Biogeochemistry of Amazon Floodplain Lakes and Associated Wetlands

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Flooding and associated lakes are important components of the biogeochemistry, ecology, and hydrology of the Amazon basin. Amazon floodplains contain thousands of lakes and associated wetlands linked to each other and to the many rivers of the immense basin. These floodplain lakes modify the passage of flood waves (Richey et al. 1989a), increase nutrient retention and recycling (Melack and Fisher 1990), and influence the chemistry of the rivers (Devol et al. 1995). The mosaic of flooded forests, open water, and floating macrophytes in the central Amazon floodplain makes a significant contribution of methane to the troposphere (Bartlett et al. 1988, Devol et al. 1990). The fishery potential of the large river systems is closely tied to the area of floodplain and the magnitude and duration of inundation (Welcomme 1979, Bayley and Pettre 1989). The majority of fishes harvested in the Amazon basin obtain nutrition in flooded forests (Goulding 1980) or from organic matter derived from floodplain algae (Araujo-Lima et al. 1986, Forsberg et al. 1993).

Much progress has been made during the last fifty years toward understanding the lakes of the Amazon floodplain. Still, the vast size of the Amazon basin poses challenges to limnologists working in the region. Recent research has been enhanced by the maintenance of functional floating laboratories in several areas, use of modern ships capable of regional surveys and equipped for hydrographic studies, and applications of remote sensing.

Our objective in this chapter is to examine the role of lakes in the hydrology of the floodplain and in the biogeochemistry of carbon, nitrogen, and phosphorus within the central Amazon basin. Particular emphasis is placed on how inundation patterns interplay with carbon balance and nutrient limitation. By combining numerous measurements of primary productivity with recent results from studies using isotopes of carbon, we will examine the contribution of the major plant groups to aquatic foodwebs, and offer a new paradigm for the processing of organic carbon on the Amazon floodplain. The interchange between the Amazon River and local catchments as sources of nutrients to the floodplain indicates the potential sensitivity of the lakes to basin-wide and local disturbances. We will focus our analysis on intensively studied lakes near Manaus (for example, Lake Calado, Melack and Fisher 1990; Lake Camaléto, Junk 1997) and on regional surveys conducted with consistent methods. When possible, we will extrapolate to the basin scale. For a review of the ecology of Amazon floodplains, we recommend Sioli (1984) and Junk (1997).
Floodplain Lakes: A Conceptual Framework

Lakes are an integral component of the Amazon floodplain, and, as defined here, encompass seasonally flooded areas, other than rivers and streams, that include open water plus vegetated areas. As water levels vary, the proportion of open water to other aquatic habitats changes considerably. At lowest water, floodplain lakes may be reduced to shallow, turbid pools and occasionally desiccate completely. During rising and high water, the lakes expand in area and encompass flooded forests and seasonal growths of emergent aquatic macrophytes; as a result, terrestrial areas surrounding the aquatic environments contract in area. Junk et al. (1989) define this seasonally flooded region as the Aquatic Terrestrial Transition Zone or ATZ. In addition, runoff from the local catchment and deposition of solutes and aerosols from the atmosphere are components of the biogeochemical system that influences floodplain lakes.

Seven types of aquatic interfaces, with differing horizontal and vertical gradients in hydrochemical and physical characteristics, can occur in floodplain lakes: river-lake interface, direct rain and throughfall-lake interface, upland stream-lake interface, lake-lake connections, epilimnion-hypolimnion interface, lake-sediment porewater interface, and lakeshore-groundwater interface.

The strong seasonal variations in depth and extent of inundation and complex hydrologic linkages and interfaces characteristic of floodplain lakes have important influences on biogeochemical processes and fluxes. Much of the discussion in subsequent sections will elaborate upon these effects. Recent efforts to model and calculate seasonal and annual rates of biogeochemical processes in Amazon floodplain lakes have provided formal expressions for the temporally and spatially varying conditions. Weber et al. (1996) and Weber (1997) present both a box and arrow conceptual picture and a mathematical model of cation fluxes in an Amazon floodplain lake. Kern and Darwich (1997) provide an algorithm for calculation of inputs and outputs of nitrogen at Lake Camaleão that incorporates temporally varying areas of aquatic and terrestrial habitats. Further research is required to extend these efforts to additional elements, such as phosphorus and carbon, and to include additional biogeochemical processes and routes of exchange.

The open water portion of floodplain lakes behaves limnologically much as other shallow tropical lakes (Melack and Fisher 1990, Melack 1990). Another major aquatic habitat within Amazon floodplain lakes is the floating meadow community: extensive beds of floating, emergent macrophytes that develop annually. Seasonally inundated forests are also ecologically important and extensive throughout the Amazon River basin and occupy varying areas within the lakes (Junk 1986, Junk 1993). The flooded plant communities have been classified based on hydromeiotic and hydrochemistry (France 1979), although a continuum of intermediate types occurs. A combination of flooding, anoxia, sedimentation, and erosion appears to result in fewer species in inundated forests than in nearby uplands (Dumont et al. 1990).

Geographical Features

The fringing floodplain along a 2600 km reach of the Amazon River from 52°5W to 70°5W contains about 6500 lakes that vary considerably in shape and size; the lower 400 km of four major tributaries (Japurá, Purús, Negro, and Madeira) contain an additional 2320 lakes (Melack 1984, Sippel et al. 1992; Fig. 14.1, reaches 1 through 12). These censuses of lakes and descriptions of morphology are based on side-looking airborne radar (SLAR) imagery (e.g., RADAMBRASIL 1978) and represent the areas of open water excluding river channels and the mouthbays of the Tapajós and Xingú rivers, paranás, and lakes less than about 250 m across, which were too small to reliably distinguish on the 1:250,000 scale images and are not abundant. Most of the imagery was acquired during moderate to low water levels. Hence, the lake areas do not reflect the complete area encompassed by our definition of a floodplain lake or the ATZ.

Area subject to flooding estimated from geomorphological maps derived from the SLAR imagery occupies about 78,000 km² along the Amazon mainstem and an additional 62,000 km² along the lower reaches of the four major tributaries (Sippel et al. 1992; 52°5W to 70°5W; reaches 1 through 12). Islands comprise a small proportion of the total main-stem floodplain, except in the Amazon delta which is excluded from our treatment. Seasonal changes in stage resulted in variations in inundated area (excluding river channels) from 10,000 km² to 81,000 km² along the Amazon River during the period from 1979 to 1987 based on passive microwave measurements (Sippel et al. 1998; Fig. 14.2). The average maximum inundated area (excluding the Amazon River) for the period from 1979 to 1987 was 67,900 km²; this area was computed by averaging the sum of the maximum inundated area for each reach (Fig. 14.1, reaches 1 through 12) in each year. These estimates of regional inundation significantly increase our ability to model biogeochemical processes responsive to changes in oxidation-reduction states or water levels such as exchanges of CH₄ or CO₂ with the atmosphere.

