Acta Limnol. Brasil.	Vol. III	1-48	1990

COMPARATIVE LIMNOLOGY OF TROPICAL FLOODPLAIN LAKES WITH AN EMPHASIS ON THE CENTRAL AMAZON

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RESUMO -

O presente estudo traz os resultados obtidos em investigações das características biogeoquímicas de um lago de várzea tropical (Lago Calado - Amazonas, Brasil). Observou-se que ocorre estratificação térmica e de oxigênio dissolvido quando a profundidade excede 5 m e deslocamentos verticais da oxiclina de 1 a 2 m a cada 3 a 5 dias. Chuvas locais e água de escoamento superficial contribuem com a maior parte do nitrogênio, enquanto a água do Rio Amazonas provê a maior parte do fósforo para o lago. Quando o lagoestá termicamente estratificado, as concentrações de nutrientes são baixas na zona eufótica e são mais elevadas no hipolímnio anóxico. Durante o período de águas baixas, na área de inundação, a água de escoamento local e a ressuspensão do sedimento promovem aumento na concentração de nutrientes, além de elevar a turbidez da água. Clorofila a e fotossíntese planctônica não ocorrem, respectivamente, em concentrações e taxas elevadas, sendo muitas vezes menos representativas do que o metabolismo heterotrófico,

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indicando entrada de matéria orgânica alóctone. Experimentos de fertilização indicam que o fósforo é limitante para o fitoplâncton durante os períodos de enchente e de cheia, enquanto o nitrogênio é limitante durante os períodos de vazante e estiagem. Medidas de absorção de amônia e nitrato (N^{15}) indicam que as concentrações de amônio e nitrato regulam a taxa de absorção no ambiente, e que a luz tem importância secundária. A rápida absorção de ^{32}P por organismos menores de 3 µm indica que o "pool" de fósforo disponível é pequeno, e que o nutriente cicla rapidamente. Medidas diretas da taxa de produção de amônio e fosfato e da taxa de liberação na interface sedimento-água revelam que há retorno de 80% do amônio e de 95% do fosfato para a coluna d'água, devido à atividade de organismos menores que 50 µm que ocorrem no epilímnio.

abstract - COMPARATIVE LIMNOLOGY OF TROPICAL FLOODPLAIN LAKES WITH AN EMPHASIS ON THE CENTRAL AMAZON

Floodplains are important to the biogeochemistry and ecology of fluvial systems. Major floodplains occur throughout the tropics where they cover at maximum inundation about 900,000 km^2, or about half the area of tropical wetlands. Limited information is available about the limnology of floodplains with the exception of the central Amazon, Brazil.

As an example of a comprehensive, long-term biogeochemical investigation of a tropical floodplain lake, the results from Lake Calado (Amazonas, Brazil) are described. L. Calado (3°15' S, 60°34'W), a moderate-sized dendritic lake, varies in area from 2-8 km^2 and in depth from 1-12 m depending on the stage of the Amazon River. Vertical profiles of temperature and dissolved oxygen obtained daily at ca 0630 for 510 days and over 100 diel cycles indicate persistent stratification when depths exceed 5 m and vertical displacements of the oxycline of 1-2 m every 3-5 days. Local rain and runoff supply the majority of nitrogen, while inflows from the Amazon River provide the majority of phosphorus to the lake. When the lake is thermally stratified, nutrient concentrations are very low in the euphotic zone and elevated in the anoxic hypolimnion. During periods of low water, riverine inundation, local runoff and sediment resuspension result in increased nutrient concentrations and high turbidity.

Chlorophyll a is moderate (1-10 μg L^{-1}). Planktonic photosynthesis is also moderate and usually less than overall heterotrophic metabolism on a daily basis which indicates inputs of organic matter to the open water. Experimental fertilization of plankton indicates phosphorus limitation during rising and high water levels.and a shift to nitrogen limitation during falling and low water levels. Measurements of uptake of ammonium and nitrate with ^{15}N indicate that ammonium and nitrate concentrations regulate the uptake rates at ambient concentrations and that light is of secondary importance. Rapid uptake of ^{32}P by organisms less than 3 μm in size indicates a small ambient phosphate pool is turning over very quickly. Direct measurements of the rate of ammonium and phosphate production in the water column and via exchange across the sediment-water interface reveal that 80% of the ammonium regeneration and 95% of the phosphate regeneration is provided by organisms in the epilimnion less than 50 μm in size.

INTRODUCTION

Floodplains are important to the biogeochemistry and ecology of fluvial systems. Interactions between rivers and their floodplains require modification or elaboration of concepts such as those of the river continuum (VANNOTE et alii, 1980) and nutrient spiralling (NEWBOLD et alii, 1982; ELWOOD et alii, 1983). Recent attempts to model the carbon biogeochemistry of large tropical rivers (e.g. RICHEY et alii, 1985) have shown that the fluxes between the floodplain and river are likely to be significant. Watersheds with wetlands export more organic carbon per unit area than drainages without wetlands (SCHLESINGER & MELACK, 1981), and destruction of existing wetlands contributes significant amounts of stored carbon to the atmosphere (CRUZ, 1986). In the Amazon, aquatic grasses grown on the floodplain contribute ca. 5% to the total organic matter transported downstream (HEDGES et alii, 1986) but occupy only ca. 0.5% of the basin. The mosaic of flooded forest, lakes, and especially floating macrophytes in the central Amazon floodplain make a significant contribution to tropospheric methane (CRILL et alii, 1988; BARTLETT et alii, 1988; DEVOL et alii, 1988). The fishery potential of large rivers is closely tied to the area of floodplain and the magnitude and duration of inundation (WELCOMME, 1979; LESACK, 1986). The majority of fishes harvested in the Amazon basin obtain nutrition in flooded forests (GOULDING, 1980) or from organic matter derived from floodplain phytoplankton (ARAUJO-LIMA et alii, 1986).

Riverine floodplains are a fertile environment as a consequence of nutrient-rich floodwaters. Recent investigations (e.g. FISHER & PARSLEY, 1979; HAMILTON & LEWIS, 1987; FORSBERG et alii, 1988) have emphasized the fertilizing role of the flood. However, as early as 1931, SVENSSON (1933) recognized that the productive floodplain swamps of the Gambia River (West Africa), could form e either from accumulation of local runoff, from backflooding from the river, or from a combination of the two mechanisms. However, it is seldom studied how the types of waters interact, and how biogeochemical processes operating within the floodplains contribute to the fertility.

The seasonal range and variability of phytoplankton productivity is now known for a wide variety of tropical lakes. With these data MELACK (1979) demonstrated the lack of a latitudinal trend in temporal variability within the tropics and proposed that three patterns of temporal change in abundance and photosynthetic rates occur. The only tropical floodplain lake include in Melack's analysis (Castanho - SCHMIDT, 1973a) had intermediate variability and regular seasonality in association with the changes in river level. However, the variability of several Indian reservoirs and a riverine bay (Ponta Negra Bay, Rio Negro - SCHMIDT, 1976) rank among the highest for tropical waters. This high variability may indicate the influence of rapid but irregular flushing possible in some riverine lakes.

In recent years measurements of primary production of phytoplankton have acquired utility for fishery management because of the demonstration of a good correlation between fish yields and gross primary production (MELACK, 1976). The successful demonstration of this correlation for tropical lakes as divergent as Lakes Tanganyika (HECKY et alii, 1981), Bangweulu (TOEWS & GRIFFITH, 1979) and Volta (MELACK, 1976) and to ponds on the Yangtze River floodplain (LIANG et alii, 1981) raises the promise of its application to tropical floodplain lakes (but see BAYLEY, 1981).

In contrast to the considerable information on phytoplankton productivity in tropical waters, the productivity of aquatic macrophytes and periphyton is difficult to evaluate. For example, the floating meadows characteristic of the Amazon floodplain cover immense areas, but fragments of the meadows leave the lakes and pass downriver. The largest portions appear to be stranded and to decay on shore as the water levels decline. Recent estimates of net productivity of *Echinochloa polystacha* (8 metric tons dry matter ha^{-1} y^{-1}) and *Paspalum repens* (3-5 metric tons dry matter ha^{-1} y^{-1}) by JUNK and his students (personal communication) are similar to those for other tropical macrophytes (DENNY, 1985; HOWARD-WILLIAMS & GAUDET, 1985) and exceed most temperate macrophytes (MITSCH & GOSSELINK, 1986). No data are available to evaluate the importance of periphyton productivity; current research in the Amazon by Fisher, Melack and their associates will provide relevant information.

