

Inorganic nitrogen uptake and river inputs in northern Lake Tanganyika

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Running title: Nitrogen cycling in northern Tanganyika Lake

ABSTRACT

Northern Lake Tanganyika is characterized by an almost permanently stratified water column which causes severe nutrient depletion in surface waters. Any external N source to surface waters, therefore, is of importance in sustaining primary production. This study attempted to quantify riverine input of dissolved inorganic nitrogen (DIN) to the extreme northern end of Lake Tanganyika (surface = 900 km²) as well as the DIN uptake by surface phytoplankton. Results showed that riverine DIN inputs (1930 tons of N/year) were of similar importance to atmospheric deposition (1520 to 1720 tons of N/year) and were maximal during the dry season. Moreover, seasonal DIN variations in river and lake waters showed maximum concentrations during part of the dry season (May to July 1999) probably due to high atmospheric inputs. Phytoplanktonic nitrate and ammonium uptake rates were measured during 9 cruises and varied from 0.01 to 19.3 nM/h. These values suggest that uptake by phytoplankton in the surface waters could represent a DIN sink of about 14400 tons of N/year, thereby utilizing all available DIN coming in from external sources. External DIN sources represent approximately 25 % of the annual phytoplankton N requirements, showing the major importance of unquantified N sources in sustaining primary production in the northern basin of Lake Tanganyika. These sources could include organic N present in the external sources, and internal N supply.

INDEX WORDS

Lake Tanganyika, Burundi, Nitrogen uptake, DIN, rivers, Rusizi River

INTRODUCTION

Lake Tanganyika (Fig. 1) is one of the world's largest freshwater lakes. Located in central Africa, this lake is 677 km long, 50 km wide (average) and exhibits a total area of 32900 km². With a maximum depth of 1470 meters, it is the world's second deepest lake. Lake Tanganyika receives water from rainfall as well as a large watershed which drains western Rwanda and Burundi, eastern R. D Congo, Tanzania and northern Zambia (Fig. 1). The outlet of Lake Tanganyika is the Lukuga River, a tributary of the Congo River. Given the extremely large volume of the lake (ca 18000 km³), the hydraulic retention time exceeds thousands of years (Coulter and Spigel 1991). Recently growing attention has focused on the ecology of the lake with large research projects supported by international organizations like the United Nations' Food and Agriculture Organization (FAO) and Developing Program (UNDP). These and other research projects have highlighted the general nutrient regime in the lake (Hecky *et al.* 1991, Edmond *et al.* 1993, Vandelannoote *et al.* 1996, Kimbadi *et al.* 1999, Vandelannoote *et al.* 1999, Langenberg *et al.* 2003a and b). This nutrient regime is strongly linked to internal water circulation characteristics.

Figure 1

The main hydrological characteristics of this lake were studied by Coulter and Spigel (1991) and more recently by Plisnier *et al.* (1999), Chitamwebwa (1999), Naithani *et al.* (2002 and 2003), and Naithani and Deleersnijder (2004). At the end of the rainy season (January to April), the water column is stable and highly stratified from North to South with surface waters depleted in nutrients and anoxic nutrient rich deep waters. During the dry season (May to September), strong southerly winds induce surface water circulation from South to North resulting in (1) the development of an upwelling region in the southern part, with nutrient-rich deep waters reaching the surface, and (2) in a marked (60 to 70 m) deepening of the nutrient-depleted epilimnion in the northern part of the lake, where the water column stays stratified. At the end of the dry season and beginning of the rainy season, South East winds

cease, and the South-North tilted epilimnion oscillates back towards equilibrium. These oscillations induce and/or reinforce small upwelling zones along the west coast which propagate cyclonically around the lake like internal Kelvin waves. Oscillations and internal waves result in nutrient pulses to the surface layers and in the North, around October-November, deep waters move back towards the surface as a secondary upwelling period.

At the whole lake scale, the importance of nutrient inputs from rivers, rainfall and vertical mixing on sustaining the primary production were estimated by Langenberg *et al.* (2003a). This study demonstrated that at lake scale, rainfall seemed to be the most important external DIN source (83 % of total external sources) compared to rivers. Estimates deduced from lake primary productivity, however, showed that these external sources only represented 1 % of nutrients used by phytoplankton. This meant that 99 % of primary productivity was supported by nutrients arising from deep nutrient-rich water layers. The Langenberg *et al.* (2003a) study, however, neglected dry deposition of nutrients (rates were not available at the time), as well as the organic fraction of N.