Apportioning the areas of floodplain occupied by one of the three major aquatic habitats, i.e., open water, herbaceous macrophytes, and flooded forests, and determining their temporal changes remains a challenge. As approximations required for calculations of the organic carbon balance.

Fig. 14.1 Central and lower Amazon River and its major tributaries, from Sippel et al. (1992). Numbered floodplain reaches indicated along bottom were used in Sippel et al. 1992; arrows mark the upriver limits of measurements along major tributaries.
of the floodplain (see below), we have utilized results from recent remote sensing studies of the Amazon basin. Sippel et al. (1992) estimated the open water area of lakes to be 10,370 km². We based our partition of vegetated habitats on analyses of Landsat thematic mapper imagery (Melack et al. 1994; Mertes et al. 1995; Novo et al. 1997; L. Mertes and E. Novo, personal communication), synthetic aperture radar data (Sippel et al. 1992; Hess et al. 1995; Melack and Hess 1998; L. Hess, personal communication), and on our aerial videography and ground-based surveys. First, we subdivided the Amazon River and its floodplain into two segments because a major shift in lake morphology and forest cover occurs between approximately 58° and 59°W. The western section encompasses about 65% of the floodplain area and extends from 70.5° to 58.5°W (reaches 1 through 8, Fig. 14.1). The eastern section contains about 35% of the floodplain area and extends from 58.5° to 70.5°W (reaches 9 through 12, Fig. 14.1). Within the western segment, open water covers about 4140 km² and within the eastern segment about 6230 km² (Sippel et al. 1992). During periods of moderate to high water levels, we estimate that the vegetated portion of the western section is dominated by herbaceous macrophytes over 30% and flooded forests over 70%. In the eastern section, herbaceous macrophytes are estimated to cover about 90% and flooded forests to cover about 10%. Based on these areas for open water in lakes and proportions of vegetated habitat, and on an average maximum inundated area of 67,900 km², we estimate that the average maximum area occupied seasonally by herbaceous macrophytes is 29,300 km² and that the average maximum area occupied seasonally by flooded forest is 28,600 km². Further basin-wide analyses with new remote sensing data will surely modify and improve our estimates and permit additional refinements in floodplain classification.

Following Sippel et al. (1992), we apply a simple morphological classification to Amazon floodplain lakes: ria or blocked-valley lakes and lateral levee lakes. Ria lakes are formed by flooding of the lower part of a tributary stream or river valley and usually have a levee bordering the main river channel. Lateral levee lakes are subdivided by a length to width ratio of 5 into dish-shaped (ratio < 5) versus channel-shaped basins (ratio > 5). All types are formed largely by fluvial processes. Based on geomorphology, most channel-shaped basins would be considered scroll bar lakes; some would be oxbow lakes, including the world's largest oxbow lake, Lake Aranaú, located between the Solimões and Tapajós rivers. Dish-shaped lakes can be called depression lakes to indicate the formation of their basin by incomplete aggradation of the post-glacial floodplain (Klammer 1984) or by tectonic subsidence (Mertes et al. 1996). As elaborated below, these differences in morphology lead to contrasting hydrologic and biogeochemical conditions.

The frequency of occurrence and area covered by the morphological classes of lakes varies by reach along the Amazon River (Sippel et al. 1992, Fig. 14.3). Much of the limnological research performed on Amazon floodplain lakes has been done in reach 7. Although lake abundances are similar in reaches 3 to 5, reach 5 has much more lake area than do the other three reaches. Reaches 10 and 11 contain the most lake area. Dish lakes are numerically the major class of lakes except in the upper four reaches, where channel lakes are of similar abundance. Dish lakes cover the largest areas, although the uncommon ria lakes are often large and make a significant contribution to total lake area, especially in reach 5.

The frequency distribution of individual lake areas has a strong positive skew, fits a hyperbolic probability distribution, and has a statistical property known as self-similarity (Hamilton et al. 1991, Sippel et al. 1992).

Figure 14.2 Monthly estimates of total flooded area (lower line, inundated floodplain plus rivers and lakes) for the mainstem Amazon River (sum of reaches 1-12 in Fig. 14.1), plotted together with river stage at Manacapuru (upper line). Horizontal line indicates open water area. Data from Sippel et al. (1998).

Figure 14.3 Abundance and total area of lakes along Amazon River, divided by lake class; from Sippel et al. (1992).
Hence, descriptive statistics such as total abundance per unit area will vary with the scale of the observations. The median open water area of lakes at low to moderate stage ranges from 0.12 to 0.44 km² among river reaches, a size much smaller than that of most of the lakes studied by limnologists in the Amazon basin.

Two major types of hydrologic and morphometric information are lacking for almost all Amazon floodplain lakes: stage data and bathymetric maps. Therefore, it is not possible to determine directly the seasonal and interannual changes in open water area, total flooded area, or volume of water residing on the floodplain. Applications of remote sensing with passive microwave sensors (Sippel et al. 1998) and synthetic aperture radar (Hess et al. 1995) help alleviate this data gap, but field surveys will be required to obtain detailed bathymetric and stage data at specific lakes.

Transport and distribution of sediments derived from Andean erosion across the cratonic landscape of Brazil have caused development of an upstream to downstream trend in geomorphic and hydrologic character of the channel-floodplain system (Mertes et al. 1996). In upstream reaches, scroll bar topography on the floodplain tends to channelize floodwater, decreasing mixing of flooding river water with locally derived water. In middle and downstream reaches, flooding river water flows onto the floodplain as diffuse, nonchannelized overbank flow, and through drainage channels. In both middle and lower reaches considerable mixing of waters from rivers and local drainages occurs.

Most limnological studies have been completed near the confluence of the Solimões and Negro rivers, which combine at Manaus to form the Amazon River. These rivers are biogeochemically distinct systems. The Solimões River, called a whitewater river, is rich in dissolved nutrients and suspended sediments and has extensive, fertile floodplains. The Negro River is nutrient poor and contains high concentrations of dissolved organic carbon, hence it is called a blackwater river.

Climate and Physical Environment

The central Amazon has a wet and warm climate with a drier period from June through November that corresponds with the northward movement of the Intertropical convergence zone. Mean annual rainfall just north of Manaus during the period 1966 to 1983 was 2410 mm; the return period for wet (2800 mm) and dry (2000 mm) years was 10 years (Lesack and Melack 1991). Local differences in the distribution of rainfall have been reported (Ribeiro and Adis 1984), although Lesack and Melack's (1995) transect of rain gauges in the Calado basin did not detect differences. Mean annual temperature is between 26°C and 27°C, with August through November slightly warmer than the mean and January through April slightly cooler than the mean (Irion et al. 1997). Diurnal variations can exceed 10°C. Cool, southern air masses occasionally influence the central Amazon, and minima can fall below 20°C for a few days during the austral winter. Relative humidity is high year round, averaging about 76% (Ribeiro and Adis 1984).