Whereas equatorial regions are characterized by equitable temperatures and insolation, marked seasonal variations in rainfall, runoff and river discharge can occur. Associated with the wet and dry seasons can be differences in the stability of thermal stratification and vertical mixing (e.g., TALLING, 1969; LEWIS, 1973; SCHMIDT, 1973b; MacINTYRE & MELACK, 1988). Nutrient pulses resulting from variations in inflows and in exchanges between tropholytic and trophogenic regions of the lake may well be a major cause of the seasonal variability in plankton productivity. At times of deep mixing or when inflows or sediment resuspension increase turbidity, light supply may take precedence as a constraint on photosynthetic rates. Grazing by zooplankton is another possible control of phytoplankton abundance, but is yet to be demonstrated as significant in tropical lakes. In fact, evidence from Lake George, Uganda (BURGIS et alii, 1973) and Lake Lanao, Philippines (LEWIS, 1978) indicates the lack of a major impact by zooplankton.

In tropical floodplains, the role of nutrient supply in the control of primary productivity has seldom been evaluated. Whereas the nutrient deposition by rain is available for several locations, comparable data for riverine inputs are lacking with one exception (LESACK, 1988). Nitrogen fixation has been measured in only one tropical floodplain lake (MELACK & FISHER, 1988). Permanent sedimentation, denitrification and outflow are the major routes of nutrient loss from lakes, and major recycling processes are excretion by heterotrophic plankton, sediment-water exchanges and turbulent mixing. Few measurements are available for any of these processes in tropical waters (see below).

The purpose of this paper is to review limnological and biogeochemical aspects of tropical floodplain lakes. First, the areal extent and distribution of tropical floodplains will be summarized. Lakes are one important habitat in these complex wetlands, and a compilation of studies concerned with lacustrine environments is provided. As an example of a comprehensive, long-term biogeochemical investigation of a tropical floodplain lake, our research at L. Calado (Amazonas, Brazil) will be the focus of the majority of the paper.

Geographical and limnological aspects of tropical floodplains

Major floodplains occur throughout the tropics where they cover hundreds of thousands of square kilometers (Tab. 1). The estimates of the maximum and minimum area inundated on these floodplains range from a few careful measurements to many rough guesses. WELCOMME (1985) has done a valuable service by compiling data from dispersed, largely unavailable sources; these data are, however, difficult to evaluate.

Maps such as the World Aeronautical Charts demark areas as seasonally inundated. However, it is nearly impossible to use these designations to distinguish riverine floodplains from areas with standing water accumulated from upland runoff or local rain. For example, the large value (70,000 km^2) assigned to the confluence of the Orinoco, Meta and Apure by WELCOMME (1985) results from the lack of such discrimination. A similar uncertainty applies to the values for the floodable savannas in the upper Madeira R. basin, Bananal and Roraima and Rupununi

Table 1 - Geographic features of tropical floodplains and limnological characteristics of floodplain lakes. Coastal deltas are excluded; list is not exhaustive and does not include many floodplains bordering small to moderate rivers. Geographic information is derived from WELCOMME (1985) and references cited therein unless noted otherwise [HOWARD-WILLIAMS & THOMPSON, 1985 (1), BALEK, 1977 (2), HAMILTON, unpubl- (3), LEWIS, 1988 (4), JUNK, in press (5), MELACK & SIPPEL, unpubl. (6), SALO et alii, 1986 (7)]. Some rounding was performed. Key primary publications and reviews are cited for limnological aspects: WELCOMME, 1985 (W); SERRUYA & POLLINGHER, 1983 (S&P); JOHN, 1986 (J); BEADLE, 1981 (B).

REGION River (Countries)	Area Inundated (approximate km²) Maximum	Minimum	Limnological Studies
AFRICA			
Senegal R.			W,J; Cogels & Gac 1982
(Senegal and Mauritania)	5500	500	Dia & Reynaud 1982
Niger			W, J, S&P,B;
(Mali)	20000-30000	4000	Dumont et alii, 1981
(Niger)	900	300	
(Benin)	300	30	
(Nigeria)	4800	1800	
Benue R.			
(Nigeria)	3100	1300	
Volta R.			
(Ghana)	8500	1000	
Oti-Pendjari R.[1]			
(Burkina Faso and Benin)	5000	?	
Nyong R.[1,2]			
(Cameroon)	7000	?	
Chari R. and Logone R. system			W,J
Yaeres			B
(Cameroon, Chad)	7000	500	
Bahr Aouk and Bahr Salamat			
(Chad, Central African Republic)	37000	3500	
Chari R. and Bahr Erguig			
(Chad)	26000	2000	

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... cont. Tab. 1

Zaire R. system			W
Concluence of Zaire R.			
Oubangui R. and Sangha R.[2]			B, S&P, DUBOIS 1959,
(Congo and Zaire)	40000	?	MARLIER 1958
Lualaba R. (Zaire)			
Kamulondo depression	12000	7000	S&P; MEEL 1953
Laupula R.			
(Zaire, Zambia)			
Kifakula depression	2000	200	
Malagarasi R.[2]			
(Tanzania)	7000	?	
Cunene			
(Angola)	10000?	>500?	
Okavango R.			B
(Botswana)	16000-20000	3000	
Zambezi R. system			B,W
Barotse plains			
(Zambia)	11000	500	
Kafue R.			
(Zambia)	4300	1500	
Zambezi R. system			
Shire R.			
(Malawi)	1400	500	
Rufiji R. and Rusha R. system			
(Tanzania)	12500	>1000?	
Kagera R.			
(Tanzania)	500	?	
Nile R. system			W, S&P; RZOSKA 1974,
(Sudan)	32000-	16000	1976, TALLING 1957
NORTH AMERICA			
Grijalva R. and Usumacinta R.			
(Mexico)	8000	?	
SOUTH AMERICA			
Atrato R.			
(Colombia)	5300	?	
Magdalena R.			
(Colombia)	20000	3300	S&P, W
Catatumba R.			
(Venezuela)	5000	?	

cont...

... cont. Tab. 1

Orinoco R. system			
Confluence of Orinoco, Meta, Arauca, Apure, Capanaparo[3] (Colombia, Venezuela)	10000-20000	500	HAMILTON & LEWIS 1987
Central Orinoco[4] (Venezuela)	7000	500	
Rupununi R. (Guyana)	6500	?	
Amazon R. system			
Amazon and major tributaries: Tapajos, Xingu, Madeira, Purus, Jurua, Japara and Negro (Brazil and Peru)[5]	300,000	?	
Central basin, main stem Amazon (Brazil)[6]	110,000	?	
Upper lowland basin (Peru)[7]	60,000	?	
Upper Madeira basin, Madre de Dios, Beni, Mamore and Guapore rivers (Bolivia)[5]	10,000	?	
Upper Branco R. Roraima (Brazil)[5]	1000	?	
Tocantins R. system			
Upper Araguaia R., Bananal (Brazil)[5]	10,000	?	
Paraguay R. system			
Gran Pantanal (Brazil and Bolivia)	80,000-100000?	?	TUNDISI & MATSUMURA TUNDISI 1985, SAIJO et alii 1987
Parana R. system			
R. Mogi-Guaçu (Brazil)	?	?	ESTEVES 1988
ASIA			
Krishna R., Godavari R. and Cauvery R. (India)	reduced and modified by dams	?	

cont...

... cont. Tab. 1

Mahawel R. (Sri Lanka)	reduced and modified by dams	?	
Ganges R. system (India, Bangladesh)	mostly deltaic mangroves, tropical freshwater portion?		
Irawaddy R. (Burma)	31000	?	
Chao Phyraya R. (Thailand)	?		
Mekong R. (Laos, Kampuchea, Vietnam)	74000? (modified and reduced by dams and canals)	4000	W, S&P
FAR EASTERN ISLANDS			
Hari, Kampar, Rokan, and Musi Rivers (examples) (Indonesia (Sumatra))	moderate?	?	
Kapuas, Barito and Mahakam (or Kutai) Rivers (examples) (Indonesia (Kalimantan))	14000 (plus Barito?)	?	
Digul R. (Indonesia (West Irian))	small?	?	
Fly R. (Papua New Guinea)	small?	?	
Sepik R. (Papua New Guinea)	7500	?	ROOM and THOMES 1985
Mindanao, Agusan, Tarlac and Cagayan Rivers (examples) (Philippines)	small?	?	
AUSTRALIA			
Alligator, Daly and Roper Rivers (examples) (Northern Territory)	small?	?	WALKER & TYLER 1984, HART et alii 1987, Office of the Supervising Scientist 1987

districts.

