Seasonal Denitrification in Flooded and Exposed Sediments from the Amazon Floodplain at Lago Camaleão

J. Kern,[1] A. Darwich,[2] K. Furch,[1] W.J. Junk[1]

[1] Max-Planck-Institute of Limnology, D-24302 Plön, Germany
[2] INPA, BR-69083-000 Manaus, Amazonas, Brazil

Abstract. Denitrification processes were measured by the acetylene-blockage technique under changing flood conditions along the aquatic/terrestrial transition zone on the Amazon floodplain at Lago Camaleão, near Manaus, Brazil. In flooded sediments, denitrification was recorded after the amendment with NO_3^- (100 μmol liter^{-1}) throughout the whole study period from August 1992 to February 1993. It ranged from 192.3 to 640.7 μmol N m^{-2} h^{-1} in the 0- to 5-cm sediment layer. Without substrate amendment, denitrification was detected only during low water in November and December 1992, when it occurred at a rate of up to 12.2 μmol N m^{-2} h^{-1}. Higher rates of denitrification at an average rate of 73.3 μmol N m^{-2} h^{-1} were measured in sediments from the shallow lake basin that were exposed to air at low water. N_2O evolution was never detected in flooded sediments, but in exposed sediments, it was detected at an average rate of 28.3 μmol N m^{-2} h^{-1} during the low-water period. The results indicate that under natural conditions there is denitrification and hence a loss in nitrogen from the Amazon floodplain to the atmosphere. Rates of denitrification in flooded sediments were one to two orders of magnitude smaller than in temperate regions. However, the nitrogen removal of exposed sediments exceeded that of undisturbed wetland soils of temperate regions, indicating a considerable impact of the flood pulse on the gaseous turnover of nitrogen in the Amazon floodplain.

Introduction

The Amazon floodplain (várzea) undergoes a periodic change in the nutrient supply driven by the hydrology of the river system with average water level fluctuations of 10 m near Manaus. The flood pulse concept describes the changing environmental

---

Correspondence to: J. Kern at present address, Institut für Agrartechnik Bornim e.V., Max-Eyth-Allee 100, D-14469 Potsdam, Germany
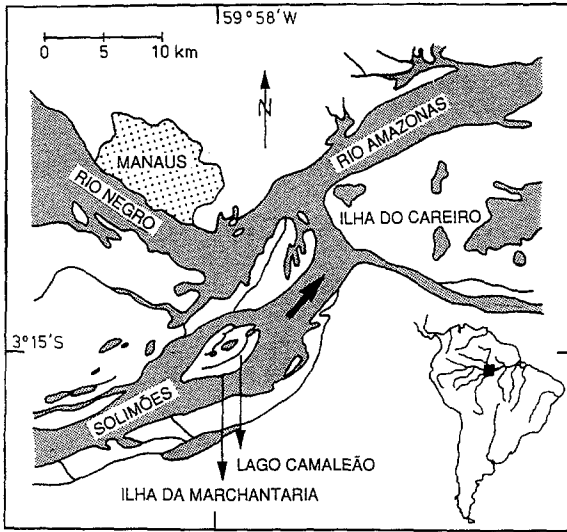
Fig. 1. Map of the investigation area. (From Furch and Junk [6].)

conditions along the aquatic/terrestrial transition zone that are associated with high productivity and rapid recycling of organic matter and nutrients [11].

Denitrification, the reduction of NO_3^- to N_2O and N_2, is the only appreciable biological process besides nitrification that releases chemically bound nitrogen into the atmosphere [3, 23]. In contrast to the northern hemisphere, little is known about the denitrifying processes in the tropics. Salati and Vose [22] estimated nitrogen gains and losses by nitrogen fixation, denitrification and volatilization for the whole Amazon basin and concluded that input and output of nitrogen are in equilibrium. On the Amazon floodplain at Lago Calado, denitrification was not detected either as a rate or as potential [17]. Other investigations of tropical and subtropical lake sediments had already succeeded in measuring denitrification as a potential after amendment with NO_3^- [8, 29, 32]. However, none of these studies was conducted continuously over a longer period of time that included seasonality and the change between terrestrial and aquatic environments. The present study is designed to clarify the extent of nitrogen loss via denitrification along the aquatic/terrestrial transition zone on the Amazon floodplain.