Meteorological data are required to calculate evaporation and to model vertical mixing within the water column of lakes, critical aspects of the hydrological cycle and fluxes of nutrients. Meteorological records from lakes in the central Amazon floodplain are short and available from only two sites (Lakes Camaleão and Calado). At Lake Calado, air temperatures typically range from 24°C to 32°C year round with occasional, brief cool periods, such as observed on days 164 to 168 in 1983 (Fig. 14.4). Insolation, measured as photosynthetically available radiation (PAR), varies as a function of cloudiness (mean ± std. dev. = 33 ± 12 Einsteins m⁻² d⁻¹). Wind speeds are generally low (near 0 to 4 m s⁻¹) during morning and around midday, but abruptly increase up to 10 m s⁻¹ as squalls pass (Fig. 14.4).

Underwater light attenuation in floodplain lakes is often high because of the high concentrations of suspended particles and dissolved organics (Schmidt 1973, Pukk and Otto 1987). Hence, the euphotic zone available to phytoplankton is often shallow. For example, Secchi disk transparency in Lake Calado varied seasonally from ca. 50 to 150 cm (J. M. Melack and T. R. Fisher, unpublished data). Consequently, emergent trees and floating macrophytes with associated periphyton are better positioned to capture sunlight than phytoplankton, and much of the primary productivity in floodplain lakes occurs in nonpelagic habitats.

Hydrological and Hydrodynamic Aspects

Regional hydrology

The Amazon River has a damped annual hydrograph with a water-stage
amplitude of about 10 m in the central basin and a 2-to-3-year cycle of interannual variation coupled to the El Niño Southern Oscillation (Richey et al. 1989b). Linked to the changes in stage are a rise and fall in flooded area, in which lakes are an important component. Large volumes of river water are stored in floodplain lakes during seasonal floods and then return to the main channel when the river level falls. In addition, the discharge of many tributaries passes through lakes, and a net flux of water from the floodplain to the river can occur even when river level is rising (Richey et al. 1989a, Lesack and Melack 1995). Further, lakes and their associated floodplain vegetation are significant sources of water vapor to the atmosphere, especially at the beginning of the dry season when inundated area is largest (Victoria et al. 1991).

In a comparison of 51 lakes located along the central Amazon River, Forseberg et al. (1988) used alkalinity as a tracer of sources of water; the Amazon River has relatively high alkalinity, while the streams draining the lowland forests have relatively low alkalinity. During high water from mid-March to mid-September, lake and river alkalinites were similar, indicating that lakes contained primarily river water in most cases. The exceptions were ria lakes with large local drainage basins. During low water from mid-September to mid-March, the influence of rivers diminished and local inputs to lakes increased in proportion to the ratio between local basin area and lake area (BA:LA). Channel and dish-shaped basins, which typically have small local catchments, appeared to receive small to moderate local runoff and had variable alkalinites at the end of low water. Alkalinities in lakes with BA:LA > 20, such as many ria lakes, approached the average values for lowland runoff by the end of low water. Corresponding to these different sources of water are differences in concentrations and fluxes of nutrients (see below).

Hydrological balance of a floodplain lake

For any period of time, the water balance of a floodplain lake can be expressed by the equation:

$$\Delta S = P + R + L + H + G - E$$  

(1)

where $\Delta S$ is the change in volume of water stored in the lake, $P$ is precipitation, $R$ is inflow from the river, $L$ is exchange of water in either direction through connections to adjacent lakes, $H$ is exchange of water in either direction through channels to an adjacent river, $G$ is exchange with the surrounding groundwater system, and $E$ is evaporation from the lake; units are volumes (Lesack and Melack 1995). During the course of the year, each of the inflows and outflows in equation 1 changes in response to temporal variations in weather and interactions with changes in stage, surface area, and volume of the lake. Evaluation of the water balance for a floodplain lake requires precise bathymetry of the basin and careful measurements or calculations of all of the variables. Bathymetric data are available for few Amazon lakes, and appropriate meteorological and hydrological measurements in floodplain lakes and their catchments rarely have been made.

The first and only detailed analysis of the terms in equation 1 for an Amazon floodplain lake was performed at Lake Calado (Lesack and Melack 1991, 1995). Lake Calado has a BA:LA ratio ranging from about 7 at high water to about 28 at low water. River water invaded the lake at the start of rising level in the mainstem, but by midrising water, lake water steadily flowed from the lake into the river, while river levels continued to rise. By the end of the water year, Lake Calado had experienced a 10 m range in water level, and local runoff had contributed 57% of the total water input, river inflow 21%, rainfall directly onto the lake 11%, inflow from an adjacent lake 6%, and seepage 4%. In contrast to the common view that flooding from river channels is expected to play the major role in the annual flushing of lakes along floodplains, at Lake Calado, local rainfall and local runoff are the dominant sources of water. Further evidence for seasonal variation in the mixture of riverine and upland runoff water in Lake Calado is provided by an analysis of the isotopic composition of the water (Martinek et al. 1996). Considerably more information about the hydrology of other types of floodplain lakes is needed before generalizations are possible.

Flow paths of inflows to floodplain lakes

Inflow of the turbid, nutrient-rich water of the Amazon River onto the floodplain helps sustain the floodplain's high fertility (Fisher and Parsley 1979, Setaro and Melack 1984, Engle and Melack 1993). The inflows follow complex flow paths that account, in part, for differences in productivity among floodplain lakes. For example, Melack et al. (1992) analyzed a rare cloud-free Landsat Multispectral Scanner (MSS) image of the initial stages of riverine inundation by the Amazon River which illustrated the complexity of the flow.

**Fig. 14.5** Limnological gradients in Lake Janauaca; from Fisher and Parsley (1979).
Table 14.1 Limnological conditions and areal coverage in Lake Janauaca, 9 December 1976.

<table>
<thead>
<tr>
<th>Water type</th>
<th>Area (km²)</th>
<th>Seston (mg L⁻¹)</th>
<th>Chlorophyll a (µg L⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amazon River</td>
<td>20</td>
<td>150 ± 42</td>
<td>2.1 ± 0.4</td>
</tr>
<tr>
<td>Mixing zone</td>
<td>24</td>
<td>41 ± 1</td>
<td>38 ± 7</td>
</tr>
<tr>
<td>Lake water</td>
<td>22</td>
<td>15 ± 2</td>
<td>49 ± 7</td>
</tr>
</tbody>
</table>

Source: From Melack et al. (1992)

paths. By chance, the date of acquisition of the image coincided with the limnological studies of Fischer and Parsley (1979) at Lake Janauaca. Hence, the gradients of turbidity in the lake could be interpreted in terms of limnological conditions (Fig. 14.5, Table 14.1). In the channel leading from the river to the lake, near the Amazon River, the water is high in suspended solids and dissolved phosphate and nitrate but low in phytoplankton. Further into the lake, transparency increases, as indicated by deeper Secchi depth and lower suspended sediment concentration, and dissolved phosphate and nitrate decline as phytoplankton abundances increase.