In the northern basin, stratification has a dramatic effect on the nutrient regime of the lake. Here, unlike what is observed in the South basin, there is almost no vertical mixing of the water column annually. Consequently, bottom waters below a depth of 150 m are permanently anoxic (Hecky 1991) while nutrients (nitrogen and phosphorus) are completely depleted in surface waters. In the euphotic zone (about 20 m deep), although both ammonium and nitrate are depleted by phytoplankton uptake, ammonium concentrations remain low up to 150 m depth (Fig. 2, from Hecky *et al.* 1991), a dark region where no phytoplankton uptake occurs. This is due to nitrification which oxidizes ammonium to nitrate in the presence of oxygen. As well, at 20 m depth when light becomes scarce, nitrate starts to increase for two reasons. First, it is no longer assimilated by photoautotrophic organisms and secondly, it is continuously generated by nitrification. Below 150 m, the anoxic water column (see above),

absence of photosynthesis and ongoing heterotrophic activity has an important effect on dissolved inorganic nitrogen profiles. Nitrate reaches a maximum between 75 to 100 m depth and then starts to decrease when approaching the depth of oxygen depletion. Indeed, when oxygen is no longer available, nitrate consumption (denitrification of nitrate to N_2 till complete depletion) replaces its production (nitrification). Also, as soon as nitrification stops (around 150 m depth), ammonium appears and accumulates further as organic N compounds are mineralized.

Figure 2

→ Under such conditions, any external N source, like rainfall or dust deposition, short local vertical mixing of the water column and/or river inputs to surface waters will be important in sustaining primary production in the northern basin. And indeed it appears that they are for in spite of the lack of water mass mixing in this basin, primary production is higher here than in any other location on the lake (Sarvala *et al.* 1999). The northern basin receives water from a number of sources including the Rusizi River. This river originates from Lake Kivu and represents one of the largest water contributors with an average discharge of 182 m³/s. Two other rivers, the Mutimbuzi and Ntahangwa Rivers have much smaller discharges - 3 m³/s and 2.5 m³/s, respectively (Institut Geographique du Burundi, see methods). These three inflowing water masses could be important nutrient sources for the lake. Atmospheric deposition and local vertical mixing may also be potentially important N sources.

The general objective of this paper is to describe and quantify seasonal variations in dissolved inorganic nitrogen (DIN) in the northern basin of Lake Tanganyika. More specifically the goals for the northern basin are: (1) to assess seasonal variability of riverine DIN inputs, (2) To measure seasonal variations in DIN concentrations (3) to estimate use of inorganic nitrogen by phytoplankton and finally (4) to estimate importance of external DIN supply (rivers and atmosphere) in sustaining phytoplankton DIN uptake.

METHODS

Sampling

Sampling was conducted from late August 1998 to November 1999. Samples were taken at a northern station on Lake Tanganyika (1 km from lakeshore, 29°19 E - 3°22 S, Fig. 1) and at the outlet of the 3 major rivers: Rusizi (1 km from the lakeshore, Fig. 1), Mutimbuzi (1.5 km from the lakeshore, Fig. 1) and Ntahangwa (3 km from the lakeshore, Fig. 1). River samples were taken with a bucket from a bridge at mid-river and lake samples from an inflatable motorboat. Samples for nutrients were stored in 10L plastic jugs (previously cleaned with 5% HCl) and subsequently transferred to the laboratory for immediate analysis.

Temperature and river discharge

Temperature was measured on lake and river samples directly after collection with a mercury thermometer. Annual, minimum and maximum discharge data for the 3 rivers were obtained from the hydrological service in Bujumbura (IGEBU, Institut Geographique du Burundi).

Dissolved inorganic nitrogen (DIN) determination

Ammonium, nitrate and nitrite were determined immediately after sampling by colorimetric methods with a Perkin Elmer lambda 2 spectrophotometer, equipped with a 5 cm optical path cell. Because of high river water turbidity, samples were first filtered through a pre-combusted GF/F glass-fiber filter (Whatman - nominal pore size 0.7 μm), whereas lake water samples were unfiltered. Ammonium concentrations were measured by the indophenol blue complex colorimetric method (Koroleff 1969). Nitrite was analyzed with the sulphanilamide colorimetric method (Bendschneider and Robinson 1952) while nitrate + nitrite were determined after nitrate reduction to nitrite on a cadmium-copper column (Gardner *et al.* 1976). Detection limits for ammonium, nitrite and nitrate were 0.1 μM and coefficient of variation on replicate measurements was less than 5 %.

Nitrogen uptake experiments

Phytoplankton nitrogen uptake was measured using the ^{15}N -tracer technique (Dugdale and Goering 1967). Transparent plastic incubation bottles were filled with 750 ml of water and then spiked with 0.1 μM of labeled $^{15}\text{NO}_3^-$ (99.5 %) or $^{15}\text{NH}_4^+$ (99.8 %). Samples were incubated *in situ* in a floating incubator (natural light conditions) for about 6 hours. At the end of incubation, particulate matter from each bottle was filtered through a pre-combusted GF/F (Whatman) glass-fiber filter. Filters were dried for 8 hours at 50°C and stored in clean Petri-dishes until analysis for particulate organic nitrogen (PN) and ^{15}N abundance. For each filter, ^{15}N abundance was measured with an emission spectrometer (model NIA 1, Jasco Corporation - Japan) (Goeyens *et al.* 1985, Kumazawa 1969) following a modified Dumas combustion technique (Fiedler and Proksh 1975). Particulate nitrogen concentration (PN) was measured using a Carlo-Erba NA 1500 elemental analyzer (Nieuwenhuize *et al.* 1994). This instrument combusts all particulate N and C to a purified stream of N_2 and CO_2 gas and analyses their concentration by thermal conductivity. Detection limit for PN was 0.1 μM and coefficient of variation on replicate analyses was less than 5 %.

