ADVANCES IN
THE ECOLOGY OF
LAKE KARIBA

Edited by Jacques MOREAU
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CONTRIBUTION OF NITROGEN FIXATION TO THE NITROGEN BUDGET OF LAKE KARIBA

Stanley M. Moyo

INTRODUCTION

Dinitrogen (N₂) constitutes about 80% of the atmosphere and is important for primary production in aquatic and terrestrial systems (Postgate 1978). A wide variety of organisms are able to fix elemental atmospheric nitrogen either in the free-living state or in symbiotic relationships. The reduction of N₂ to ammonia is referred to as biological nitrogen fixation (BNF) and is an energetically expensive reaction catalysed by nitrogenase or dinitrogenase (Postgate 1978, Carr and Whitton 1982). However, nitrogen fixation may provide significant inputs to a large variety of ecosystems (Postgate 1978). BNF is carried out by a wide range of autotrophic and heterotrophic bacteria. Most nitrogen is fixed in aquatic ecosystems where cyanobacteria are the dominant plankton (Howarth et al., 1988). This is so particularly if the cyanobacteria can form heterocysts (Postgate 1978, Stewart et al. 1967). The phytoplankton of Lake Kariba is known to be dominated by heterocystous cyanobacteria in the hot season (Ramberg 1984, Cronberg this vol.) There was sufficient reasons to expect that BNF might be an important process in the lake.

There is very little information about nitrogen fixation in tropical lakes in general and even less in tropical man-made lakes (Thornton 1986, Wetzel 1983). The literature reveals that apart from the processes of nitrification and denitrification there is a dearth of information on nitrogen cycling in African aquatic ecosystems (Thornton 1986). There is no information on the relative contribution of cyanobacterial N₂ fixation to the nitrogen budget of Lake Kariba. Such information can be of vital importance as this input of nitrogen might be one important source of nitrogen. This is particularly important for Lake Kariba as it is located in a basin which is not only highly leached but has inflows that are low in nutrients (Begg 1970, Coche 1974).

The main objectives of the current study were therefore to determine (1) the rates of BNF in the lake (2) the spatial and temporal variations and (3) the importance of BNF to the nitrogen economy of Lake Kariba.

MATERIAL AND METHODS

The study site

The study site was Lake Kariba (Zimbabwe/Zambia) whose characteristics have been thoroughly discussed elsewhere (Coche 1974, introduction in this volume). The stations that were sampled during the study period (1986–1988) are depicted
in Figure 2.1. They have been used for other sampling procedures (see, for instance, Machena this volume, Kautsky this volume).

**Methods of evaluation of BNF**

Rates of BNF were measured by the simple and sensitive acetylene reduction assay that was developed during the 1960s (Stewart *et al.* 1967; Hardy *et al.* 1968). Five millilitres of lake water were pipetted into 15 ml Hungate tubes that were then sealed with butyl-rubber septa and screw caps and kept in dark prior to incubation. To initiate the assay, 2 ml of acetylene, which had been scrubbed through concentrated sulphuric acid and water, were injected into each of the tubes. The incubations were carried out in triplicate with two blank tubes; one without acetylene and the other containing 0.15 ml of Lugol's iodine to kill and preserve the phytoplankton. Incubations were either conducted on-board, in deck incubators (in 1986 and 1987) or under *in situ* conditions (during 1988). Incubations lasted two hours, after which time acetylene reduction was terminated by injecting 0.15 ml of Lugol's iodine. The tubes were then stored upside-down (to minimize ethylene loss) in darkness prior to ethylene analysis. Correction for possible loss of ethylene during storage was operated according to Leonardson (1984). Prior to analysis for ethylene, samples were first equilibrated to room temperature and then shaken for 30–60 seconds. One millilitre of the gas phase was then withdrawn for ethylene measurement using flame ionisation gas chromatography on a Shimadzu 4-CM (PF) gas chromatograph fitted with a stainless-steel column (4 m long by 1/8 inch internal diameter. The column was packed with Porapak T (mesh 80–100 and obtained from Waters Assoc., Inc. Framingham, Mass., USA) and operated at 110°C. The carrier gas used was N₂ at a flow rate of about 60 ml min⁻¹. Chemically pure ethylene standards (Alfax Ab. Malmo, Sweden) at a concentration of 2.1 and 4.2 x 10⁻¹⁰ mol ml⁻¹ were used for calibration. The conversion rate from ethylene reduced to N₂ reduced was the theoretical ones of 3:1 (Peterson and Burris 1976, Stewart *et al.* 1967) since the acetylene reduction assay was not calibrated with the N₁⁵ isotopic measurements in this study.