Mertes et al. (1993) estimated concentrations of suspended sediment in the surface waters of the Amazon River and adjacent floodplain from Landsat images. They documented patterns of decreasing concentration from the main channel onto the floodplain and through channels. Rates of sediment transport into the floodplain were estimated by combining the Landsat-derived sediment concentrations with hydraulic calculations (Mertes 1994).

As lake levels rise and inundate upland stream channels, water and sediments from streams often pass through flooded vegetation before reaching open water in lakes. At Lake Calado (Alves 1991; Fig. 14.6), the cool waters (24°C) of Mota Brook flowed beneath the warm lake water (about 28°C). After an initial mixing in the first 50 m, stream water high in nitrate remained distinct from lake water low in nitrate for about 400 m. Alves (1991) attributed consumption of nitrate within the inundated channel to plankton, periphyton, and benthos. Further advances in understanding of how riverine and upland stream inflows interact and influence the biogeochemistry of floodplain lakes will require the merging of remote sensing data and hydraulic and hydrological modeling with information on biogeochemical processes.

**Vertical mixing within floodplain lakes**

Hundreds of vertical profiles of temperature and dissolved oxygen obtained in Lake Calado permitted an analysis of the frequency of mixing (Melack and Fisher 1983, MacIntyre and Melack 1984, 1988), an important factor influencing nutrient supply to the euphotic zone and oxidation-reduction conditions at the sediment–water interface. When water depths were less than 3 to 4 m, diel mixing from top to bottom was usual. When depths exceeded 5 m, anoxic water developed below a thermocline at about 3 m, and oxygen displacements downward of 1 to 2 m occurred every 3 to 5 days in conjunction with mixing events. When depths exceeded 8 m, mixing to the bottom was rare. Detailed analyses of heat inputs and losses, wind speeds, and thermal structure indicated that evaporative heat losses resulting in convective mixing predominated over direct, wind-induced mixing (S. MacIntyre and J. M. Melack, unpublished data).

**Figure 14.6** Stratification and horizontal variation from Mota Brook to Lake Calado during high water; SLI is stream–lake interface; from Alves (1991).
Biogeochemical Processes and Fluxes: Carbon Dynamics

Floodplain lakes and their associated wetland habitats play an important role in the organic carbon balance of the Amazon River system. Lakes are the main sites of aquatic plant production, the principal source of organic carbon for aquatic food chains. They are also a major source of methane and other biogenic gases to the troposphere. The temporary storage and transformation of riverine organic matter in lacustrine environments contributes significantly to the downstream spiraling of carbon along the Amazon River. We will describe principal aspects of the organic carbon cycle in Amazon lakes, emphasizing the dominant fluxes, the factors that control them, and their contribution to the organic carbon balance at local, regional and global scales.

Primary production

Four groups of plants contribute to autochthonous primary production in floodplain lakes: phytoplankton, herbaceous macrophytes, flooded forest trees, and periphytic algae. The distribution and production dynamics of each of these plant groups varies within and between lakes in response to spatial and temporal variations in lake morphology, geochemistry, and flooding pattern.

Phytoplankton

Phytoplankton communities are limited generally to the open waters of lakes where underwater light availability is sufficient. The Amazon River, while rich in nutrients, is too turbid to support significant levels of planktonic production (Wissmar et al. 1981). As the river flows onto the floodplain, sediments settle from the water column and light availability and phytoplankton production can increase (Schmidt 1973, Fisher and Parsley 1979, Forberg et al. 1988; Fig. 14.5). For example, more than 90% of the suspended material entering Lake Calado from the Solimões River was lost from the upper water within 2 km of the river during periods of channelized and overbank flow (Engle and Melack 1993). Phytoplankton populations in Lake Calado had moderate abundance (1 to 10 µg chlorophyll l⁻¹) and modest gross photosynthesis (0.4 to 1.2 g C m⁻² d⁻¹) (Melack and Fisher 1983, Fisher et al. 1988a, Smith-Morrill 1987). Seasonal minima in phytoplankton biomass and production tended to occur during low water when the water was turbid from resuspension of sediments. Annual gross planktonic production was estimated to be about 300 g C m⁻² yr⁻¹ in Lake Calado. A similar rate of annual production was reported for Lake Castanho by Schmidt (1973).

Daily integral rates of phytoplankton production, (daily integral photosynthesis), (I) are known to vary inversely with the vertical light attenuation coefficient (Ed) and as a direct positive function of the light saturated rate of photosynthesis (Pmax) (Falling 1957, Vollenweider 1965), reflecting the effects of light limitation and nutrient or temperature limitation (Smith 1979), respectively. B. R. Forberg (unpublished data) has investigated the influence of variation in Ed and Pmax on levels of primary production in 36 lakes associated with the Amazon River and its major tributaries in the central Amazon floodplain (Table 14.2). Daily integral gross production, averaged over all lakes, was 0.82 g C m⁻² d⁻¹, which corresponds to an annual production rate of about 300 g C m⁻² yr⁻¹. Daily integral production was higher in floodplain lakes associated with whitewater rivers due primarily to higher Pmax levels. The average light saturated rate of photosynthesis in whitewater lakes was more than twice that encountered in lakes fed by clear and blackwater rivers. Daily integral production tended to be lower during low water, and this was attributed to a lower light availability (i.e., higher average Ed) associated with resuspension of sediments. The average I value determined for whitewater lakes (0.96 g C m⁻² d⁻¹) corresponded to an annual rate of 350 C t C km⁻² yr⁻¹.

Total daily phytoplankton production can vary considerably in Amazon floodplain lakes due to large seasonal changes in surface area linked to water-level variations. This variability makes it difficult to calculate the total annual production of individual lakes and to estimate the combined contribution of phytoplankton in all lakes to total floodplain production. A reasonable approach is to use the total lake area of 10,370 km² determined by Sippel et al. (1992) for the central Amazon floodplain. Since images used by Sippel et al. (1992) were acquired at different times during the year, their value is assumed to approximate average open water area. The average areal production value of 300 t C km⁻² yr⁻¹ determined by B. R. Forberg reflects the proportional area of different lake types along the central floodplain. Using these two values, we estimate the total gross production of phytoplankton on the central Amazon floodplain to be 3.1 Tg C yr⁻¹, where Tg indicates teragrams or 10¹² g. Converting this value to net production for better comparison to production estimates for herbaceous macrophytes, flooded forests and periphyton (see below), is difficult. Although approximate conversions are possible, they are confounded by assumptions about rates of respiration in the dark versus light, bottle effects on measurements of photosynthetic rates which usually reduce rates, and difficulties calculating integrated daily rates. We judge our estimate of gross production by phytoplankton to be not more than 50% above net production, that is, net production is about 2 Tg C yr⁻¹.