A few detailed, local or regional surveys have been conducted as a result of economic interests. The Magela Creek is the focus of a major study because it is downstream from a large uranium mine in Northern Australia (Office of the Supervising Scientist 1987); a digital elevation map with a 0.5 m vertical resolution has been made for this small floodplain. The Sudd in southern Sudan is the site of a diversion project, the Jonglei Canal, and regional surveys are therefore available (HURST & PHILLIPS, 1931; MEFIT-BABTIE, 1983).

Remote sensing holds the greatest promise for quantitative evaluation of floodplain extent. The recent mapping of the Brazilian Amazon basin with aircraft-borne, side-looking, synthetic aperture radar (SLAR) has provided improved estimates of the Amazon floodplain (e.g. NASCIMENTO et alii, 1976). Although compromised by cloudcover, imagery produced by the Landsat multispectral scanner or thematic mapper can be used to help delimit floodplains (e.g. SALO et alii, 1986; HAMILTON, personal communication; MELACK, unpublished). A promising technique to detect inundated areas is synthetic aperture radar (SAR) systems mounted on satellites. Preliminary examination of the Amazon with Space Shuttle-borne SAR is encouraging (MELACK, unpublished). Other techniques with potential for recognizing flooded lands are thermal inertia mapping (e.g. ROSEMA & FISELIER, 1988) and passive microwave mapping (CHOUDHURY, personal communication). The major advantages offered by satellite-based remote sensing of floodplain extent is that repeat coverage is possible which permits mapping of seasonal and annual variations in inundation.

With due regard to the uncertainties of the estimates of floodplain extent, if the maximum areas inundated are summed, approximately 900,000 km^2 of tropical floodplain are obtained from the data in Tab. 1. Previous estimates of the global area covered by wetlands range from

2 million km² (WHITTAKER, 1974) to 5.3 million km² (MATTHEWS & FUNG, 1987). The tabulation of wetland extent by 10° latitude bands in MATTHEWS & FUNG (1987) permits an approximate calculation of tropical wetland area, i.e. 1.6 million km². Hence, tropical floodplains may represent about half the area of tropical wetlands.

Tab. 1 includes a compilation of published data on tropical floodplain lakes. The purpose is to indicate the availability of information about key hydrological, physical, chemical and biological features. While not exhaustive, an attempt to be comprehensive and representative was made. With the exception of the Amazon, there is a paucity of data. In general, if any information is available, it is limited to the lakes' size and depth, a few measurements of chemical composition and of dissolved oxygen and temperature profiles and species lists, especially of fish. The literature is widely scattered and much is difficult to obtain, hence the efforts of reviewers with access to local sources is valuable (e.g. WELCOMME, 1985; JOHN, 1986).

Amazon floodplain lakes

The Amazon and its floodplain is the world's largest river system, draining 37% of South America and discharging about 20% of the freshwater reaching the world's oceans (SIOLI, 1975; 1984). Bordering the middle reach of the river is a ca. 110,000 km² floodplain--a freshwater habitat with exceptional biological diversity and increasing economic importance. The ca. 8000 lakes in the central Amazon basin (MELACK, 1984) are a freshwater resource comparable to the myriad of lakes formed by continental glaciers at higher latitude.

The dominant seasonal pattern in the central Amazon basin is a ten meter rise and fall of river level. As the waters rise, a mosaic of flooded forests, floating grasses, and open water forms on the floodplain which functions as a capacitor and reaction vessel for the energy and nutrient fluxes that sustain its fertility (FISHER & PARSLEY, 1979; JUNK, 1980). Much more information about floodplain lakes is needed before the dynamics of the Amazon basin and other tropical river systems will be understood (RICHEY, 1983) and before a definitive global analysis of productivity and factors affecting it can be made (SCHINDLER, 1978). Studies of the Amazon floodplain, such as those summarized here, expand the insights and generality of freshwater ecology and will be valuable in planning the rational use of this important resource.

The goal of our current research is to understand the processes that influence the input, recycling, and loss of nitrogen and phosphorus in Amazon floodplain lakes. Examination of these processes requires experiments and measurements spanning several years because of the considerable spatial and temporal variability in the central Amazon. Therefore, we selected one floodplain lake (L. Calado) for intensive study and three neighboring lakes for less intensive sampling: L. Paru (immediately east of Calado), L. Miriti (immediately west of Calado), and L. Janauaca (Fig. 1). We emphasize the importance of long-term, multi-station data to adequately understand the dynamics of floodplains. Significant ecological variability occurs over a spectrum of times, and we have investigated processes on scales of minutes, hours, days, weeks, months, and years in L. Calado.

Our primary study site, Lake Calado (3°15' S, 60°34' W), is located on the north side of the Solimões River 80 km upriver from the Negro River. Depending on the stage of the river, the lake is about 2-8 km^2 in area and 1-12 m in depth (Fig. 2). A detailed bathymetric map has been constructed from aerial photographs, local soundings, and surveying, and can be used to convert lake levels to volumetric changes (LESACK, 1988).