Materials and Methods

Study Site

Lago Camaleão is an elongated lake on Marchantaria Island (3° 15' S and 59° 58' W, Fig. 1), which is 300–500 m wide and 7-km long at middle water. Marchantaria Island, 15-km upstream of the confluence of Rio Negro and Rio Solimões/Amazon near Manaus, is influenced only by water from the Rio Solimões and by rain. Every year from May to July the high water usually inundates the island entirely, so that the chemistry of the Rio Solimões and the water on Marchantaria Island are similar [4].

The sampling site for flooded sediments was the deepest part of Lago Camaleão (18.4 m above sea level), which was covered with water even during the low-water period (Fig. 2). Sampling sites
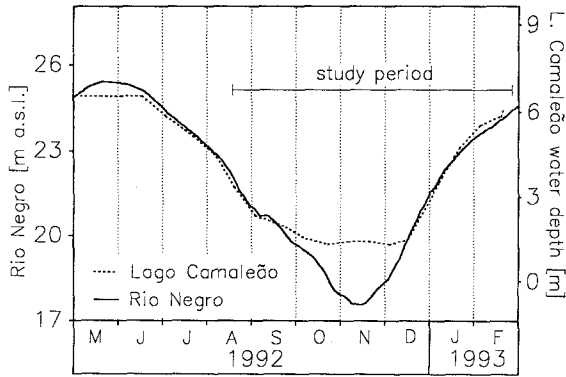
Fig. 2. Water level of Rio Negro in meters above sea level (m a.s.l.) in relation to the water depth of Lago Camaleão from May 1992 to February 1993.

for exposed sediments were located at a distance of about 50 m from the deepest part of the lake at 1 and 5 m from the water line (19.8–20.0 above sea level).

Sampling

Lake water and river water samples were taken with a Ruttner sampler from the surface at 2- to 3-week intervals. Water from the bottom of Lago Camaleão was also sampled. The samples were transported to the laboratory in polyethylene bottles that were placed in ice-filled coolers. Flooded sediments were sampled from August 1992 to February 1993 at monthly intervals with a gravity corer (Ø = 6 cm). Samples were cut into 0- to 5-cm slices, placed in plastic bags, and stored in ice-filled coolers. Exposed sediments were sampled three times after in situ incubation, once in November and twice in December 1992.

Physical and Chemical Methods

The pH was measured with a glass electrode immediately after sampling in the field. Measurements of dissolved oxygen were made in situ with a polarographic electrode that was equipped with a submersible stirrer. The water content of flooded and exposed sediments was determined gravimetrically after drying at 105°C.

Pore water from flooded and exposed sediments was obtained by taking the upper layer (0–5 cm) and centrifuging at 3000 rpm for 20 min. NO_3^- and NH_4^+ were determined from filtered samples (Sartorius SM 111, pore size 0.45 μm) according to Grasshoff: NH_4^+ was measured by applying the indophenol blue method, and NO_3^- was measured by the sulfanilamide method after reduction to NO_2^- with copperized Cd [7].

N_2O Evolution

N_2O that was naturally produced during an incubation without applications of C_2H_2 and NO_3^- was defined as N_2O evolution.

The incubation of flooded sediments was started on the same day of sampling after an acclimation period of 1 h to environmental temperature of 28°C. Wet weights of 1.5–2.0 g homogenized sediment (0–5 cm) were enclosed in sterilized 55-ml flasks, which were filled with lake bottom water. Then 15 ml of water was replaced by the same volume of N_2 (Linde, purity ≥99.999%) to create a vapor phase for the accumulation of N_2O. Incubations were carried out in duplicate for 24 h in the dark. Microbial activity within sediment slurries generally provides only a relative measure of in situ activity

Table 1. Chemical and physical properties of flooded sediments from Lago Camaleão at 0- to 5-cm depth