**Other parameters recorded**

Simultaneously, additional parameters were monitored: carbon dioxide fixation (CDF) (phytoplankton primary production), light penetration (LP), turbidity (TU), alkalinity (ALK), conductivity (CON), concentrations in phosphates (PO₄), ammonia (NH₄), nitrate-nitrite (NO₃N), chlorophyll *a* (CHLA) and phaeopigments. The methods used in order to measure these parameters are given in Moyo (1991).

**Data analysis**

The whole data set was initially split into littoral and pelagic data on the basis of expected differences in the productivity of these two zones and then analysed using multi-variate methods, the rationale of which was to summarize the data set and to determine the relationships between the variables measured. Multi-variate techniques used were principal component, factor analysis and multiple regression analysis (see Moyo 1991 for details). The whole set of data is available on request to the author.
Figure 2.1 Map of Lake Kariba showing sampling locations
RESULTS

Volume based rates of BNF ranged from 0 to 5 μg N l⁻¹ h⁻¹ (Figure 2.2). After integration on a surface area basis, rates of BNF ranged between 0.040 and 0.202 g N m⁻² yr⁻¹ with an average of 0.121 gN m⁻² yr⁻¹.

Values of BNF varied with time (Figure 2.2). BNF was usually highest in the hot season (October–February), although peaks occurred much earlier than this in the more lacustrine basins of the lake. Variations of BNF on the longitudinal axis were noted with rates being higher in the lacustrine basins (Basins 3, 4 and 5) compared with in the riverine basins (Basins 1 and 2).

The values of BNF measured here were used in the construction of a nitrogen budget for Lake Kariba (Table 2.1).

Table 2.1 Nitrogen budget for Lake Kariba (tonnes yr⁻¹)

<table>
<thead>
<tr>
<th>Source</th>
<th>Inputs</th>
<th>Amounts</th>
<th>Source</th>
<th>Outputs</th>
<th>Amounts</th>
</tr>
</thead>
<tbody>
<tr>
<td>Surface inflow</td>
<td></td>
<td></td>
<td>Outflow</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Zambezi</td>
<td></td>
<td>1199a</td>
<td>Zambezi</td>
<td></td>
<td>793.1e</td>
</tr>
<tr>
<td>Other rivers</td>
<td></td>
<td>147b</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>BNF</td>
<td></td>
<td>630c</td>
<td>Fish harvesting</td>
<td></td>
<td>830.1f</td>
</tr>
<tr>
<td>Rainfall</td>
<td></td>
<td>100d</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>2,026</td>
<td>Total</td>
<td></td>
<td>1,623.2</td>
</tr>
</tbody>
</table>

Notes:
(a) Value calculated on the assumption that the concentration of the Zambezi River is 40.54 μg l⁻¹ and the flow is 29.58 km³ yr⁻¹ (Coche 1974)
(b) Value calculated on the basis of the value of Nitrogen concentration of 50 μg l⁻¹ for secondary rivers in the Zambezi basin (Davies 1986). The inflow of these river (2.925 km³ yr⁻¹) was computed from data provided by the Zambezi River Authority and by the Meteorological Office of Zimbabwe.
(c) Value based on results of current study (0.121 g m⁻² yr⁻¹) for the whole surface of the lake during the study: 5 000 km²
(d) Value calculated on basis of rainfall measurements at Kariba and Binga (Meteorological Office, Harare) with a content of 17.4 μgN l⁻¹ (Caulton unpublished)
(e) Data from Magadza et al. (1986) where nitrogen in the outflow is given as 26.8 μg l⁻¹ and the flow is 29.58 km³ yr⁻¹
(f) Calculated from assumption that
   (i) Kapenta catches are 29615 t (Lupikisha, 1992) and inshore catches are 3590 t for the whole lake (Sanyanga et al. 1990, Scholtz and Mweetwa 1990)
   (ii) 2.5% of the wet weight of kapenta is nitrogen (Chemistry and Soil Research Institute Laboratory Report No 1489/GF, June 1980). This value has been used for every fish species.