Table 14.2 Average values of phytoplankton production parameters for 36 Amazon floodplain lakes.

<table>
<thead>
<tr>
<th>River type</th>
<th>I</th>
<th>Pmax</th>
<th>Ed</th>
<th>TP</th>
<th>TN</th>
<th>TSS</th>
<th>TN/TP</th>
</tr>
</thead>
<tbody>
<tr>
<td>Whitewater</td>
<td>959</td>
<td>114</td>
<td>3.0</td>
<td>37</td>
<td>460</td>
<td>33</td>
<td>17</td>
</tr>
<tr>
<td>Black-and clearwater</td>
<td>366</td>
<td>48</td>
<td>2.9</td>
<td>18</td>
<td>472</td>
<td>19</td>
<td>36</td>
</tr>
<tr>
<td>River stage</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>High water</td>
<td>894</td>
<td>82</td>
<td>2.2</td>
<td>25</td>
<td>468</td>
<td>19</td>
<td>25</td>
</tr>
<tr>
<td>Low water</td>
<td>684</td>
<td>124</td>
<td>4.1</td>
<td>42</td>
<td>473</td>
<td>43</td>
<td>19</td>
</tr>
<tr>
<td>Lake average</td>
<td>818</td>
<td>98</td>
<td>2.9</td>
<td>32</td>
<td>470</td>
<td>28</td>
<td>30</td>
</tr>
</tbody>
</table>

* I = daily integral photosynthesis (mg C m⁻² d⁻¹), Pmax = light saturated rate of photosynthesis (mg C m⁻² d⁻¹), Ed = vertical attenuation coefficient of PAR (m⁻¹), TP = total P (mg m⁻³), TN = total N (mg m⁻³), TSS = total suspended sediments (mg l⁻¹) and TN/TP = total N to total P ratio by weight.
the annual flooding cycle (Junk and Piedad 1997). At lowest water, the surface area of many lakes is reduced and much of the lake bed is dry mud flats. These dry areas are colonized by a variety of perennial and annual macrophytes. Some of these plants (e.g., Alternanthera philox, A. brasiliana, Paspalum conjugatum, Ludwigia dencia and Sorghum arundinaceum) are exclusively terrestrial, while others (e.g., Eichhornia polystachya, Hymenachne amplifoliaus, Leetia haxandra, Oryza perennis, Paspalum repens, and Montrichardia arborescens) have both terrestrial and aquatic growth phases. All of these species are rooted in the exposed lake sediment during the terrestrial phase. When flooded, the obligate terrestrial species die and decompose while transitional species continue growing as emergent aquatic macrophytes and dominate the herbaceous plant community during the early rising water period. As the water level continues to rise, some of these species (for example, P. repens and L. hexandra) become free-floating and, together with other obligate floating species (e.g., Pistia stratiotes, Scirpus cubensis, Eichhornia crassipes, and Salvinia auriculata), form an extensive floating meadow community (Junk 1970). Rooted, submerged macrophytes are generally absent and submerged unrooted species (e.g., Utricularia foliosa) are restricted by the shallow eutrophic zones encountered in floodplain lakes. When the water level falls, the aquatic macrophyte community begins to decompose; annual species generally die and perennial species persist as rhizomes. The cumulative, sequential net production of terrestrial, semi-aquatic, and aquatic macrophyte communities is all potentially available to the lacustrine ecosystem.

The seasonally changing biomass of floating macrophytes was determined at Lake Calado with a combination of sampling and airborne videography (Fisher and Moline 1992; T.R. Fisher, personal communication; Fig. 14.7). Further analysis of these data indicate that the biomass of the macrophytes turned over 2 to 3 times per year. Casual observations of the area covered by floating plants at Lake Calado during the 1980s suggest large variations occur with low coverage in years with high floods and possibly increased human activities reducing abundance, except where deforestation of the floodplain has increased habitat for macrophytes.

While many species of macrophytes in Amazon floodplain lakes are C-3 species, a few C-4 grasses (especially Echinochoia polystachya and Paspalum repens) frequently dominate community production and biomass (Junk and Piedad 1997). Growth in C-4 plants is efficient under drought stress conditions (Feer and Stowe 1976), and this characteristic gives C-4 plants a competitive advantage over C-3 plants during the terrestrial growth phase. C-4 plants also tend to have a higher photosynthetic efficiency than C-3 plants under the high light conditions which prevail in the tropics. Piedad et al. (1991, 1994) measured an average photosynthetic efficiency of 2.3 g dry wt MJ⁻¹ and an average energy conversion of 4% in natural stands of Echinochoia polystachya growing in Lake Camaleo, one of the highest efficiencies measured for a vascular plant. The high rates of photosynthesis in C-4 plants allow them to grow faster during the rising water period and colonize deeper water than C-3 plants. The combination of high growth rates and high drought efficiency thus provides a competitive advantage to C-4 plants through the year and appears to explain their dominance in the herbaceous plant community of Amazon floodplain lakes.

The complex structure and seasonal dynamics of herbaceous macrophyte communities make it difficult to estimate their total annual contribution to floodplain lake production. Annual production estimates must incorporate the cumulative, sequential production of terrestrial, semi-aquatic and aquatic plant communities and the spatial and temporal variation in their distributions. To date all measurements of macrophyte production have been made in a limited area on the central Amazon floodplain near Manaus. Only a few of these estimates have included contributions of more than one species. Junk and Piedad (1995) estimated the cumulative biomass increase of three successive macrophyte communities (terrestrial, semi-aquatic, and aquatic) growing under favorable conditions on the central Amazon floodplain to be 3000 t dry wt. km⁻² yr⁻¹. Assuming a monthly biomass loss of 10-25% during the growing season, they estimated net annual primary production to be 5000 t dry wt km⁻² yr⁻¹. Assuming a dry weight carbon content of 50%, this represents a net annual production of 2500 t C km⁻² yr⁻¹. Using 29,300 km² as the area of floodplain potentially covered by herbaceous macrophytes (see section on geographical features) together with the cumulative, net areal production estimated above (2500 t C km⁻² yr⁻¹), we estimate the total contribution of herbaceous macrophyte communities to floodplain net production along the central Amazon to be about 75 Tg C yr⁻¹.