Uptake rates were then calculated according to the following equation (Dugdale and Wilkerson 1986, Collos 1987):

$$U = PN \times \frac{Apf - An}{(Adi - Apf) \times dt}$$

With:

U (nM/h): uptake rate;

An (%): natural abundance of $^{15}\text{N} = 0.367$ %;

Adi (%): abundance of ^{15}N in the ammonium or nitrate of the sample after tracer addition (calculated);

dt (h): incubation time;

Apf (%): abundance of ^{15}N in PN at the end of the incubation (measured);

PN (nM): particulate nitrogen concentration (measured).

RESULTS

River discharge and temperature

Table 1

Maximum, minimum and annual river discharges for the Mutimbuzi, Ntahangwa and Rusizi rivers are given in Table 1. River water temperatures varied from 22 to 28°C (Fig. 3) and were slightly higher in the surface waters of the lake (27 to 29°C). Peak temperatures were generally observed during the rainy season (September to April). During the dry season, southerly winds induced evaporative cooling of surface waters and temperatures were slightly lower (Coulter and Spiegel 1991) as observed in the rivers and the lake. In January (wet season), a sudden decrease of 2°C is observed in the surface waters of the lake.

Figure 3

DIN concentrations

All species of dissolved inorganic nitrogen showed maximum concentrations during part of the dry season for both lake and rivers (June to August 1999; Fig. 4). According to the similarity of June -August N profiles in all water-bodies, it seems likely that one single event caused increased N concentrations observed. In the lake: During the wet season (September to April), nitrate and nitrite were all below the detection limit while ammonium was higher (around 0.15 µM). In early January, 0.4 µM of nitrate and 0.1 µM of nitrite were detected while ammonium disappeared completely. This feature corresponded to a sudden temperature decrease (see Fig. 3). At the end of the wet season (March-April), ammonium also became undetectable. During the beginning of the dry season (April to June), nitrate, nitrite and ammonium were all at undetectable levels. From June to August, nitrite, nitrate and ammonium increased to 16 µM, 6.5 µM, and >40 µM, respectively. In the rivers: During the wet season (November to February), nitrite and nitrate decreased from around 5 µM and 10 µM, respectively, to undetectable levels. For all rivers, the beginning of the dry season was

characterized by low nitrite and nitrate levels, followed by a sharp increase from June-August, when nitrate concentrations reached 150 - 200 μM and nitrite 15 - 85 μM . In the Mutimbuzi River ammonium levels were low throughout the year. During the wet season, (November to February), ammonium levels in the Rusizi and Ntampangwa rivers increased reaching a concentration of 5 μM . During the dry season, while concentrations were low in Rusizi waters they increased sharply in the urban Ntampangwa River reaching 475 μM in July 1999.

Figure 4

Nitrogen uptake rates

N-uptake rates were mostly measured when ammonium and nitrate were undetectable (Fig. 4 B and C). Consequently the 0.1 μM ^{15}N -DIN spike added in these uptake experiments likely increased ambient DIN by a factor ≥ 2 . Spike concentrations used here were therefore well above the recommended maximum 10 % increase generally allowed. Uptake rates obtained under these conditions, therefore, should not be regarded as in situ rates, but rather as instantaneous in situ phytoplankton responses to small DIN pulses (0.1 μM). Phytoplankton nitrate and ammonium uptake rates were measured during 9 cruises (Table 2). Although organisms were submitted to low DIN concentrations, they were able to use ammonium and nitrate at rates varying between 0.01 to 19.3 nM/h. During the wet season, DIN uptake rates varied between 1 and 1.5 nM/h when both nitrate and ammonium were depleted, and were higher when nitrate or ammonium was available (5 to 19 nM/h) (Table 2). During the dry season, rates varied between 3 and 12 nM/h when both nitrate and ammonium were depleted, but were also higher when nitrate or ammonium was available (16 nM/h) (Table 2).

Table 2

DISCUSSION

With respect to DIN distribution two differing regimes were observed in northern Lake Tanganyika and its 3 major inflowing rivers: a period of relatively low DIN concentration in the wet season followed by higher DIN concentrations during the dry season. Similar findings

have been reported by other researchers. Langenberg *et al.* (2003b), for example, observed that DIN concentrations in the euphotic zone of the lake during the dry season were twice as high as during wet season. For rivers (Rusizi, Malagarasi and Lufubu), however, Langenberg *et al.* (2003a), found the opposite pattern reported here, with highest concentrations and inflow during the wet season and lowest during the dry season. As the Langenberg study relied on rather limited data (2 observations in each season), it is possible that events with accompanying higher DIN concentrations were missed.

Rivers input

Using nutrient profiles, we calculated integrated wet season, dry season and yearly average nitrogen concentrations for the 3 rivers (Table 3). These calculations indicated that the Ntakangwa River, with its high NH_4^+ concentration, was clearly contaminated with urban effluents (see also Vandelannoote *et al.* 1996). The yearly average DIN concentration in the Rusizi River (22.5 μM) reported in this study, however, was lower than that reported by Vandelannoote *et al.* (1999 – 36 μM) or Langenberg *et al.* (2003a - 47 μM). Year to year variations and differences in sampling frequency (every 2 weeks approximately in this study, every 3 months from August 1994 to August 1995 in the study of Langenberg *et al.* 2003a, and 10 times between March 1994 and July 1995 in the study of Vandelannoote *et al.* 1999) could explain these differences.