		1992					1993	
		Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.
N_2O evolution	(nmol N g^{-1} DW h^{-1})	0	0	0	0	0	0	0
Denitrification								
Rate	(nmol N g^{-1} DW h^{-1})	0	0	0	1.0	12.5	0	0
Potential	(nmol N g^{-1} DW h^{-1})	238.4	491.3	763.6	543.5	290.7	153.6	ND
Rate	(μmol N m^{-2} h^{-1})	0	0	0	1.2	12.2	0	0
Potential	(μmol N m^{-2} h^{-1})	279.3	491.4	640.7	339.3	257.6	272.5	192.3
NH_4^+	(μmol liter^{-1})	205.6	301.4	519.6	146.1	181.8	206.4	155.2
NO_3^-	(μmol liter^{-1})	ND	ND	ND	0	0	0.1	0.6
% Water content		61.6	66.3	63.8	68.5	68.5	66.7	72.1
pH		ND	ND	ND	6.9–7.0	ND	ND	ND

Data of N_2O evolution and denitrification are averaged by duplicates from sediment slurries. NH_4^+ and NO_3^- concentrations resulted from the pore water of two sediment cores, which were joined before analysis. ND, not determined.

[19]. Exposed sediments were incubated in the field under glass domes with a 20-ml headspace of air in accordance to Stal [27]. Each sample was conducted with four replicates. After an incubation time of 3 h, the headspace was transferred into 7-ml vacutainers (Becton Dickinson, Plymouth, England).

Denitrification Rate

Denitrification was measured by the acetylene-blockage technique [33]. The denitrifying activity in an atmosphere of 20 kPa C_2H_2 was defined as denitrification rate. The incubations of flooded and exposed sediments were conducted in the same manner as for N_2O evolution. The vapor phase, however, was enriched with C_2H_2 (Linde, purity $\geq 99.5\%$) to obtain a partial pressure of 20 kPa C_2H_2. The amount of dissolved N_2O in the aqueous phase of the slurries from flooded sediments was taken into account by correction at the incubation temperature with the solubility coefficient [31]. Results are given in Table 1 as average rates, expressed in nmol N g^{-1} DW h^{-1}. The rate and the potential (see below) of denitrification were related in units of surface area of the sediment slurry within the incubation flask and expressed in μmol N m^{-2} h^{-1} for comparison with exposed sediments. The definition in units of surface area was employed because it has been shown that denitrifying activity was significantly more close to the area of the sediment–water interface than to the mass of sediment within the incubation flasks ($P = 0.020$, n = 38).

Denitrification Potential

The potential of denitrification was measured only in flooded sediments after the amendment with NO_3^- (100 μmol liter^{-1}). In contrast to the denitrification rate (Fig. 3A), there was a constant accumulation of N_2O throughout 3 days (Fig. 3B), indicating that NO_3^- remained saturating in the treatment amended with NO_3^-.

Gas Chromatographic Analysis

Gas samples of 250 μl were withdrawn by a gastight syringe (Dyntach, Precision Sampling Corp., Baton Rouge, Lousiana, USA). The headspaces of flooded sediments were sampled directly from the
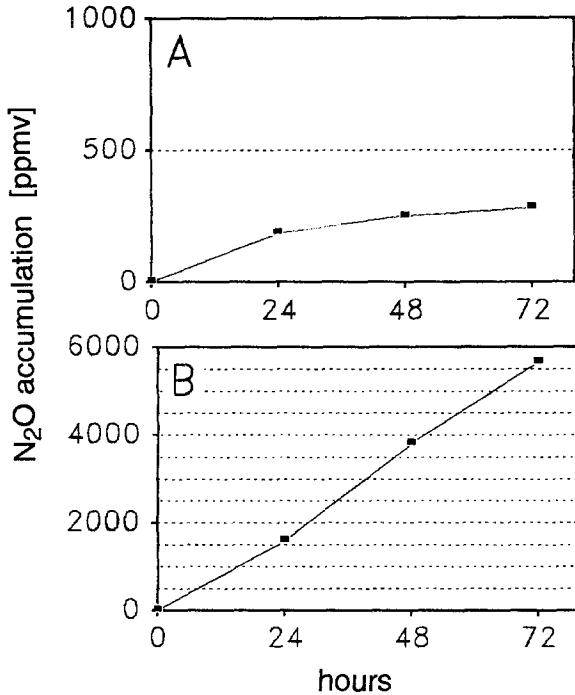
Fig. 3. Kinetics of denitrifying activity in slurries from flooded sediment (0–5 cm) of Lago Camaleão in December 1992. **A,** N_2O accumulation without additional NO_3^- → Denitrification rate. **B,** N_2O accumulation after the amendment with NO_3^- (100 μmol liter^{-1}) → Denitrification potential.