**Flooded forest trees**

Floodplain forests often occupy a significant portion of the littoral region of Amazon floodplain lakes. Their distributions are generally restricted to the shallower portions of lakes where the annual flooding period is less than 230 - 270 days (Junk and Piedad 1997). The biomass and species diversity of floodplain forests vary spatially as a function of geographical and flooding characteristics. Inundation forests associated with white-water and black-water rivers are taxonomically distinct (Kubitzi 1989, Filoso 1996) and have been classified as várzea and igapó forests, respectively (France 1979). Várzea forests tend to be more productive and have a lower species diversity than igapó forests due to the higher nutrient inputs from white-water rivers (Worbes 1997). Species diversity and biomass also tend to diminish within a given forest with increasing annual inundation period, reflecting the physiological stress of long-term root inundation (Ferreira 1991). Local variations in floodplain forest community structure have been identified as successional sequences related to riverine

**Figure 14.7** Periphyton and macrophyte biomass and areal coverage at Lake Calado, dominant genera are listed in bottom panel: T. R. Fisher, D. Engle, and R. Doyle, unpublished data.

Net production estimates for Amazonian floodplain forests have been based primarily on litterfall data collected at sites near Manaus (Junk 1985, Bayley 1989). Litter production rates of 670 and 1030 t dry wt. km⁻² yr⁻¹ have been estimated for igapô (Adis et al. 1979) and várzea forests (J. Adis, unpublished data cited in Worbes 1997), respectively. The higher litterfall in várzea forests has been attributed to the higher levels of phosphorus and potassium present in soils (Worbes 1997). In addition to fine litterfall, large woody detritus and root production can contribute significant amounts of carbon to floodplain lakes. Worbes (1997) estimated the combined production of fine litter and large woody detritus to vary from 1600–2500 t dry wt. km⁻² yr⁻¹ in well-developed várzea forests. He estimated root production to be 30% of the live wood increment (that is, 730 and 860 t dry wt km⁻² yr⁻¹ of 219 to 258 t dry wt km⁻² yr⁻¹). We assume that fine root production and some coarse litter derived from roots is available to benthic organisms. However, we did not include Worbes' measurements of increment in wood or his estimates of aerial grazing losses in our production values because we considered that production unavailable to aquatic organisms. The total contribution of várzea forests to floodplain lake production thus varied between about 1820 - 2760 t dry wt km⁻² yr⁻¹. Taking the average of these two values and assuming a dry weight carbon content of 50% results in an average net production rate of 1150 t C km⁻² yr⁻¹. This production, which includes inputs during both flooded and dry conditions, is all potentially available to the lacustrine ecosystem. Applying this value to a maximum highwater flooded forest area of 28,200 km², we estimate the total contribution of flooded forests to production along the central Amazon floodplain to be about 52 Tg C yr⁻¹.

**Periphyton**

Periphytic algae require solid substrata and adequate light levels for growth. They are generally found near the water surface in the littoral regions of lakes attached to the submerged portions of emergent macrophytes and flooded forest trees. The highest biomass is usually encountered at the interface between flooded vegetation and open water areas where light availability is greatest. However, significant densities can also occur in the middle of macrophyte and forest stands when light penetration is sufficient for growth. Periphyton community structure has been found to vary among lakes associated with geochemically distinct rivers. In a study of periphytic algae grown during in situ incubations on roughened cellulose-acetate, Putz and Junk (1997) found differences in species composition between white- and blackwater rivers. The periphyton communities in blackwater environments were generally dominated by diatoms throughout the year while those in whitewater contained predominantly green algae during high water with diatoms and cyanophytes increasing in importance at lower water levels. The increased importance of nitrogen fixing cyanophytes at low water provided evidence for the existence of nitrogen-limiting conditions in whitewater lakes at low water.

The underwater stems and roots of the floating plants, so common in lakes such as Calado, are colonized by periphyton. These epiphytic algae, whose biomass per unit area can exceed that of phytoplankton (Engle and Melack 1990), are responsible for high rates of primary productivity (Doyle 1991) and can be an important food for fishes (Forsberg et al. 1993). Doyle (1991) measured using closed, recirculating chambers in situ photosynthesis and respiration of intact periphyton growing on macrophyte roots and stems. Biomass-specific photosynthetic rates were high, and biomass-specific respiration rates averaged 37% of biomass-specific photosynthesis rates, indicating considerable heterotrophic activity in the periphyton. Depth- and time-integrated annual, gross primary productivity for the periphyton attached to floating macrophytes in Lake Calado for 1989 was 1.2 t C km⁻² d⁻¹ (Doyle 1991). Converting this value to net primary productivity is confounded by the difficulty of distinguishing the considerable heterotrophic respiration from autotrophic respiration. Based on Doyle's (1991) measurements of community respiration and biomass increments of periphyton, we estimate net primary productivity to be at least half of gross productivity.

Periphyton accumulations on leaves and branches within flooded forests may be lower than those in floating meadows. For example, Doyle (1991) reported a mean of about 40 mg chlorophyll m⁻² in the periphyton of floating meadows of Lake Calado, while Alves (1991) measured an average of 10 mg chlorophyll m⁻² in the periphyton of the flooded forest near an upland stream in Lake Calado. However, more data on periphyton biomass from a variety of sites are needed before generalizations are warranted.

Putz (1997) estimated production as uptake of 14C by periphyton that grew on artificial cellulose-acetate substrata suspended in several habitats near Manaus. Her results could not be used to compute an areal value for periphyton associated with floating macrophytes due to the complex surface of the natural substrata. To extrapolate her results to areal rates in floodplain forests requires an estimate of leaf area in the euphotic zone per unit area of water. Alves (1991) reported between about 0.5 and 1.5 m² of leaves in the euphotic zone of flooded forest per m² of water; for simplicity we used 1.0. Based on net productivities measured by Putz (1997) at a site dominated by Solimões River water in Lake Camaleão and at a site receiving a mixture of Solimões and Negro river water in Lake Catalão, we estimate average areal periphyton production in várzea forests to be 0.76 t C km⁻² d⁻¹.