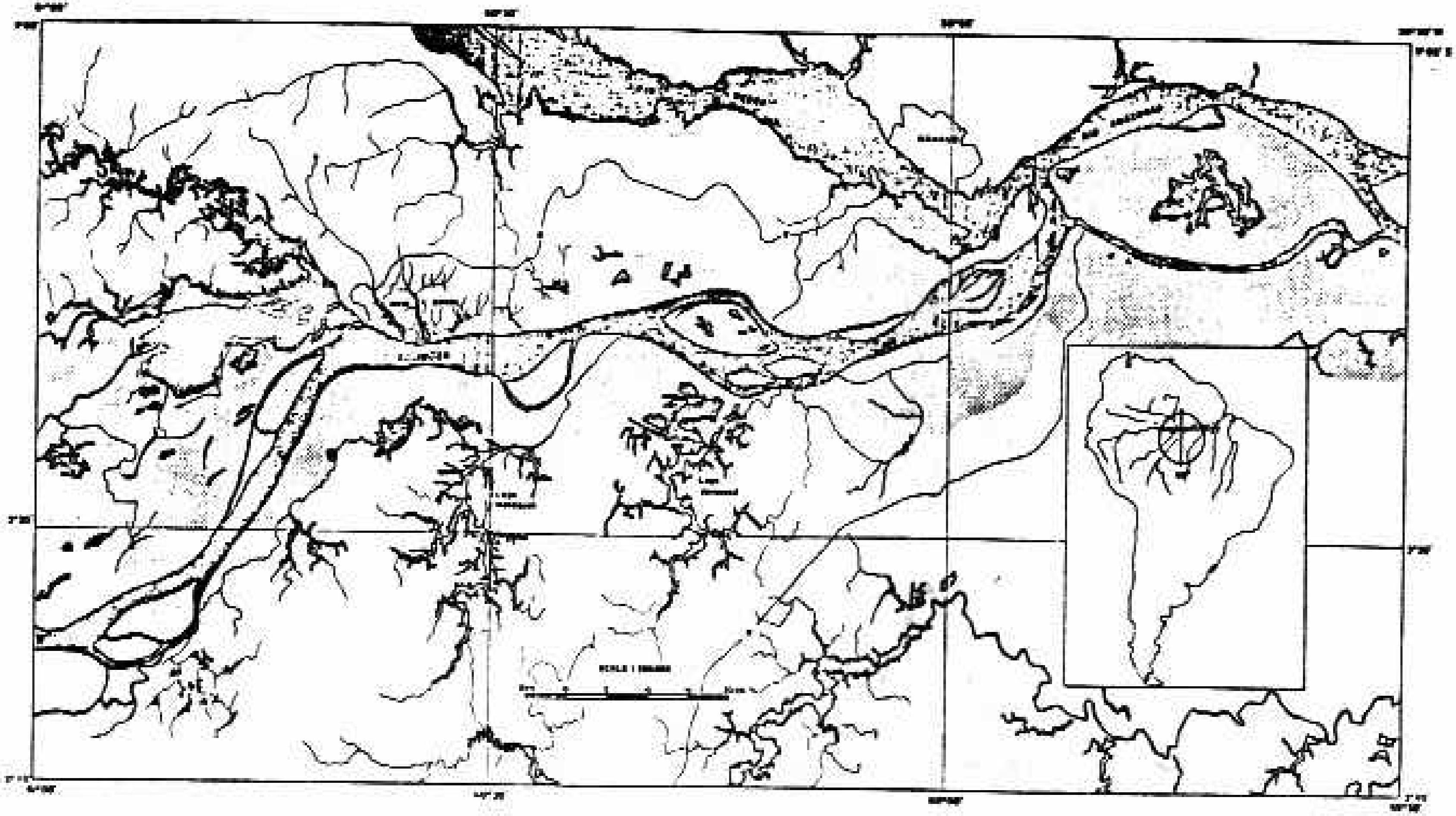
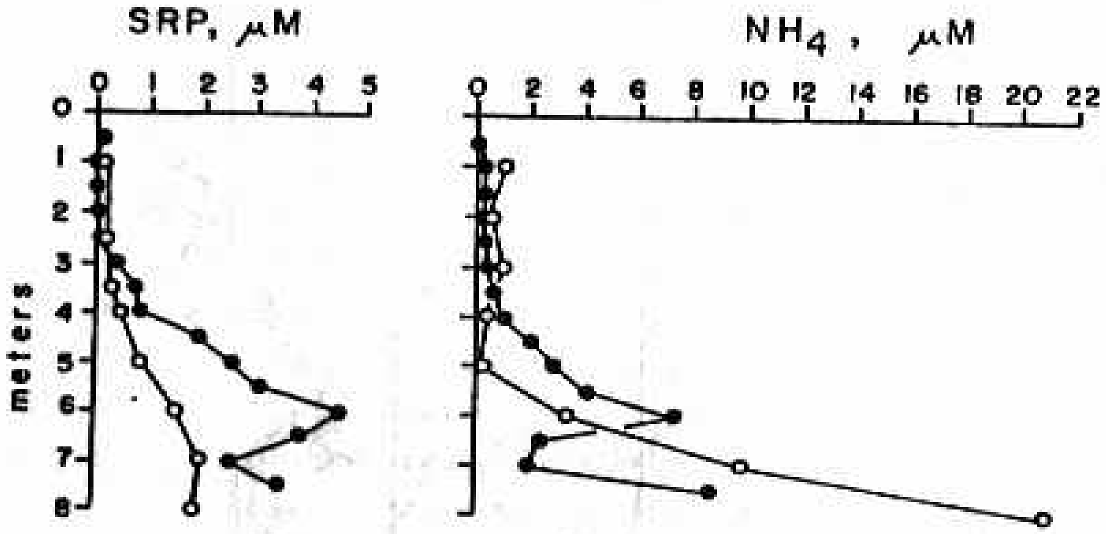
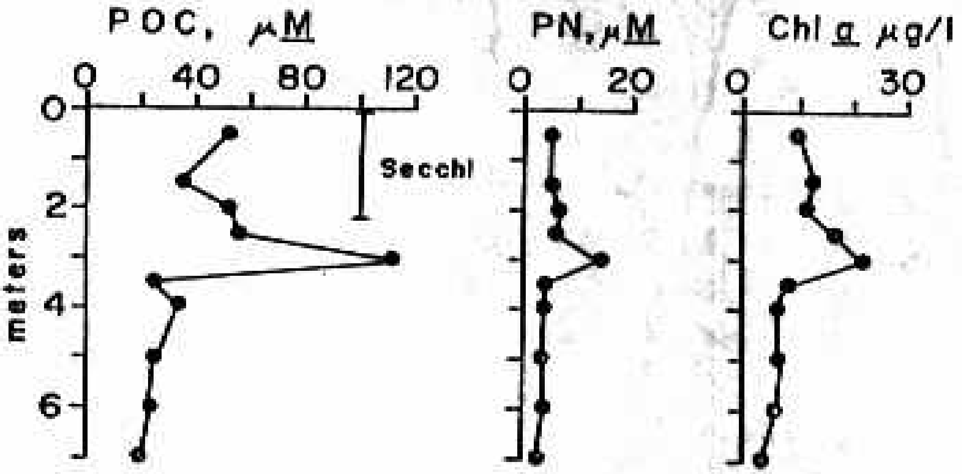


Figure 1 - Central Amazon basin near confluence of Solimões River and Negro River showing location of lakes studied (Calado, Miriti, Paru, Janauaca).



LAGO CALADO, 9 May 80 ● ; 19 July 80 ○ (SRP),
21 July 80 ○ (NH4)



LAGO CALADO, 29 May 1980

Figure 2 - Lake Calado. High and low water outlines of lake are marked.

The lakes in the central Amazon basin vary considerably in size and shape (MELACK, 1984). A common shape of larger lakes is dendritic, and Lake Calado is a moderate-sized, dendritic lake. Our auxiliary lakes include examples of small (Paru), moderate (Miriti), and large (Janauaca) dendritic lakes.

Lake Calado combines a number of characteristics that make it well suited to our study of nutrient dynamics. It has a single, well-defined channel connecting it to the Solimões River all year. During high water, connections to the two neighboring lakes (Miriti and Paru) exist, but only the channel to L. Miriti is significant and can readily be gauged. The moderate size of the lake and its basin permits efficient sampling at several stations and adequate monitoring of rainfall and runoff. The local drainage basin is largely forested; however, portions are under various degrees of agricultural use, as is typical of the floodplain throughout the central Amazon. The three major habitats of the Amazon floodplain are represented in L. Calado. The oblong portion parallel to the Solimões River is about half open water and half covered by floating vegetation at high water. The major north/south axis and dendritic fingers of the lake extend into uplands and are largely open water and flooded forest.

Although no intensive study of nutrient dynamics in L. Calado or other Amazon floodplain lakes had been performed prior to our work, a number of investigations of value to us have been done at L. Calado and neighboring lakes (e.g. FITTKAU et alii, 1975; JUNK, 1970; 1973; 1980; 1983; GROTH, 1971; RAI & HILL, 1980; REISS, 1976; GEISLER & SCHNEIDER, 1976; KNOPPEL, 1970; FURCH, 1976; 1982; 1984; HOWARD-WILLIAMS & JUNK, 1976; 1977; LOPES et alii, 1983; SCHMIDT, 1969; 1970; 1973a,b; TUNDISI et alii, 1984; ZARET et alii, 1981; FORSBERG, 1984; FORSBERG et alii, 1988). We have investigated L. Calado since 1979 and summarize below our experimental and descriptive results.

Our limnological program has evolved from a series of one to two week expeditions in river boats to a near full-time operation made possible by a floating laboratory. This facility is securely moored in L. Calado, and allows nutrient chemistry to be performed at the lake, intensive experiments to be attended readily, and meteorological instruments to be located on the lake. Diel cycles are especially important in tropical lakes, and we are ideally situated to sample repetitively over diel cycles (e.g. MELACK & FISHER, 1983; MacINTYRE & MELACK, 1988). Our main station is centered in the southern oblong portion of L. Calado; this is where we anchored the river boats and moor our floating lab.

The hydrology of an Amazon floodplain lake such as L. Calado is complex. The Solimões River rises and either fills L. Calado directly or functions as a dam that forces the local runoff, rain, or adjoining lakes to fill the lake. As this occurs, L. Calado gradually increases in depth and area. Although river stage is usually plotted as a function of time to illustrate the annual cycle, a more useful plot for our purposes is the rate of change of level, which clearly illustrates three distinctive portions of the annual cycle (Fig. 3): (1) During the initial stages of river rise (November-January) the rates of change are variable and range from -10 to +30 cm week^{-1}. (2) Maximum rates of rise during the period February-April can exceed 50 cm week^{-1}. (3) Rates of rise decline as the flood peaks in June and eventually the levels fall as rapidly as 80 cm week^{-1} during August.