From this budget, it appears that BNF contributed about 32% of the total annual nitrogen inputs into Lake Kariba during the study period.

Factor analysis of biological nitrogen fixation and other limnological parameters measured produced the factor diagram shown on Figure 2.3.
Figure 2.2 Variation of BNF (ordinate: unit $\mu g \, l^{-1} \, h^{-1}$) with time in each basin.
Three clearly distinct clusters of variables are evident when the first two components were plotted. The analysis showed that the group comprising pH, alkalinity and conductivity was inversely related to that of BNF, phytoplankton primary production and turbidity.

The equations obtained when the data set was subjected to multiple regression analysis are given below. They show the relationships between BNF and various limnological parameters:

\[
\text{BNF} = 12.79 - 0.51 \text{LP} + 0.002 \text{PO}_4 - 0.97 \text{pH} - 0.02 \text{NH}_4 + 0.020 \text{COND} - 0.01 \text{TU} - 4.61 \text{ALK} \quad (R^2 = 0.371)
\]

\[
\log \text{BNF} = 13.79 - 0.47 \log \text{TU} + 0.32 \log \text{pH} - 0.11 \log \text{CHLA} - 5.90 \log \text{ALK} - 0.073 \log \text{PO}_4 - 0.33 \log \text{NH}_4 - 0.34 \log \text{LP} - 1.49 \log \text{COND} \quad (R^2 = 0.88)
\]

\[
\log \text{BNF} = 11.84 - 4.13 \log \text{ALK} - 1.97 \log \text{COND} \quad (R^2 = 0.79)
\]

It should be noticed that there was no inverse correlation between BNF and ammonia N or nitrate-nitrite N. However, alkalinity, conductivity, light penetration and pH are potentially the most useful predictors of the BNF in Lake Kariba.

The temporal variation noted for BNF correlates well with the abundance of *Cylindrospermopsis raciborski*, a heterocystous cyanobacterium, as quoted by
Ramberg (1984 and 1987). The latter noted an increased cyanobacterial biomass in the hot dry and hot wet season (between October and April) whereas the lake experiences high temperatures, stratification and nutrient inflow. These parameters are possibly the major determinants of cyanobacterial biomass increase.

The basin-related spatial variations observed in BNF levels may be a result of the differential riverine influence on the sampling stations. Stations in riverine basins 1 and 2 are markedly affected by the Zambezi River which, although low in nutrients, exerts itself lumetrically. The lacustrine basins 3 and 4 have no major riverine inputs, whereas lacustrine basin 5 (Sanyati basin) is under the influence of the nutrient rich Sanyati River which drains agricultural lands.

**DISCUSSION**

The rates of BNF found in Lake Kariba (0–5 μg N l⁻¹ h⁻¹) are comparable to those from other lakes and the oceans (Goering, Dugdale and Menzel 1966, Horne and Goldman 1972). Aerial cyanobacterial nitrogen fixation rates in Lake Kariba ranged from 0.04 to 0.202 g N m⁻² yr⁻¹, values which lie at the lower end of the range (0.9 to 9.2 g N m⁻² yr⁻¹) given by Howarth et al. (1988).