The contribution of periphytic algal communities associated with herbaceous macrophytes and floodplain forests to lacustrine production along the central Amazon floodplain was determined by multiplying the maximum area of each habitat (28,000 and 25,300 km² for floodplain forest and herbaceous macrophytes, respectively) by the corresponding daily areal production rate and the average estimated inundation period. Since most lakes along the central Amazon floodplain are associated with the main or side channels of the Amazon River, the areal production values of Doyle (1991) for macrophyte habitat (1.2 t C km⁻² d⁻¹) and Putz (1997) for várzea forest (0.76 t C km⁻² d⁻¹) were considered appropriate. The maximum inundation period for the most flood-tolerant trees in flooded forests along the central Amazon floodplain has been estimated as 270 days (Junk and Piedade 1997). Assuming an average inundation period of half this value (135 days), the annual areal and total regional, net production of periphyton communities associated with floodplain forests were estimated to be 100 t C km⁻² yr⁻¹ and about 3 Tg C yr⁻¹, respectively. Aquatic macrophyte communities can be encountered throughout the year in Amazon floodplain lakes (Junk and Piedade 1997). Assuming an average inundation period of half a year (182.5 days), the annual areal and total regional, gross production of periphyton associated with herbaceous macrophytes were estimated at 220 t C km⁻² yr⁻¹ and about 6 Tg C yr⁻¹, respectively; total regional, net production of periphyton associated with herbaceous macrophytes is about 3 Tg C yr⁻¹. Hence, the regional, net production of periphytic
The table below shows the regional net production estimates for four plant groups contributing to primary production on floodplain of the Amazon River between 70.5°W and 52.5°W.

<table>
<thead>
<tr>
<th>Plant Group</th>
<th>Total area (km²)</th>
<th>Regional Net Production Tg yr⁻¹ (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phytoplankton</td>
<td>10,370</td>
<td>2 (2%)</td>
</tr>
<tr>
<td>Herbaceous macrophytes</td>
<td>29,300</td>
<td>73 (65%)</td>
</tr>
<tr>
<td>Floodplain forest</td>
<td>28,300</td>
<td>32 (28%)</td>
</tr>
<tr>
<td>Periphytic algae: flooded forest</td>
<td>28,300</td>
<td>3</td>
</tr>
<tr>
<td>Periphytic algae: aquatic macrophytes</td>
<td>29,300</td>
<td>3 (3%)</td>
</tr>
<tr>
<td><strong>Total production</strong></td>
<td><strong>113</strong></td>
<td></td>
</tr>
</tbody>
</table>

* See text for information regarding individual estimates.

In an analysis of planktonic production and respiration rates measured by incubating samples in bottles from 30 Amazon floodplain lakes, B. R. Forsberg (unpublished data) found an average respiration to production ratio of 5.4 for oxygen and 6.5 for carbon. The predominance of respiration in these systems is due, in part, to the input of significant quantities of allochthonous carbon from riverine and upland sources. The main cause for the imbalance is the predominance of aerial photosynthesis and aquatic respiration in the plant communities. Emerging macrophytes and flooded forest trees, which account for the bulk of lacustrine production, both have aerial photosynthetic parts and respire predominantly through submerged roots (Hamilton et al. 1995). Hence, these plants contribute organic carbon to the aquatic environment and consume dissolved oxygen, but they return almost no oxygen to the water column, which results in a major deficit of O₂ and excess of CO₂.

Quay et al. (1995) reported lower respiration to production ratios (1.0 to 1.7) in seven Amazon floodplain lakes. These ratios were derived from stable isotope ratios of dissolved oxygen in surface waters where light availability and photosynthesis are often high. The higher ratios calculated by B. R. Forsberg were based on depth-integrated rates and thus more accurately reflect the total pelagic carbon balance.

Inputs of organic carbon to floodplain lakes from the Amazon River are largest during rising river stage and reach a cumulative maximum at high water. Using alkalinity as a hydrological tracer, Forsberg et al. (1998) calculated that many lakes along the central Amazon floodplain contain predominantly river water at high water, but the larger lakes often are ria lakes with a considerable contribution of water from uplands (Lesack and Melack 1995). Based on Sippel et al. (1992), ria lakes cover about 2,400 km² and other lakes the remaining 7,970 km². Based on Forsberg et al. (1988) and Lesack and Melack (1991), we estimate that 90% and 30% of the water in nonia and ria lakes, respectively, at high water, is derived from the Amazon River. Using an average high water lake depth of about 7 m (n = 86, B. R. Forsberg, unpublished data) and the appropriate areas and percent contributions for ria and nonia lakes, we estimate a cumulative annual input of 55 x 10⁶ m³ of river water to open water in lakes. In the remaining 57,530 km² of floodplain occupied by flooded forests and floating macrophytes at high water, after approximating the average depth to be 4 m based on numerous sampling transects into these habitats and estimating that 80% of the water is derived from the Amazon River in these habitats based on examination of optical remote sensing imagery, we calculate an annual input of 184 x 10⁶ m³ of river water. The sum of riverine inputs to the whole floodplain is 239 x 10⁶ m³.

The particulate and dissolved organic carbon in the Amazon River have been shown to be predominantly terrestrial in origin and highly refractory (Hedges et al. 1986, Ertel et al. 1986). The average concentrations of fine particulate organic carbon (PPOC > 63 μm), fine particulate organic carbon (PPOC < 63 μm), and dissolved organic carbon (DOC) in the Amazon River were determined by Richet et al. (1999) to be 0.5, 2.7, and 5.6 g C m⁻³, respectively. Using this average composition and the cumulative water storage on the floodplain, we estimate the total riverine, organic carbon input to the floodplain to be 1.5 Tg C yr⁻¹.

The distribution on the floodplain of particulate carbon derived from riverine inputs depends on its route of entry. In an investigation of sedimentation patterns during diffuse overbank flow onto the central Amazon floodplain, Mertes (1994) estimated that > 80% of the riverine partici-
lates entering the floodplain were deposited within a few hundred meters of the river-floodplain boundary. Riverine sediments entering lakes through discrete channels tend to penetrate further into floodplain lakes. For example, during an early rising water period, Fisher and Parsley (1975) found evidence of turbid river waters penetrating over 30 km into Lake Janaucu.

Riverine DOC is expected to behave conservatively and to be distributed throughout the floodplain. In a stable isotopic study of autotrophic carbon sources for heterotrophic bacteria in Lake Calado, Waichman (1996) found that DOC in all lacustrine habitats was derived predominantly from C-3 plants and was refractory, characteristics similar to those of riverine DOC.

Inputs of water to lakes from upland drainage basins occurs year around (Lesack and Melack 1995) but makes a major contribution to the water occupying lakes during falling and low water (Forsberg et al. 1988). Richey et al. (1986, 1989a) estimated that up to 50% of the discharge of the Amazon River passes through the central floodplain and that part of this flow represents diffuse upland runoff and discharge from small tributaries passing through floodplain lakes. The magnitude of inputs from local upland runoff and direct precipitation to the floodplain was estimated by Richey et al. (1989) and plotted for upriver, midriver, and downriver reaches. We integrated the flow volumes in their plot, subtracted an estimate of direct precipitation and scaled the integrated sum to the entire floodplain. Assuming that all of upland runoff flowed across the floodplain, we calculated the annual input of upland runoff to the floodplain to be 400 x 10^6 m^3 yr^-1.