The annual rise of the Amazon River causes inundation of the floodplain lakes to varying extent. Using digitally--enhanced Landsat imagery we have examined the spatial heterogeneity in the extent of inundation within and among lakes near Manaus. Furthermore, we have documented kilometer-scale heterogeneity in the early stages of Amazon inundation in Lakes Calado, Paru, Miriti,

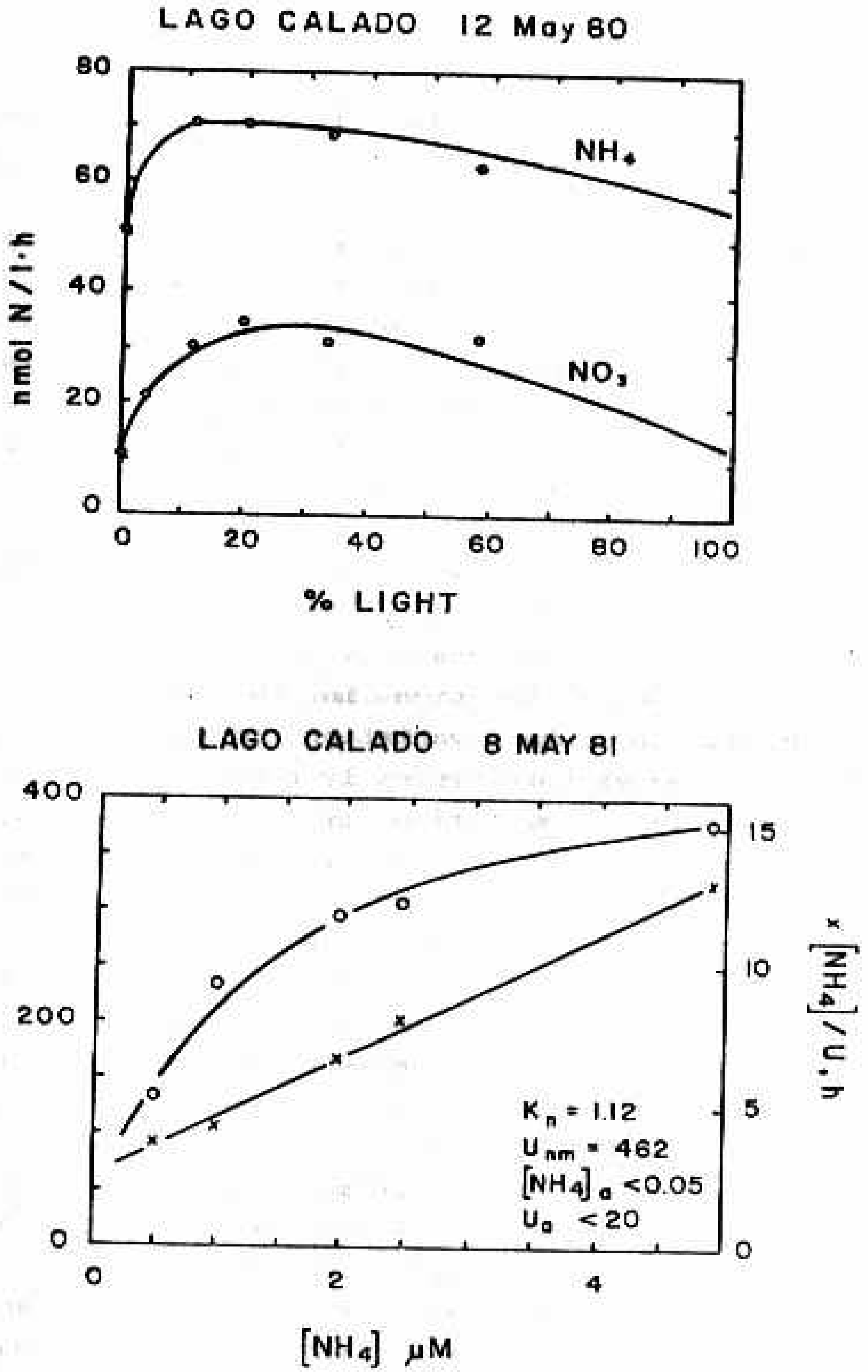


Figure 3 - Rate of change in stage height, Lake Calado, 1980-1981.

and Janauaca. FISHER & PARSLEY (1979) report similar gradients for L. Janauaca.

Meteorological, hydrological and limnological measurements--To characterize the seasonality and annual variations in meteorology, hydrology, and limnology of Lake Calado, we conducted a sampling and measurement program from 1980-1986. We instrumented our main station for the following measurements: insolation as recorded by an Eppley pyranometer (280-2800 mm) and a PAR sensor (400-700 mm), wind speed and direction, air and surface water temperature, rain intensity and quantity, and humidity. Most of the data are recorded on solid state data loggers and are backed up by manual observations.

Lake Calado's location in the humid, lowland tropics results in muted variation in meteorological conditions. Air temperature typically ranges from 24-32°C year round, with brief, exceptionally cool periods (20°C) once or twice each year. Insolation, measured as photosynthetically available radiation, varies as a function of cloudiness with a mean ± std. dev. of 33 ± 12 Einsteins $m^{-2}d^{-1}$. Wind speeds are generally low at night (0-4 m s^{-1}) and increase to maxima at mid-day (4-8 m s^{-1}) but can abruptly increase as squalls pass (10-12 m s^{-1}). Winds from SE-NE are usual during the day, as are northerly flows from the uplands at night.

Vertical profiles of temperature and dissolved oxygen obtained daily in the water column at ca. 0630 h for 510 days and 100 diel cycles permit an evaluation of the frequency of mixing unattained in any other study of shallow tropical lakes (MELACK & FISHER, 1983; FISHER et alii, 1983; MacINTYRE & MELACK, 1984; 1988). The stability of the thermal stratification depends on depth of the lake and on the duration of periods with moderate to high insolation versus periods with low insolation, strong winds and rain. When water depths are less than 3-4 m, diel mixing from top to bottom is usual. When depths exceed 5 m, anoxic water develops below a thermocline at ca. 3 m, and oxycline displacements downward of 1-2 m occur every 3-5 days. When depths exceed 8 m, holomixis occurs rarely during unusually cool periods. Detailed analyses of heat inputs and losses, wind speeds, and thermal structure indicate that evaporative heat losses result in convective mixing which predominates over direct, wind-induced mixing (MacINTYRE, unpublished).

Dissolved oxygen is usually undersaturated in Amazon floodplain lakes (MELACK & FISHER, 1983). In L. Calado planktonic gross photosynthesis is modest, and is considerably less than respiration on a daily basis. Diel oxygen variations depend largely on air-water exchanges and vertical mixing. Diffusion-corrected, daytime changes in dissolved oxygen are usually negative, and this result implies that the plankton consumes more organic matter than it produces. The sources of this additional organic matter consumed in the water column are periphyton, macrophytes, and forest litter inputs on the margins of Lake Calado, but the quantities and relative propostions from each are unknown.

L. Calado receives inputs of water, solutes, and particulates from the Solimões River and from local rain, runoff, and connections with monitored the following: (1) lake level, (2) currents in the channels that connect the lake to the river and to neighboring lakes, (3) rainfall, (4) discharge of local streams, (5) groundwater levels and seepage, and (6) meteorological parameters required to calculate evaporation by the energy budget method. The Solimões River is an important but not the only significant source of N and P for L. Calado. During the period from October 1983 through October 1984, the inputs of N from local rain and runoff were about three times greater than those from the river; however, the river was the dominant supply of P (LESACK, 1988).

Our chemical and biological sampling program provides a description of temporal and spatial differences. We have routinely sampled four stations in L. Calado, one each in L. Miriti and L. Paru and several in L. Janauaca. We determined vertical profiles of temperature, dissolved oxygen, conductivity, pH, CO_2, NO_3, NH_4, PO_4, total N, total dissolved N, total P, total dissolved P, particulate N(PN), particulate P(PP), particulate organic C(PC), and chlorophyll a; less often we determine SiO_4, Fe, and the major cations (Ca, Mg, Na, K) and anions (SO_4, Cl, HCO_3). Concurrently, we collected zooplankton and phytoplankton samples and measured photosynthetic rates. In general, when the lake is stratified, the nutrient concentrations are low in the euphotic zone, but elevated in the hypolimnion (FISCHER et alii, 1983; SETARO & MELACK, 1984; Fig. 4). A metalimnetic peak in particulate concentrations is common (Fig. 4). During low water (e.g. Oct.), riverine inundation, local runoff, and sediment resuspension result in elevated nutrient concentrations and high turbidity.

Planktonic biomass, productivity and chemical composition are summarized in Tab. 2. Phytoplankton populations are moderate (1-10 μg chl L^{-1}). Atomic ratios of seston indicate the presence of C-rich material with low N and P content. Gross production of phytoplankton was estimated with the oxygen and short-term ^{14}C methods, and the results were not significantly different. Negative values for net productivity result from the high respiration rates sustained by lateral transfer of organic matter from the margins of the lake. Although there are no striking seasonal patterns in phytoplankton biomass or productivity, there is pronoundec spatial variability. Planktonic biomass and productivity are highest near the river and decline by about a factor of two up the axis of the lake away from the river.