incubation flasks at the end of the incubation time. The headspaces of exposed sediments, which were stored in vacutainers, were analyzed within 1 week after sampling.

Gas samples were injected into the gas chromatograph (Hewlett Packard 5890 Series II) equipped with a 25-m-long capillary column (Poraplot U). Oven temperature was 40°C. N_2O was detected by a ^{63}Ni electron capture detector operating at 300°C. Carrier gas was pure nitrogen (99.999% N_2) with a flow rate of 15 ml min^{-1}. For calibration, 100 ppm N_2O in N_2 (Scotty I) was used.

Results

Lake Water Chemistry

During the flood phase, microbial activity in the sediments was influenced by physical, chemical, and biological parameters of the overlying water. The main fraction of inorganic nitrogen was NH_4^+ from the water of Lago Camaleão and NO_3^- from the water of Rio Solimões (Fig. 4A,B), which corresponds to previous studies [6]. Both during the high-water and the low-water phases in June and December, a stagnation of the water flow inside of Lago Camaleão was coupled with an increase in NH_4^+ concentration in the water at the bottom of the lake. At the beginning of December 1992, the NH_4^+ concentration reached a maximum of 32.6 μmol liter^{-1}. After a 2-week delay, NO_3^- increased to 4.9 μmol liter^{-1}, a concentration that was 10-fold more than that measured during receding water (Fig. 4B). This increase may be explained by nitrification, which was enabled by increasing O_2 input into the diminishing water column. As long as the water depth remained below 1.5 m, relatively high O_2 concentrations between 150 and 200
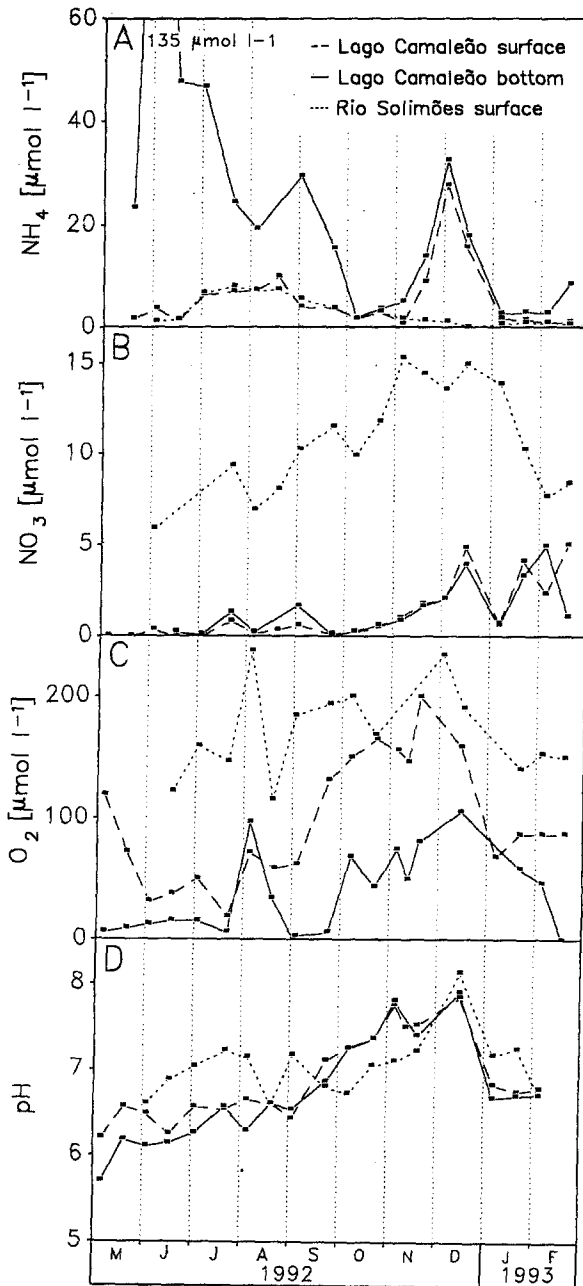
Fig. 4. Seasonal variability of ammonium, nitrate, and oxygen concentration and pH in the Rio Solimões and the Lago Camaleão. Sampling at 2- to 3-week intervals from May 1992 to February 1993. **A,** NH_4^+ concentration in the Rio Solimões (surface) and the Lago Camaleão (surface and bottom). **B,** NO_3^- concentration in the Rio Solimões (surface) and the Lago Camaleão (surface and bottom). **C,** O_2 concentration in the Rio Solimões (surface) and the Lago Camaleão (surface and bottom). **D,** pH in the Rio Solimões (surface) and the Lago Camaleão (surface and bottom).