The contribution of BNF to the total annual nitrogen inputs in Lake Kariba is higher than those given for a few aquatic ecosystems (e.g. Carr and Whitton 1982, Horne and Fogg 1970, Horne and Viner 1971, Leonardson 1984, Toetz 1983). The contribution of BNF by cyanobacteria to the nitrogen budget in Lake Hefner was 1.5% (McFarland and Toetz 1988). In the Western Sargasso, *Oscillatoria (Trichodesmium) thiebauti*, a non-heterocystous cyanobacteria made an insignificant input of nitrogen (Carpenter and McCarthy 1975).

On the opposite, BNF has been shown to be a quantitatively important source of nitrogen for the nitrogen budgets of a number of lakes. This process contributed up to 80% of the annual nitrogen supply to Lake Erken, Sweden (Granhall and Lundgren 1971), and 43% in Clear Lake, California (Horne and Goldman 1972). In eutrophic Rietvlei dam, South Africa, the process contributed between 1.4 and 46.5% of the total nitrogen (Ashton 1981). In oligotrophic Skaha Lake, Canada, a cyanophyte bloom contributed up to 60% of the annual nitrogen income into the lake (Findley et al. 1973). In Pyramid lake, nitrogen fixed by a short-lived bloom of *Nodularia* sp. constituted 99.5% of the alga's needs and 81% of the nitrogen input (Horne and Galat 1985). The value reported for Lake Kariba is as high as the 33% attributed to this process in Lake George, Uganda (Horne and Viner 1971). Possible reasons for the similarity of the two figures could be investigated: Cyanobacteria are abundant in the two lakes which are both mesotrophic or even eutrophic.

Factors influencing BNF were investigated for instance by Horne and Fogg (1970) who concluded that although nitrogen fixation was confined to periods of low nitrate N, there was no significant negative correlation noted. Horne and Goldman (1972), in their multiple regression equation, found that fluctuations in NBF were best explained by variations in heterocysts, cyanobacterial biomass, orthophosphates levels, nitrate levels and temperature. In Lake Kariba, a model incorporating alkalinity and conductivity may be of significant predictive value for BNF.
BNF showed spatial variation along the longitudinal axis of Lake Kariba. This observation is similar to that made for BNF and heterocyst frequency in Lake Valencia (Levine and Lewis 1985). Spatial variations of several other variables have been reported in Lake Kariba. For example, Coche (1974), Moyo (1991) and Lindmark (this volume) noted variations of several physico-chemical variables along the longitudinal axis of the lake. Magadza (1980) also found that riverine influences affected the distribution of plankton in the Sanyati basin.

CONCLUSION

The present study aimed at quantifying the level of BNF in Lake Kariba and finding out how this process was related to biological physical and chemical parameters in the lake. Such knowledge can be of useful modelling and predictive value, particularly when attempting to approach the transfers of nutrients and biomass inside the whole ecosystem.

SUMMARY

There is no information on the relative contribution of cyanobacterial N\textsubscript{2} fixation to the nitrogen budget of Lake Kariba. The main objectives of the current study were therefore to determine (1) the rates of BNF in the lake (2) the spatial and temporal variations and (3) the importance of BNF to the nitrogen economy of Lake Kariba.

Volume-based rates of BNF ranged from 0 to 5 mg N l\textsuperscript{-1} h\textsuperscript{-1}. After integration on a surface area basis, rates of BNF ranged between 0.040 and 0.202 g N m\textsuperscript{-2} yr\textsuperscript{-1} with an average of 0.121 gN m\textsuperscript{-2} yr\textsuperscript{-1}.

Values of BNF varied with time. BNF was usually highest in the hot season (October-February), although peaks occurred much earlier than this in the more lacustrine basins of the lake. Variations of BNF on the longitudinal axis were noted with rates being higher in the lacustrine basins (Basins 3, 4 and 5) compared with in the riverine basins (Basins 1 and 2).

The values of BNF measured here were used in the construction of a nitrogen budget for Lake Kariba which shows that BNF contributed about 32% of the total annual nitrogen inputs into Lake Kariba during the study period. A factor analysis was also performed which helped to establish that alkalinity, conductivity, light penetration and pH are potentially the most useful predictors of the BNF. Lake Kariba is compared with other water bodies for BNF contribution to the nitrogen budget of the lake.
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