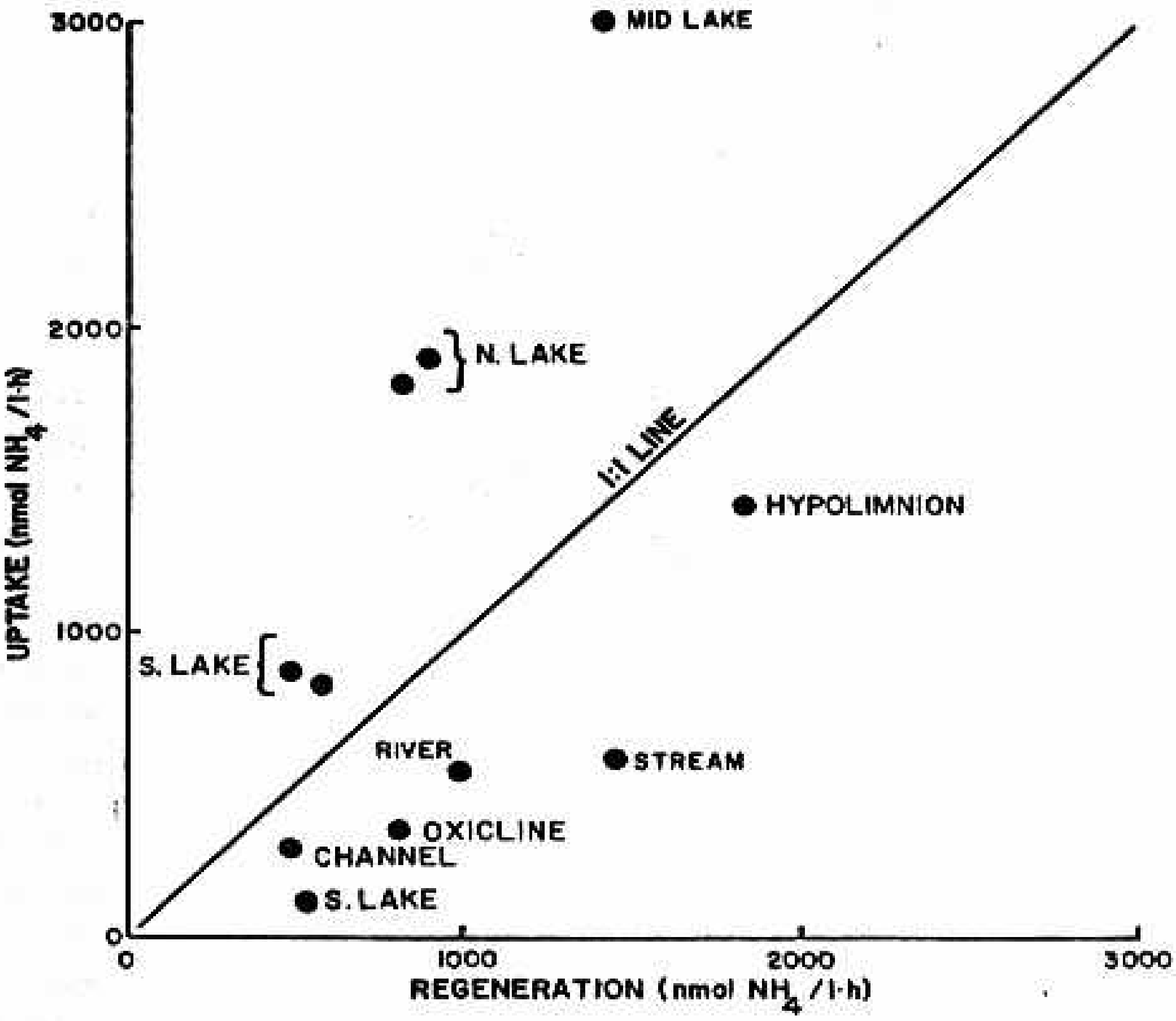


Figure 4 - Vertical profiles of dissolved N and P (top) and particulates (bottom), L. Calado. SRP, soluble reactive phosphate; NH_4, ammonium; POC, particulate organic carbon; PN, particulate nitrogen; chl.a, chlorophyll a.

Table 2 - Plankton biomass, primary production, and respiration in Lake Calado. Abbreviations: chl.a = chlorophyll a, PC = particulate carbon, PN = particulate nitrogen, PP = particulate phosphorus, GP = gross photosynthesis, R = respiration, NP = net photosynthesis. Data are from SMITH-MORRILL, 1987; MELACK & FISHER, 1983 and FISHER et alii, 1988.

$g\ m^{-2}$	$mg\ m^{-2}$	-------mmol m^{-2}-------				-----------gC m^{-2} d^{-1}-----------		
seston	chl.a	PC	PN	PP	PC:PN:PP	GP	R	NP
50±10	23±5	700±30	75±10	2.7±1.2	260:28:1	0.92±0.22	-1.60±0.27	-0.68±0.35

Experimental nutrient enrichments--To determine the influence of enrichments of nitrogen and phosphorus on the phytoplankton, we performed a series of experiments during rising, high, falling, and low water (SETARO, 1983; SETARO & MELACK, 1984). We based our fertilizations on ambient concentrations of the major inputs. Following enrichment with ammonium, nitrate, and phosphate alone or in combination, we monitored changes in standing crop and physiological condition of the phytoplankton. These experiments were performed in 4 liter, 10 liter, or 700 liter enclosures. Standing crop was assessed as chlorophyll, particulate N and C, and cell counts. Physiological condition was assessed as photosynthetic rate, ammonium enhanced dark ^{14}C fixation, P and N debt, initial saturated uptake rates, alkaline phosphatase activity, and sestonic C-N-P ratios. The responses in terms of standing crop implicate phosphorus limitation during rising and high water and a shift to nitrogen limitation during falling and low water levels. However, even during rising water, week to week differences in the relative importance of N or P occur. Furthermore, the physiological indices imply some impoverishment with respect to nitrogen and phosphorus throughout the year. Further corroborative work on the nutritional status of the phytoplankton in L.

Calado is described in PINHEIRO (1985).

Nutrient uptake--Uptake of ammonium and nitrate has been measured in L. Calado with the stable tracer ^{15}N. We have measured the uptake rates as a function of light intensity and the concentration of ammonium or nitrate. Initially, we used known additions of ^{15}N-labelled ammonium and nitrate and measured ambient concentrations to calculate uptake rates (FISHER et alii, 1988); later we corrected ammonium uptake rates for isotope dilution (MORRISSEY & FISHER, 1988), using a new method that we developed for precipitation of ammonium (FISHER & MORRISSEY, 1985).

Fig. 5 shows an example of the affect of light and nutrient concentration on the rate of N uptake in L. Calado. Light influences the uptake of nitrogen in a manner similar to that of carbon incorporation, except for a large uptake rate in the dark, especially for NH_4^+. Concentrations of NH_4 and NO_3^- also strongly influence the rates of uptake. Under optimal light conditions, the half-saturation constants (K_m) for ammonium and nitrate averaged 1.6 ± 0.9 and 0.8 ± 0.3 uM, respectively. These values are typical of those observed in other systems (e.g. EPPLEY et alii, 1969), and are higher than prevailing ambient concentrations. This indicates that N uptake is less than half-saturated under ambient conditions, and suggests that N is limiting algal growth or abundance in Lake Calado. This is consistent with the bioassays reported by SETARO & MELACK (1984) and PINHEIRO (1985).