Table 2. Chemical and physical properties of exposed sediments 1 and 5 m from the water line at Lago Camaleão

		1 m		5 m	
N_2O evolution	(μmol N m^{-2} h^{-1})	18.3 ± 5.3	(n = 12)	28.3 ± 6.8	(n = 8)
Denitrification rate	(μmol N m^{-2} h^{-1})	18.1 ± 6.4	(n = 12)	73.3 ± 6.5	(n = 8)
NH_4^+	(μmol liter^{-1})	98.5 ± 41.1	(n = 3)	345.2	(n = 2)
NO_3^-	(μmol liter^{-1})	0.5 ± 0.3	(n = 3)	0.5	(n = 1)
% Water content		62.7 ± 6.1	(n = 3)	56.9	(n = 2)

Data are average rates ± standard errors measured in November and December 1992. NH_4^+ and NO_3^- concentrations resulted from the pore water of exposed sediments.

μmol liter^{-1} could be measured in the surface water (Fig. 4C). The pH in the water column also reached its highest values, ranging between pH 7 and 8, during December 1992 (Fig. 4D).

N_2O Evolution

N_2O evolution was not detectable in slurries from flooded sediments of Lago Camaleão throughout the whole study period (Table 1). However, during low water, N_2O evolution was detected in exposed sediments that always had a water content above 50%. The average rate was 18.3 μmol N m^{-2} h^{-1} and 28.3 μmol N m^{-2} h^{-1} at 1 and 5 m from the water line, respectively (Table 2).

Denitrification Rate

In slurries from the flooded sediments, denitrification was detectable only during low water in November and December (Table 1), when maximum water depth declined to 1.5 m and the lake became isolated from the river by a sediment bar. In December 1992, corresponding to the highest NO_3^- concentration in the overlying water of the sediment, denitrification defined in units of surface area reached its maximum rate of 12.2 μmol N m^{-2} h^{-1} in the 0- to 5-cm sediment layer.

Exposed sediments of Lago Camaleão were obviously more affected by denitrification and had an average rate of 18.1 μmol N m^{-2} h^{-1} at 1 m from the water line in November and December 1992 (Table 2). Much higher rates of denitrification with an average rate of 73.3 μmol N m^{-2} h^{-1} were measured at 5 m from the water line and more inside the stands of *Echinochloa polystachya,* a semiaquatic C_4 grass, which provided large amounts of rotting organic material. A high decomposition rate in this zone was reflected by a high NH_4^+ concentration of 345.2 μmol liter^{-1} in the pore water. In contrast, NO_3^- concentrations remained below 1 μmol liter^{-1} (Table 2).

