{15}N was not recovered in the soil profile beyond the 25 cm depth. Denitrification probably accounted for large losses of nitrogen from this ecosystem. Soil organic-N is converted to gaseous end products by ammonification of soil organic-N to ammonium-N, followed by the upward

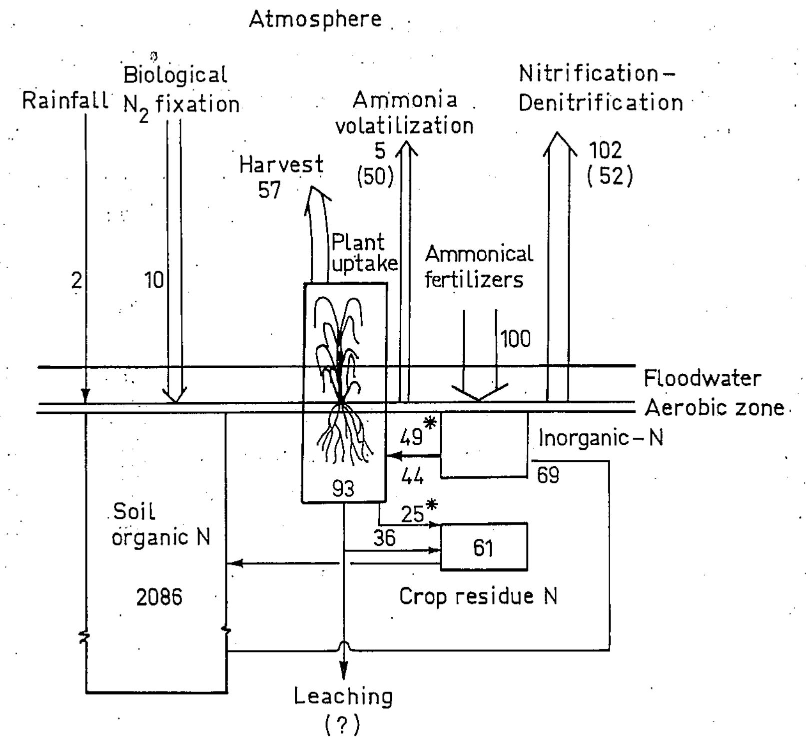

Fig. 4. Schematic representation of the main aspects of the nitrogen cycle during the rice growing season. Arrows are fluxes (kg N ha^{-1} growing $season^{-1}$). Boxes represent pool sizes (kg N ha^{-1}) at harvest. Soil N is to 30 cm depth. Asterisks indicate fertilizer derived-N.

diffusion of ammonium-N to the aerobic layer, its oxidation to nitrate in this layer, the downward diffusion of nitrate to the anaerobic soil layer, and finally the reduction of nitrate-N to gaseous end products such as N_2 and N_2O (Fig. 1). Nitrogen losses in flooded soils can also be enhanced by the aerobic layer around the root zone. Although no experimental evidence is available, it is possible that nitrogen in the aerobic root rhizosphere and the adjacent anaerobic soil acts in much the same way as in the interface described above. Unless all types of nitrogen losses are identified and measured quantitatively under field conditions, it is difficult to obtain a reliable mass balance for nitrogen in a flooded soil ecosystem.

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