Using the above information, we have analyzed the relative importance of light and nutrient concentrations to influence uptake of ammonium and nitrate under "in situ" conditions in the epilimnion. The data indicate that ammonium and nitrate concentrations principally regulate the uptake rates under "in situ" conditions, and that light affects are secondary. The rates of supply of nitrate and ammonium are less than the potential maximum rates of

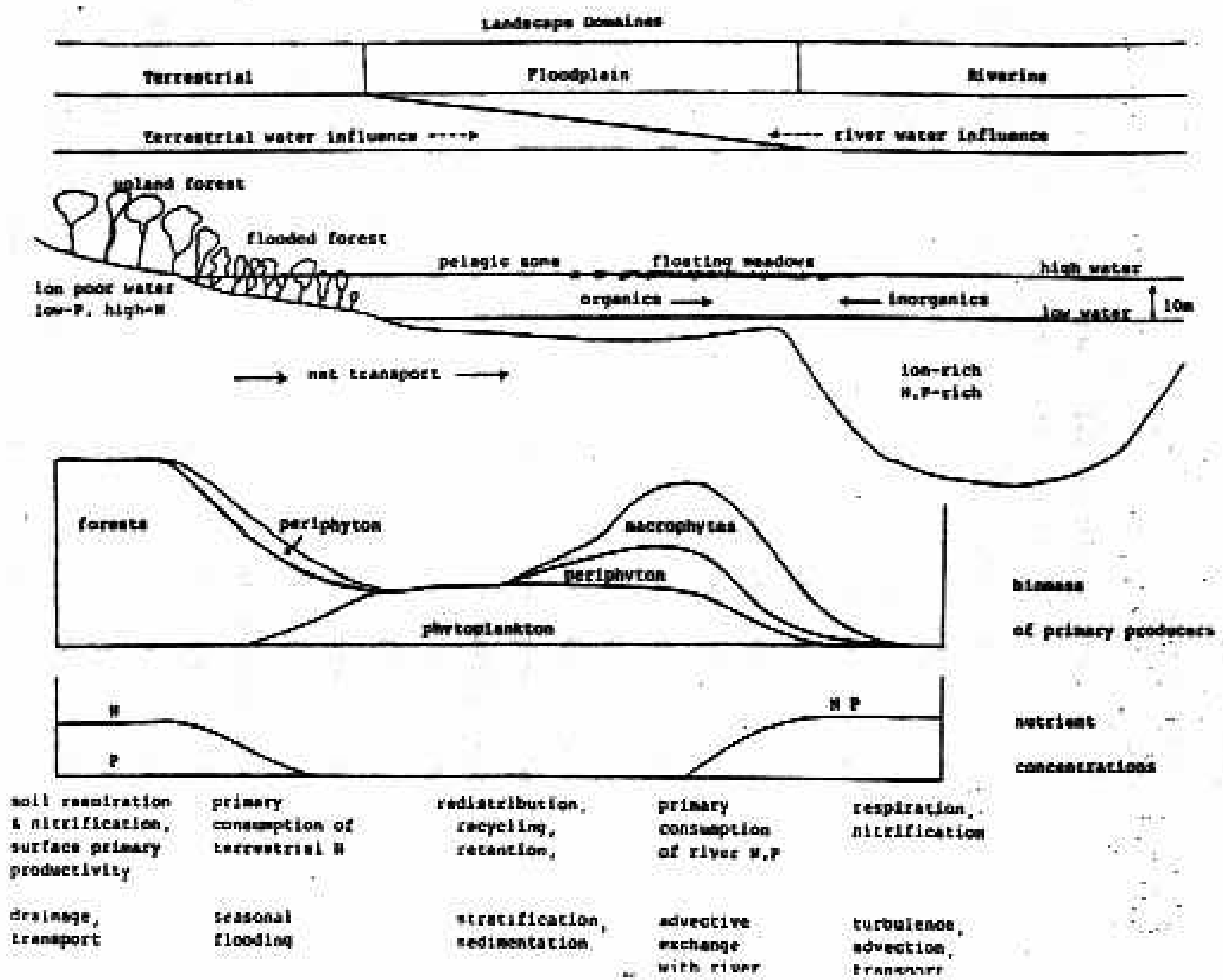


Figure 5 - Light and concentration effects on uptake of ammonium and nitrate. K_n is the half saturation constant (μM), U_m is the saturated uptake rate (nmol L^{-1} h^{-1}), and the subscript a refers to uptake rate at the ambient concentration.

uptake, and the rates of the processes supplying dissolved inorganic nitrogen appear to be regulating the rates of uptake.

Uptake of phosphate has been measured in L. Calado with ^{32}P, using Nuclepore filters of 0.2 and 3.0 µm porosity, as well as Gelman A/E filters (nominal pore size 1 µm). In surface waters of the lake, 60-90% of the ^{32}P uptake occurred in the 0.2-3.0 µm size fraction; however, in the metalimnion, more than 60% was in the >3.0 µm fraction. In a single experiment with Gelman A/E filtered surface water, the plankton remaining in the filtrate removed in one hour virtually all of the radiolabel added after filtration, as judged by retention on a Nuclepore 0.2 µm filter. Very small organisms in the surface waters are clearly involved in phosphorus cycling in L. Calado, in agreement with the results of others for freshwaters (NALEWAJKO & LEAN, 1980; LEAN & WHITE, 1983) and marine environments (TAFT et alii, 1977).

Turnover times of the phosphate pool (defined here as "filterable molybdate - reactive phosphate" = FRP) varied from 4-60 minutes (ave + se = 19 + 7, n = 8) at ambient phosphate concentrations. In experiments where unlabelled phosphate was added (up to 2 µM), net uptake rates calculated from disappearance of phosphate were 5-100 times less than gross uptake rates calculated from ^{32}P turnover times and FRP. This indicates that a small ambient phosphate pool is turning over very rapidly due to continuous uptake and release of phosphate (LEAN & WHITE, 1983).

<u>Nutrient regeneration in the water column</u>--We have made direct measurements of the rate of ammonium production in the water column of L. Calado using the ^{15}N isotope dilution method (MORRISSEY & FISHER, 1988). Measurement of the appearance of ^{15}N label in the PN pool and the dilution of the label in the NH_4 pool enables simultaneous

measurements of the rates of uptake and regeneration of ammonium.

Rates of ammonium production in the epilimnion of L. Calado ranged from 580-1410 nmol NH_4 $L^{-1}h^{-1}$, and the total amount of ^{15}N in the ammonium and PN pools remained constant, indicating that the main cycling pathways were ammonium and particulate N (LAWS, 1984; FISHER & MORRISSEY, 1985). Ammonium production in the hypolimnion under "in situ" conditions was lower than in the epilimnion, 50-100 nmol NH_4 $L^{-1}h^{-1}$. However, the same hypolimnion samples experimentally exposed to oxygen gave rates that were considerably higher (1600-1830 nmol NH_4 $L^{-1}h^{-1}$); this suggests that the rate of ammonium production was limited by oxygen availability and that large quantities of labile organic nitrogen were present in the anoxic water.

In river and stream samples, we obtained rates of ammonium production that ranged from 480-1460 nmol NH_4 $L^{-1}h^{-1}$, and in these the total amount of ^{15}N label in the PN and ammonium pools decreased significantly during the incubations. The disappearance of ^{15}N suggests loss of label to an unmeasured pool such as nitrate; these samples also had significant amounts of nitrate (0.8-8.8 µM), in contrast to the lake samples. While we have no direct evidence, we suspect that nitrification was occurring in the river and stream samples.

Fig. 6 compares the rate of ammonium production in the epilimnion with the saturated rate of uptake. The rate of ammonium production that we measured in the surface waters of the lake was typically less than the saturated rate of uptake of ammonium. These points fall above the 1:1 line in the figure. In the bottom left-hand corner, the points marked "channel" and "S. lake" are data obtained from samples collected during river invasion. In the stream and river water samples, including those during the river invasion of the lake, the rate of regeneration exceeded the saturated uptake rates; therefore, ammonium should

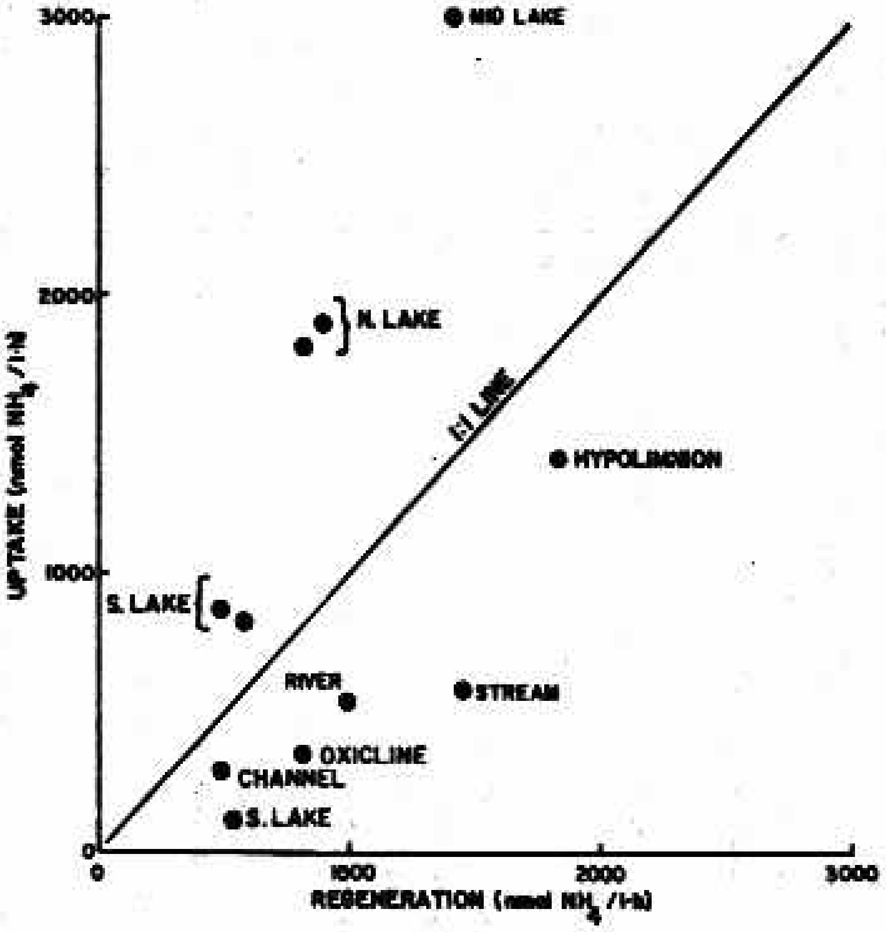


Figure 6 - Comparison of uptake and regeneration of ammonium in L. Calado and neighboring streams and river.