Denitrification Potential

Denitrification measured as potential (+100 μmol NO_3^- liter^{-1}) in slurries from flooded sediments was detectable throughout the whole study period, indicating a

limitation by NO_3^- for denitrifiers (Table 1). In the 0- to 5-cm sediment layer, N_2O accumulation ranged between 192.3 and 640.7 μmol N m^{-2} h^{-1}. Particularly high denitrification potential was measured during receding water from September to November. Limitation by NO_3^- in the Lago Camaleão was obvious, because throughout the whole study period NO_3^- concentrations only ranged between 0 and 1 μmol $liter^{-1}$ and 0 to 5 μmol $liter^{-1}$ in the sediment interstitial and the overlying water, respectively (Table 1, Fig. 4B).

In December 1992 denitrification potential was 257.6 μmol N m^{-2} h^{-1} and should have removed completely the amount of added NO_3^- within 1–2 days [13]. However, a continuing N_2O accumulation up to 6 days as shown by Kern [13] excludes a NO_3^- depletion within this time. This phenomenon is not fully understood but might be the result of accelerated mineralization of particulate nitrogen coupled with nitrification and denitrification.

Discussion

Denitrification did not play an important role in the loss of nitrogen at Lago Camaleão as long as sediments were covered by lake water. Low oxygen concentrations in the water column restricted nitrification and the supply of NO_3^- into the sediment. This was reflected by an always measurable denitrification potential, which indicates there is a limitation of NO_3^-. Only at low water, sedimentary denitrification could be detected in slurries from flooded sediments without NO_3^- amendment. We suggest that it was the last step of four consecutive physicochemical processes between sediment and overlying lake water. These steps were as follows: (a) NH_4^+ leached into the lake water when it was released from the interstitial sediments and by seepage from exposed sediments. (b) Nitrification in the mixed and oxygenated lake water led to an increase of NO_3^- concentrations to 4.9 μmol $liter^{-1}$. (c) NO_3^- was transported from the lake water into the sediment. (d) Denitrification in the sediments progressed at a maximum rate of 12.2 μmol N m^{-2} h^{-1} in December 1992. Although NO_3^- concentrations in the water of Lago Camaleão increased from 0.2 to 4.9 μmol $liter^{-1}$ from October to December, they were far too low to allow an intensive denitrification as reported for the temperate regions. In nutrient-rich Danish streams with NO_3^- concentrations between 300 and 1,000 μmol liter $^{-1}$, the accumulation of N_2O in the sediment achieved 1,400 μmol N m^{-2} h^{-1}, two orders of magnitude greater than Lago Camaleão sediments [2].

Exposure of Lago Camaleão sediments to the air during low water was favorable for a subsequent oxidation of NH_4^+. Rates of N_2O evolution and denitrification of recently exposed sediments increased by greater distance from the water line of Lago Camaleão, probably as a result of high NH_4^+ concentrations, favorable O_2 conditions, and a great source of organic matter from decomposing macrophytes.

The N_2O evolution we measured in exposed sediments on Marchantaria Island was much higher than measured on other várzea soils near Manaus [16]. The explanation for this discrepancy may lie in the fact that our study was performed on waterlogged sediments located between 19.0 and 20.0 m above sea level in contrast to the results from Matson et al. [16]. Their results were derived from a more elevated location (>25.0 m above sea level) where sediments had been

exposed to air for a longer period. That points to a decisive influence by the flood pulse on N_2O evolution during the exposed period.

N_2O evolution may have different microbial sources, especially denitrification, which favors N_2O as a final product with respect to the reduced N_2 under aerated soil conditions, high NO_3^- concentrations, and low pH values [18, 28, 30]. At Lago Camaleão oxygen was the most important factor controlling the N_2/N_2O ratio because NO_3^- concentrations were very low in flooded and exposed sediments, and pH values, both in the water column (Fig. 4D) and the interstitial of flooded sediments (Table 1), were high enough to let denitrification run mainly to N_2. For the pore water of exposed sediments, we assume similar pH data because of high decomposition rates, which are accompanied by an increase of pH up to the neutral range, as shown by Furch and Junk [5] in decomposition experiments with *Echinochloa polystachya*. The high N_2O evolution rates we observed in exposed sediments may have been derived from other microbial processes not just by denitrification. In recent years it has been proved that nitrification can play an important role in N_2O evolution as well [1, 10, 25].