Table 3

By multiplying these average concentrations by the average annual, wet and dry season discharges of the Rusizi, Ntakangwa and Mutimbuzi rivers, riverine DIN contributions to the lake were calculated (Table 3). According to these calculations, the most important contributor of DIN to the lake was the Rusizi River which supplied 1810 tons of N/year mostly (98 %) as oxidized N (nitrite and nitrate). The Ntakangwa River, although showing the highest N-nutrient concentrations (due to contamination with urban effluents), only represented an input of 92 tons of N/year to the lake (around 5 % of total river inputs). Most

of its' input (53 %) was in the form of ammonium making it the most important riverine ammonium supplier to the northern lake basin. The Mutimbuzi DIN-load only represented 2 % of the total river inputs mainly as oxidized DIN (94 % - similar to the percentage from the Rusizi River). Considering wet and dry seasons separately, most (more than 70 %) of the DIN coming into the lake entered during the dry season, which is characterized by the lowest river discharge, but also the highest DIN concentrations. This is in accordance with the highest concentrations observed in surface lake water during part of the dry season.

Rusizi River inflow mixes with Tanganyika waters over a relatively short distance from mouth (800 m), merges with epilimnetic lake water (surface layer) and spreads horizontally, due to shore-bound currents (Vandelannoote *et al.* 1999). Therefore, the influence of the Rusizi inflow, and of other rivers in that area in providing nutrients to the lake is likely only of importance locally i.e. to the Bujumbura or northern basin, – see Fig. 1. For this area (900 km²) river inputs represent about 2140 kg N/km²/year, 90 % of which arrives during the dry season and 10 % during the wet season (Table 4).

Table 4

Why then are N loads so important in rivers during the dry season? The N load at river outlets is governed by the balance between external N inputs to the watershed and in-stream N retention (by for example denitrification and vegetation uptake). In stream retention in tropical watersheds is mostly controlled by runoff (Downing *et al.* 1999) and should increase in the dry season. This factor can thus not explain the high dry season N loads. Sources of N to rivers can be point and diffuse. Point sources are mainly linked to wastewater discharge and are a function of population size and industrialization. They are thus relatively independent of climatic conditions. Diffuse sources are mainly linked to groundwater inflow and atmospheric deposition. Groundwater inflow is strongly related to rainfall with lowest N inflows for dry periods (Downing *et al.* 1999). Again, this factor can thus not explain our observations. The most likely factor is thus atmospheric deposition. This should occur over

river basins and lake, and is thus likely the event responsible for the high concentrations observed in all water bodies between June and August. Also as atmospheric N input increases with watershed surface, the largest increase of N load between wet and dry season is found for the river with the largest basin: the Rusizi.

Atmospheric deposition

Wet and dry atmospheric deposition in the lake occurs concomitantly with wet and dry seasons, respectively. Estimates of nutrient wet deposition (Langenberg *et al.* 2003a) suggested that DIN atmospheric inputs were more important than riverine inputs at the whole lake scale: rain and the Rusizi River accounted for 95 % of the total DIN input to the lake, with rain accounting for 6.9 times the river inputs (Langenberg *et al.* 2003a). According to these authors, estimated wet deposition for the whole lake is 22.10^3 tons of DIN/year (estimated from 1200 mm/year precipitation; DIN concentration of 48 mmol/m²/year; lake surface area of 32900 km²). Applying these deposition rates to the northern Bujumbura basin of the lake (surface 900 km²) where our station is located, wet deposition was estimated at 610 tons of N-DIN/year or 680 kg N/km²/year. Another recent and detailed study on atmospheric N deposition in Africa by Galy-Lacaux *et al.* (2003) estimated a total N deposition on wet savanna type landscape in west and central Africa of 1700 kg N/km²/year, of which 440 kg N/km²/year occurred as wet deposition, (similar to the data of Langenberg *et al.* 2003a), and 1260 kg N/km²/year as dry deposition. These extremely high deposition rates (especially dry deposition) are comparable to values observed in industrialized regions like northern Europe (720 to 1920 kg N/km²/year, Van Boxtel *et al.* 1991). Comparing these deposition rates to other lakes, wet DIN deposition into Lake Tanganyika is about 10 times higher than Lake Baïkal, a similar large lake (van Marrewijk 2003). Data of Bootsma *et al.* (1996) estimated wet N deposition to neighboring Lake Malawi to be 12.4 kg N/km²/year, much lower than estimates from Langenberg *et al.* (2003a) and Galy-Lacaux *et al.* (2003), but

much higher than average values reported for other tropical lakes (7.5 to 19 kg N/km²/year, Bootsma *et al.* 1996).