accumulate in these environments. However, ammonium does not accumulate, although nitrate does. This lends further support for the argument for nitrification in the river and stream samples.

The recycling rates in L. Calado are quite high. The N and P requirements of phytoplankton computed from gross primary productivity data are only 20% and 5% of the N and P regeneration, respectively. This indicates that heterotrophic consumption of nutrients (immobilization) is an important component of uptake and is consistent with the large planktonic respiration rates. Although the pelagic zone is dominated by heterotrophic processes, inorganic N and P do not accumulate in surface waters. Therefore, the epilimnion must be receiving inputs of C-rich organic matter from other primary producers, such as the floating meadows on the lake margins, in order to keep heterotrophic immobilization at such high levels in the pelagic zone.

We have measured production of ammonium and phosphate by the larger zooplankton (i.e., cladocera and copepods) in filtered lake water (method of GANF & BLAZKA, 1974) and when feeding on nutrient replete phytoplankton (method of LEHMAN, 1980). Animals were obtained from vertical net tows (>53 µm) in the upper 4 m and excretion rates were measured as accumulation of ammonium and phosphate using colorimetric methods (LENZ et alii, 1986). Measurements were made during rising and falling water, at several stations and over diel cycles.

Regeneration by the macrozooplankton of L. Calado was low compared to other lakes and compared to the microzooplankton and bacteria in L. Calado. Macrozooplankton rates averaged 25.5 ± 3.1 µmol NH_4 $m^{-2}h^{-1}$ and 3.30 ± 0.34 µmol PO_4 $m^{-2}h^{-1}$. The low rates are probably the result of low macrozooplankton abundance due to grazing by fish.

<u>Nitrogen fixation and denitrification</u>--We have

used acetylene reduction and $^{15}N_2$ uptake to assess nitrogen fixation by plankton during rising and falling water but have found no detectable fixation (MELACK & FISHER, 1988). In contrast, we measured nitrogen fixation by filamentous cyanobacteria associated with floating aquatic macrophytes. Furthermore, we have occasionally found heterocystous cyanobacteria in the plankton. Nitrogen fixation appears to be temporally and spatially variable and requires additional examination to determine its quantitative importance.

To estimate denitrification in L. Calado we have used the acetylene blockage method (YOSHINARI & KNOWLES, 1976). Our experimental design included aerobic and anoxic conditions with and without nitrate additions. Sediment samples from the lake and streams, and water samples from the hypolimnion, streams and mixed water column at low water were assayed. No denitrification was detected (MELACK & FISHER, 1988). However, N_2O profiles from a variety of Amazon floodplain lakes are suggestive of some denitrification (RICHEY et alii, 1988), and we have measured consumption of experimental additions of nitrate in bottom chambers in L. Calado.

<u>Sedimentation and burial rates</u>--We have deployed sediment traps at three open water stations and one within the floating macrophyte beds at the south end of the lake (SMITH-MORRIL, 1987). Sedimentation was highest near the river and decreased by a factor of about two in a northerly direction away from the river. The macrophyte bed had sedimentation rates up to 140% higher than the open water station. The C, N and P content of the sinking particulates was similar to that of the seston and periphyton attached to the floating grasses.

Sediment cores obtained along the axis of the lake and dated with ^{210}Pb indicate that about 45% of the particulate C, 25% of the particulate N and 20% of the particulate P settling from the epilimnion is permanently buried (SMITH-MORRIL, 1987).

Sediment-water nutrient fluxes--We have estimated the fluxes of dissolved oxygen, ammonium, nitrate, phosphate, iron and silicate across the sedimentwater interface of Lake Calado (SMITH & FISHER, 1985; FIGUEIREDO, 1986; SMITH-MORRILL, 1987). Two methods were used to estimate the fluxes: (1) a chamber which directly measured the "in situ" rates as changes in dissolved material in the bottom waters trapped in the chamber above the sediments, and (2) an interstitial water sampler which measured the concentration gradients of the dissolved nutrients.

Under isothermal conditions at low water, dissolved oxygen is present at the sediment-water interface and fluxes of all constituents across the sediment-water interface were less than under stratified conditions at higher water levels (SMITH-MORRIL, 1987). Phosphate fluxes were near zero or negative at low water, suggesting seasonal sequestering on ferric oxyhydroxide complexes. Nitrate fluxes were near zero and quantitatively unimportant compared to those of ammonium. Fluxes of ammonium were highest at the north end of the lake and decreased towards the river; in contrast, the fluxes of phosphate and iron were highest at the river-end and decreased towards the uplands. These trends are consistent with our data on N and P inputs; the sediments under greater riverine influence released more PO_4, whereas sediments under greater terrestrial influence released more NH_4^+.

Comparison of recycling mechanisms--We have summarized information on recycling processes in Lake Calado in Tab. 3. Rates of ammonium production in the water column were transformed from volumetric to areal units assuming a 3 m epilimnion and a 5 m hypolimnion; areal

Table 3 - Comparison of direct measurements of recycling in L. Calado. Data are from MORRISSEY & FISHER, 1988; FISHER et alii, 1988; FISHER & DOYLE in press; SMITH-MORRILL, 1987 & LENZ et alii, 1986.

source	μmol $m^{-2}.h^{-1}$ ammonium production	%	μmol $m^{-2}.h^{-1}$ phosphate production	%
epilimnion (whole)	2600 ± 260	80	720 ± 50	95
(macrozooplankton)	26 ± 3	(< 1)	3.3 ± 0.3	(<1)
hypolimnion (whole)	380 ± 60	12	-	?
sediments	270 ± 60	8	37 ± 19	5
Total	3750 ± 270	100	760 ± 50	100

importance of the rates varies seasonally with water level changes. In this example the routes of recycling differ significantly in relative magnitude; epilimnetic regeneration provides 80% of the total ammonium supply and 95% of the total phosphate supply. Macrozooplankton within the epilimnion appear to be relatively unimportant in the production of ammonium; similar conclusions have been reached recently in several studies of marine systems (CAPERON et alii, 1979; GILBERT, 1982; PAASHE & KRISTIANSEN, 1982). Anaerobic regeneration in the hypolimnion and sediments provide 5-20% of the total, although vertical mixing is necessary to bring the recycled nitrogen into the euphotic zone. The vertical mixing may also transport labile organic nitrogen into the epilimnion and may contribute to the high ammonium production rates there. The dominance of epilimnetic ammonification and the relative unimportance of the macrozooplankton indicate that the smaller epilimnetic heterotrophs such as bacteria, fungi, protozoans, and rotifers are the organisms most important in the production of ammonium.

Overview--Our research and that of others enables us to draw conclusions concerning the Amazon's floodplain. Nutrient inputs from the river are important, but terrestrial inputs from the surrounding local watershed and airshed are also significant. Nutrient cycling occurs primarily via heterotrophic processes in the epilimnion, and small organisms such as bacteria and microzooplankton are the most important agents. Primary productivity by phytoplankton in the open waters of the floodplain is modest, and respiration is generally larger, resulting in oxygen undersaturation. The high rates of respiration presumably result from lateral movements of organic matter produced at the lake margins in the floating meadows and flooded forests. The net heterotrophic nature of the open waters is an important ecological feature of Amazon floodplain lakes.

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