Because there was no accumulation of NO_3^- in the pore water of the exposed sediments, a strong coupling of nitrification with denitrification has to be considered. That means that NO_3^- derived by nitrification was very rapidly consumed by denitrifiers as long as there was no limitation in electron donors. The latter was not the case at Lago Camaleão, with its high availability of organic carbon fixed by C_4 grasses and other macrophytes [12, 20]. Taking a denitrification rate of 73.3 μmol N m^{-2} h^{-1} at 5 m from the water line as representative for the whole exposed sediment, a nitrogen loss of 14.8 kg N ha^{-1} occurred throughout the 2 dry months. This value was more than 20 times higher than that measured by Jordan et al. [9] in an undisturbed terra firme forest, and it was three times higher in relation to denitrification rates in unfertilized wetland soils of temperate regions [14, 34]. Therefore, the studied várzea ecotope represents an important source of nitrogen that is released into the atmosphere (i.e., accelerated gas turnover of nitrogen in the exposed sediments).

The C_2H_2 inhibition technique is the most practical method in the field for measuring denitrification because of its high sensitivity and its low cost. However, the blockage of N_2O reductase by C_2H_2 may be incomplete at low NO_3^- concentrations [15, 19, 21, 24, 26]. It was shown that C_2H_2 also inhibited nitrification by causing denitrifiers to reduce N_2O in the case of NO_3^- deficiency. Thus, in the presence of low NO_3^- concentrations as in the studied ecotopes, denitrification in the nonpotential assays may have been underestimated. Nevertheless, the actual results already indicate a high nitrogen release during the transition from an aquatic to a terrestrial ecotope and point to a considerable impact of the flood pulse on the gaseous nitrogen turnover within the Amazon floodplain.

References

1. Bremner JM, Blackmer AM (1978) Nitrous oxide: emission from soils during nitrification of fertilizer nitrogen. Science 199:295–296
2. Christensen PB, Nielsen LP, Sørensen J, Revsbech NP (1990) Denitrification in nitrate-rich streams: diurnal and seasonal variation related to benthic oxygen metabolism. Limnol Oceanogr 35:640–651
3. Conrad R, Seiler W (1980) Field measurements of the loss of fertilizer nitrogen into the atmosphere as nitrous oxide. Atmos Environ 14:555–558
4. Furch K (1984) Seasonal variation of the major cation content of the várzea-lake Lago Camaleão, middle Amazon, Brazil, in 1981 and 1982. Verh Int Verein Limnol 22:1288–1293
5. Furch K, Junk WJ (1992) Nutrient dynamics of submersed decomposing Amazonian herbaceous plant species *Paspalum fasciculatum* and *Echinochloa polystachya*. Rev Hydrobiol Trop 25:75–85.
6. Furch K, Junk WJ (1993) Seasonal nutrient dynamics in an Amazonian floodplain lake. Arch Hydrobiol 128:277–285
7. Grasshoff K (1976) Methods of seawater analysis. Verlag Chemie, New York
8. Howard-Williams C, Esteves F de, Santos JE, Downes MT (1989) Short term nitrogen dynamics in a small Brazilian wetland (Lago Infernão, São Paulo). J Trop Ecol 5:323–335
9. Jordan C, Caskey W, Escalante G, Herrera R, Montagnini F, Todd R, Uhl C (1983) Nitrogen dynamics during conversion of primary Amazonian rain forest to slash and burn agriculture. Oikos 40:131–139
10. Jørgensen KS, Jensen HB, Sørensen J (1984) Nitrous oxide production from nitrification and denitrification in marine sediment at low oxygen concentrations. Can J Microbiol 30:1073–1078
11. Junk WJ, Bayley PB, Sparks RE (1989) The flood pulse concept in river-floodplain systems. In: Dodge DP (ed) Proceedings of the International Large River Symposium. Can Spec Publ Fish Aquat Sci 106:110–127
12. Junk WJ, Piedade MTF (1993) Biomass and primary-production of herbaceous plant communities in the Amazon floodplain. Hydrobiologia 263:155–162
13. Kern J (1995) Die Bedeutung der N_2-Fixierung und der Denitrifikation für den Stickstoffhaushalt des amazonischen Überschwemmungssees Lago Camaleão. Dissertation, University of Hamburg, Germany, p 178
14. Klingensmith KM, Cleve K van (1993) Denitrification and nitrogen fixation in floodplain successional soils along the Tanana River, interior Alaska. Can J For Res 23:956–963
15. Knowles R (1990) Acetylene inhibition technique: development, advantages, and potential problems. In: Revsbech NP, Sørensen J (eds) Denitrification in soil and sediment. Plenum Press, New York, pp 151–166
16. Matson PA, Vitousek PM, Livingston GP, Swanberg NA (1990) Sources of variation in nitrous oxide flux from Amazonian ecosystems. J Geophys Res 95 D10:16789–16798
17. Melack JM, Fisher TR (1988) Denitrification and nitrogen fixation in an Amazon floodplain lake. Verh Int Verein Limnol 23:2232–2236
18. Nägele W, Conrad R (1990) Influence of soil pH on the nitrate-reducing microbial populations and their potential to reduce nitrate to NO and N_2O. FEMS Microbiol Ecol 74:49–58
19. Oremland RS, Umberger C, Culbertson CW, Smith RL (1984) Denitrification in San Francisco Bay intertidal sediments. Appl Environ Microbiol 47:1106–1112
20. Piedade MTF, Long SP, Junk WJ (1994) Leaf and canopy photo-synthetic CO_2 uptake of a stand of *Echinochloa polystachya* on the Central Amazon floodplain—Are the high potential rates associated with the C_4 syndrome realized under the near-optimal conditions provided by this exceptional natural habitat? Oecologia 97:193–201
21. Rudolph J, Frenzel P, Pfennig N (1991) Acetylene inhibition technique underestimates in situ denitrification rates in intact cores of freshwater sediment. FEMS Microbiol Ecol 85:101–106
22. Salati E, Vose PB (1984) Amazon basin: A system in equilibrium. Science 225:129–138
23. Schuster M, Conrad R (1992) Metabolism of nitric oxide and nitrous oxide during nitrification and denitrification in soil at different incubation conditions. FEMS Microbiol Ecol 101:133–143