Where, then, does this large amount of atmospheric N originate? One possible source is biomass burning (Langenberg *et al.* 2003a, Bootsma *et al.* 1996). In Africa, the magnitude and importance of this burning has been assessed by several methods and investigators (e.g. Andreae 1991, Barbosa *et al.* 1999, Wooster *et al.* 2003 and 2004) and has included associated NO_x emission estimates. “Best guess” emission flux estimates from African savanna fires for NO_x were 6 Tg N/year (Andreae and Fishman 1998). Barbosa *et al.* (1999) estimated trace gas and particulate matter emissions for 1985-1991 and obtained an average value of 6.7 Tg N/year. If we make the assumption that all NO_x emitted during biomass burning on a surface equal to that by atmospheric deposition into the lake, we reach to a value of 45x10³ tons of N-NO_x/year. In this calculation a total burned area of 4376x10³ km² was used as an average surface of the 2 scenarios reported by Barbosa *et al.* (1999). The amount of 45x10³ tons of N-NO_x/year emitted during biomass burning is of the same magnitude as the 22 x 10³ tons of N/year wet deposition reported by Langenberg *et al.* (2003a). Moreover, according to Barbosa *et al.* (1999), there are two main periods of mass burning in Africa: from November to March (wet season), mainly in the northern hemisphere and from June to October (part of dry season), mainly in the southern hemisphere. So, intense biomass burning around the lake occurs during the dry and wet season and could potentially result in important wet and dry deposition fluxes. Although these rough calculations seem to support the notion that biomass burning is behind the high N deposition rates observed, more research is required. Clearly robust estimates of deposition rates must be based on reliable data. This should be a priority for future research on N-cycling in Lake Tanganyika.

Comparing atmospheric deposition rates to river input rates for the northern Bujumbura basin (Table 4), one can see that on an annual scale, they are of similar importance (2140 kg

N/km²/year for rivers and 1700 to 1920 kg N/km²/year for atmospheric deposition). Considering wet and dry season separately, atmospheric deposition dominates during the wet season, while river and atmospheric inputs are of the same importance during the dry season.

Internal water masses circulation

In addition to river and atmospheric inputs, other hydrodynamical mechanisms may enhance nutrient inputs during wet and dry seasons. As mentioned in the introduction, the region around the lake is characterized by strong and persistent southeast winds during the four months of dry season (May to August). At the end of the dry season and beginning of the wet season, thermocline oscillations occur (Naithani *et al.* 2002), and from time to time small coastal upwelling zones are propagated clockwise around the western boundaries of the lake (internal Kelvin water packets - Naithani and Deleersnijder 2004). These short upwelling events could explain the small nitrite and nitrate peaks (Fig. 4), and lower surface water temperature (Fig. 3) observed in January in lake surface waters.

Nitrogen uptake by organisms in response to DIN pulses

Considering both the range of DIN uptake rates obtained here (0.1 to 19 nM/h) and a photic depth of 20 m, a DIN sink ranging from 0.0005 to 0.125 g N/m²/day can be estimated for the northern Bujumbura basin. In order to evaluate if this range is realistic, it was compared to primary production (Sarvala *et al.* 1999) for a northern basin station close to Bujumbura. This rate varied between 1 and 4.5 g C/m²/day and was converted into nitrogen by using the average Tanganyika phytoplankton C/N molar ratio of 8.8 (Jarvinen *et al.* 1999). The resulting range was 0.1 to 0.6 g N/m²/day. Although values estimated from this study are at the lower end of the range estimated from primary production, they would still seem realistic. Moreover, our specific uptake rate values (obtained by dividing the uptake rates by PN concentration) can be compared to algal growth rate measurements made in the northern part of the lake by Hecky (1991). Indeed, the specific N uptake corresponds to an apparent growth

rate in term of nitrogenous biomass. Hecky (1991) reported an algal growth rate of 0.0042 to 0.079 h⁻¹ for October 1975, so our September and October 1999 specific N-uptake rates (0.013 and 0.0056 h⁻¹ respectively) fall in the range of measurements. In conclusion, although DIN uptakes in this study were measured with a significant increase in substrate concentration, they are in the range of previously reported in situ rates. We will thus assume that rates obtained were representative of in situ rates and we will use them to estimate the uptake of N by phytoplankton at the scale of the northern Bujumbura basin.

Considering a photic depth of 20 m, DIN uptake by phytoplankton corresponds to a median DIN sink in the northern Bujumbura basin of 16000 kg N/km²/year. For the dry season, the median DIN sink is 11850 kg N/km² and for the wet season, 3250 kg N/km². These estimates are 4 times higher than the total external inputs of DIN here. Consequently external DIN inputs represent only 25 % of phytoplankton N requirements, whatever the season considered. Although, this fraction is higher than that of Langenberg *et al.* (2003a) for the whole lake (1 %) as he did not take into account DIN dry deposition. Other important external sources of N include organic N (dissolved and particulate) not quantified in this or previous studies. For example, it has been shown that dissolved organic nitrogen (DON) represents between 60 and 70 % of the total N pool in all aquatic systems except deep-ocean waters (Bronk 2002). DON and particulate organic nitrogen (PON) can also be present in the atmosphere in dust particles or dissolved in aerosols. Estimates have shown that organic N represented 50 % of N wet deposition for tropical Lake Maracaibo (Venezuela) (Morales *et al.* 2001). Clearly, good approximations of the importance of this organic fraction in external N sources are lacking. Moreover, they are sorely needed in order to fully understand the role of external N sources in sustaining primary production, not only in Lake Tanganyika, but other aquatic ecosystems as well. Nevertheless, even when considering the underestimation of external N sources, our

results suggest that internal sources of N are important in sustaining primary production in the surface waters of Lake Tanganyika's northern basin.