24. Seitzinger SP, Nielsen LP, Caffrey J, Christensen PB (1993) Denitrification measurements in aquatic sediments: a comparison of three methods. Biogeochem 23:147–167
25. Skiba U, Smith KA, Fowler D (1993) Nitrification and denitrification as sources of nitric oxide and nitrous oxide in a sandy loam soil. Soil Biol Biochem 25:1527–1536
26. Slater JM, Capone DG (1989) Nitrate requirement for acetylene inhibition of nitrous oxide reduction in marine sediments. Microb Ecol 17:143–158
27. Stal LJ (1988) Nitrogen fixation in cyanobacterial mats. In: Packer L, Glazer AN (eds) Methods in enzymology, vol. 167. Academic Press, Orlando, pp 474–484
28. Thomsen JK, Geest T, Cox RP (1994) Mass spectrometric studies of the effect of pH on the accumulation of intermediates in denitrification by Paracoccus denitrificans. Appl Environ Microbiol 60:536–541
29. Viner AB (1982) Nitrogen fixation and denitrification in sediments of two Kenyan lakes. Biotropica 14:91–98
30. Weier KL, Doran JW, Power JF, Walters DT (1993) Denitrification and the dinitrogen/nitrous oxide ratio as affected by soil waters, available carbon, and nitrate. Soil Sci Soc Am J 57:66–72
31. Weiss RF, Price BA (1980) Nitrous oxide solubility in water and seawater. Mar Chem 8:347–359
32. Whitaker V, Matvienko B (1992) A method for the study of N_2O evolution in tropical wetlands. Hydrobiologia 230:213–218
33. Yoshinari T, Knowles R (1976) Acetylene inhibition of nitrous oxide reduction by denitrifying bacteria. Biochem Biophys Res Commun 69:705–710
34. Zak Dr, Grigal DF (1991) Nitrogen mineralization, nitrification and denitrification in upland and wetland ecosystems. Oecologia 88:189–196