CONCLUSIONS

This study demonstrated that riverine (about 1900 tons/year) and atmospheric inputs (literature estimates 1500-1700 tons/year) are important sources of inorganic nitrogen for the northern part of Lake Tanganyika. The majority of DIN inputs occurred during the dry season, when river and atmospheric inputs were highest (90 % of total river input and 65% of total atmospheric inputs). At the same time, DIN uptake by phytoplankton in surface waters (14500 tons/year) exceeded DIN coming from external sources. In fact, external DIN sources only provided ~ 25 % of the annual phytoplankton N requirements. This indicated that other, un-quantified, N sources like organic N in external inputs and N supplied internally were likely important in sustaining primary production in the northern Bujumbura basin of Lake Tanganyika. More information concerning particulate and dissolved organic nitrogen pools, ammonium and nitrate assimilation and regeneration, wet and dry deposition of DIN and organic N and the occurrence of upwelling events will improve our understanding of the N-cycling in the northern part of Lake Tanganyika.

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TABLES

TABLE 1. Minima, maxima and yearly average flows of the Mutimbuzi, Ntakangwa and Rusizi Rivers (from IGEBU).

m ³ /s	Mutimbuzi	Ntakangwa	Rusizi
Minima (dry season)	3.2	1.9	148.4
Maxima (wet season)	6.7	14.4	221.9
Yearly Average	3.0	2.5	182.4

TABLE 2. Ammonium and nitrate uptake rates (*Up*) measured in Lake Tanganyika from December 1998 to October 1999. Underlined rates were measured when nitrate or ammonium were below the detection limit. Dry season extends from April to September.

Date	NH ₄ ⁺ μM	NO ₃ ⁻ μM	Up NH ₄ ⁺ nM/h	Up NO ₃ ⁻ nM/h	Up DIN nM/h
31 Dec 1998	< 0.1	0.40	<u>5.69</u>	-	> 5.69
12 Jan 1999	0.18	< 0.1	13.84	<u>5.51</u>	19.35
23 Feb 1999	< 0.1	< 0.1	<u>0.11</u>	<u>0.99</u>	1.10
29 Mar 1999	< 0.1	< 0.1	<u>0.21</u>	<u>1.25</u>	1.46
27 Apr 1999	< 0.1	0.14	<u>0.06</u>	0.01	0.07
28 May 1999	< 0.1	1.12	<u>1.90</u>	14.55	16.45
14 Jul 1999	< 0.1	< 0.1	<u>6.86</u>	<u>0.51</u>	7.37
09 Sept 1999	< 0.1	< 0.1	<u>6.08</u>	<u>5.85</u>	11.93
28 Oct 1999	< 0.1	< 0.1	<u>2.49</u>	<u>0.16</u>	2.65

TABLE 3. Yearly (A), dry season (B) and wet season (C) averages of river discharge (Q in m^3/s), nitrite, nitrate, ammonium and DIN concentration (C in μM); annual DIN, nitrite, nitrate and ammonium loads (L in tons of N/year).

Period	River	Q	C(NO ₂ ⁻)	C(NO ₃ ⁻)	C(NH ₄ ⁺)	C(DIN)	L(N-NO ₂ ⁻)	L(N-NO ₃ ⁻)	L(N-NH ₄ ⁺)	L(N-DIN)
A-YEAR	Mutimbuzi	3.0	4.8	18	1.1	24	6.4	24	1.4	32
	Ntakangwa	2.5	14	26	44	84	15	28	49	92
	Rusizi	182	3.7	18	0.32	22	300	1480	26	1810
	Total rivers	188					322	1540	76	1930
B-DRY	Mutimbuzi	3.2	9.4	39	0.14	49	6.6	28	0.10	34
	Ntakangwa	1.9	33	60	113	205	14	25	47	86
	Rusizi	148	7.4	44	0.06	51	242	1440	1.9	1680
	Total rivers	153					262	1490	49	1800
C-WET	Mutimbuzi	6.7	2.2	6.0	2.5	11	3.3	8.9	3.6	16
	Ntakangwa	14.4	1.6	4.2	3.0	8.8	5.1	13	9.5	28
	Rusizi	222	1.3	2.0	0.59	3.9	63	99	29	191
	Total rivers	243					71	121	42	234

TABLE 4. Yearly, dry season and wet season averages of DIN fluxes in the Bujumbura basin (900 km²) linked to rivers, atmospheric deposition and median phytoplankton uptake. Wet deposition rates estimated by Langenberg et al. (2003a) and Galy-Lacaux et al. (2003). Dry deposition rates estimated by Galy-Lacaux et al. (2003).

	Year	Wet season	Dry season
	kg N/km ² /year	kg N/km ² /wet season	kg N/km ² /dry season
Rivers	2140	210	1600
Wet deposition	440-680	440-680	-
Dry deposition	1240	-	1240
Phytoplankton uptake	16000	3250	11850

FIGURES

FIG. 1. Lake Tanganyika and its inflows. Black dots represent sampling locations on the Rusizi, Ntampangwa and Mutimbuzi Rivers and in the Lake.

FIG. 2: Typical vertical profile of dissolved inorganic nitrogen and oxygen measured in the northern basin of Lake Tanganyika. Adapted from Hecky et al. (1991).

FIG. 3. Seasonal variation in temperature at the outflow of Mutimbuzi, Ntampangwa and Rusizi Rivers and at a station of Lake Tanganyika. Dry season extends from April to September.

FIG. 4. Seasonal distribution of DIN in Lake Tanganyika (A, B, C) and at the outflow of the Mutimbuzi, Ntampangwa and Rusizi Rivers (D, E, F). Symbols surrounded by squares show periods when uptake rates were determined. Dry season extends from April to September.

Figure 1

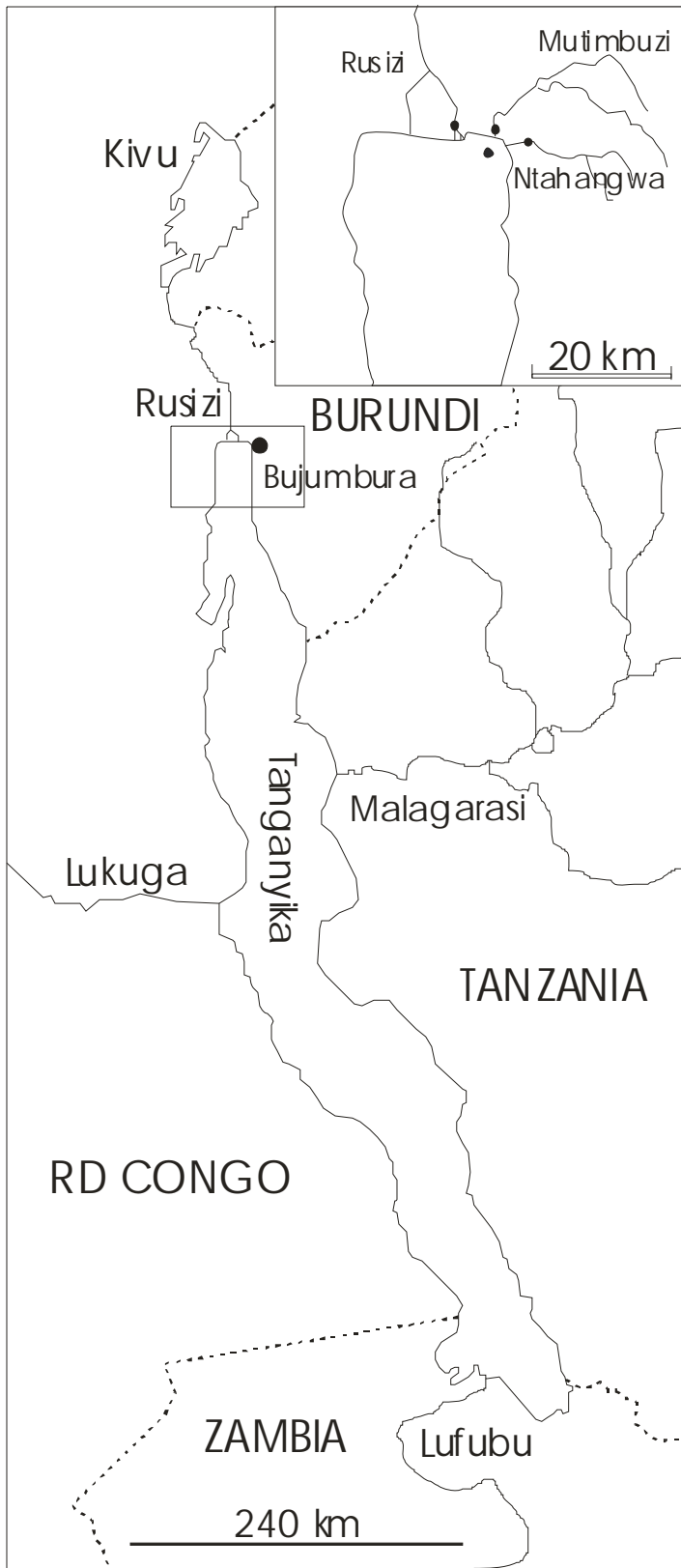


Figure 2

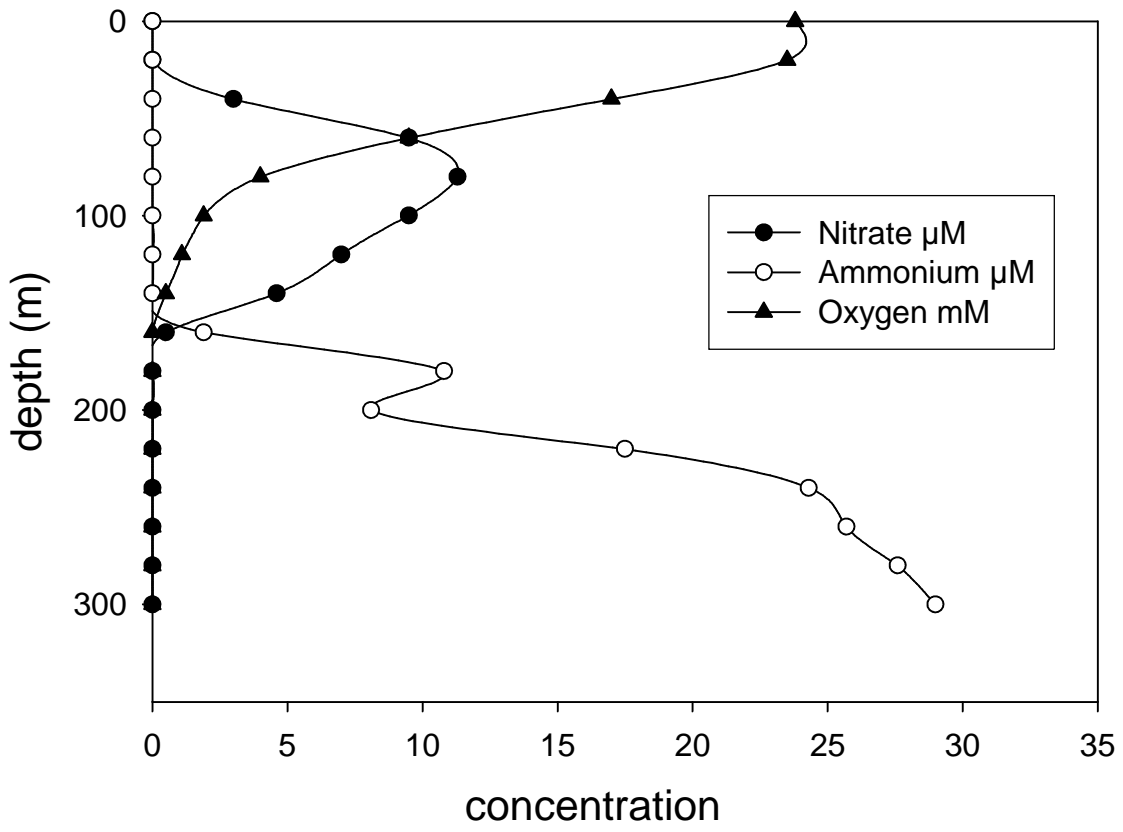


Figure 3

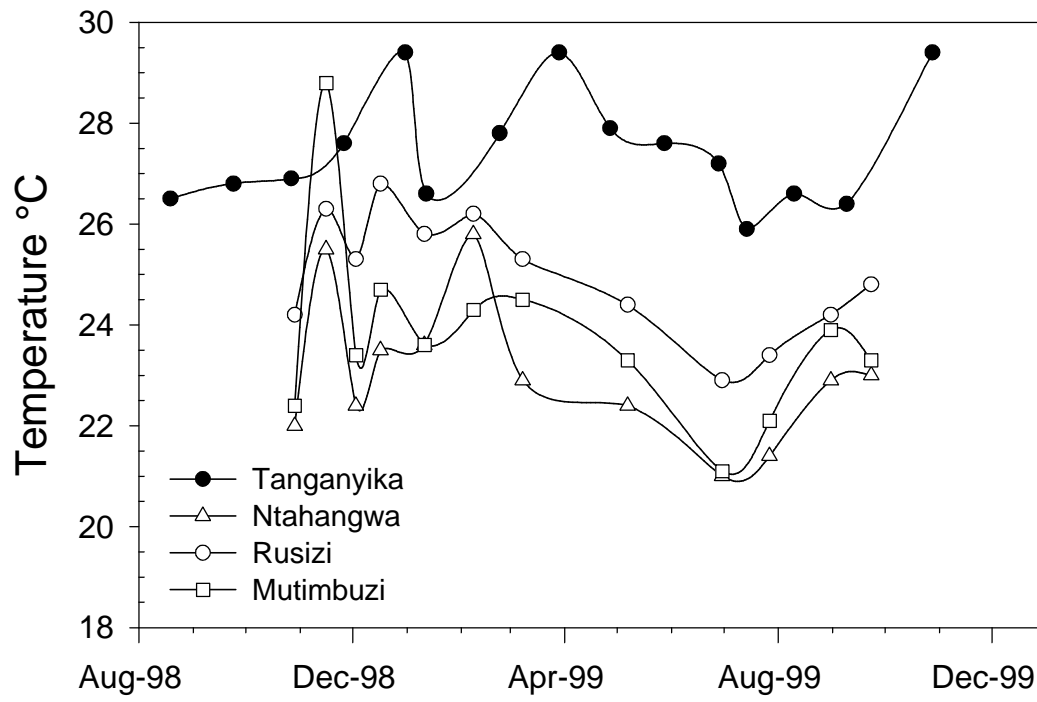


Figure 4