The organic carbon in upland runoff is expected to be refractory and predominantly terrestrial in origin (Hedges et al. 1986). The local drainage basins of Amazon floodplain lakes are generally forested and local runoff is low in suspended particulates. The concentrations of dissolved and particulate organic carbon in these waters can be estimated from values for black- and clearwater tributaries of the Amazon River which have predominantly unforested basins. The average concentration of suspended sediments in these black- and clearwater tributaries was determined by Forsberg et al. (1988) to be 12 g m^-3. The suspended sediments in black and clear water tributaries are predominantly fine (<63 μm, Richey et al. 1986) and have an average carbon content of 5.4% (Hedges et al. 1986). The average particulate organic carbon concentrations in these rivers is estimated to be 0.65 g C m^-3. The corresponding average concentration of DOC, determined from measurements in seven different black and clear water tributaries (J. E. Richey, unpublished data, n = 29), is 6.08 g m^-3. Using this average carbon composition and the estimated regional input of local runoff, we calculate the total organic carbon input from local drainage basins to floodplain lakes to be 2.7 Tg C yr^-1.

Allochthonous inputs from the Amazon River and local drainage thus contribute 4.3 Tg yr^-1 of organic carbon to floodplain. This represents approximately 4% of total plant production within the floodplain. However, the majority of the allochthonous inputs are refractory carbon, while most of the aquatic plant production is available to other trophic levels.

Heterotrophic activity and foodwebs

Once organic carbon is produced in or transported into floodplain lakes, it is potentially available to heterotrophic organisms. The point at which the organic carbon enters the foodweb, and the rate at which it is assimilated depend on a variety of factors including its physical form, its nutritional quality, and the spatial and temporal distributions of the carbon source and its potential consumers.

Measurements made in Lake Calado indicate that bacteria are responsible for 60 to 90% of the planktonic respiration (E. Peele and T. R. Fisher, personal communication). While bacterial abundances were intermediate (2 to 5 x 10^6 cells per liter), rapid division rates produced bacterial doubling times of about 15 hours. Grazing measurements with tritium-labeled bacteria indicated that bacterial growth was about balanced by bacterial mortality by flagellates (0.2 to 25 x 10^6 per liter), ciliates (10^2 to 10^5 per liter), rotifers (900 per liter) plus cladocera and copepod nauplii (E. Lessard and E. Peele, personal communication). Abundances of adult calanoid and cyclopoid copepods and cladocera were low (1 to 100 per liter) (Fisher et al. 1983, Lenz et al. 1986, Silva 1991), and this may reflect predation by fish larvae.

Macrophytes are apparently the principal source of labile DOC for bacterial communities due to their high production rates and small losses from grazing. The DOC leached from decomposing macrophytes is nutritious and rapidly consumed by heterotrophic bacteria. In enclosure experiments with freshly cut Echinodorus polystachya, the dominant C-4 plant in many macrophyte communities, Furch and Junk (1992) observed an initial weight loss accompanied by a rapid decline in dissolved oxygen concentrations and increase in CO₂ associated with rapid bacterial metabolism of labile DOC. Based on analyses of stable carbon isotope ratios, DOC derived from C-4 plants was found to be the principal carbon source for bacteria, accounting for 89% of bacterially respired CO₂ (Waichman 1996). The DOC present in lake water, in contrast, was found to be predominantly derived from C-3 plants. These results suggest that there are two distinct pools of DOC in lakes: a small pool of labile DOC dominated by C-4 macrophyte inputs with a fast turnover time, and a large pool of more refractory DOC dominated by inputs from C-3 plants with slower turnover times. The refractory DOC component may include degraded terrestrial carbon derived from upland and river inputs or older carbon leached from flooded forest soils or sediments.

The contribution of different plant groups to carbon flow in aquatic foodwebs on the central Amazon floodplain has been investigated in a series of studies utilizing natural variations in carbon stable isotope ratios (Araujo-Lima et al. 1986, Padovani 1992, Fernandez 1993, Forsberg et al. 1993, and Waichman 1996). In an investigation of carbon sources for fish species (Forsberg et al. 1993) found that a minimum of 82% of carbon in fishes was derived from C-3 plants (phytoplankton, periphyton, C-3 macrophytes, and floodplain forest trees), of which 36% was derived from algae. Eleven fish species, including 8 characiform detritivores, derived all of their carbon from algae. Recent results indicate that the delta 13C of periphyton is variable and can be quite negative as are the values from some detritivores (B. R. Forsberg, unpublished data). C-4 plants, which are responsible for the bulk of herbaceous macrophyte production and more than half of all aquatic primary production, accounted for less than 18% of carbon in fishes (Forsberg et al. 1993). In a similar study of carbon sources for larval fish, Fernandez (1993) found a higher contribution of C-4 plant carbon, especially in smaller species, in larvae of Semaprochilodus insignis and Prochilodus nigricans smaller than 55 mm, C-4 plants accounted for 43% and 36% of their carbon, respectively. Percent C-4 carbon diminished above lengths of 55 mm, indicating a shift to C-3 carbon sources in both species as they became fingerlings. In a study of carbon sources for detritivorous shrimp species, Padovani (1992) obtained results similar to those for adult fish. While living in close association with C-4 macrophyte beds, the shrimp derived more than 85% of their carbon from C-3 plants, predominantly periphytic algae associated with macrophyte roots.
The relative lack of carbon derived from C-4 plants in higher organisms is surprising considering the large contribution of C-4 macrophytes to floodplain primary production and suggests that these plants are selectively avoided by aquatic herbivores. Forsberg et al. (1993) presented data on the nutritional quality of plant materials available in floodplain lakes which indicated C-4 grasses to have low food value. The occurrence of C-4 carbon in larval fish can be explained by their spatial distribution and available food sources. Since parental care is rare in Amazonian fish, larvae are vulnerable to predation and tend to seek refuge under the abundant floating macrophytes present in most lakes. These fish are forced to consume the less nutritious C-4 plant detritus which is plentiful under these beds.

The predominance of C-3 plant carbon in most higher organisms reflects the selective consumption of C-3 plants by herbivores and detritivores. Forsberg et al. (1993) found tree fruits and seeds and C-3 macrophytes and algae to have high nutritional value. The high percentage of fruits and seeds encountered in the diets of herbivorous and omnivorous fish tends to support this conclusion (Goulding 1980, Goulding et al. 1988).

The predominance of phytoplankton-derived carbon in diets of many fish species, despite its small contribution to floodplain production, can be explained by the selective consumption of algae. However, Bayley (1989) argued that phytoplankton production was too low to contribute significantly to regional fish production. He based his argument on a food chain with three trophic levels (phytoplankton—zooplankton—fish), and a 10% transfer efficiency between trophic levels. This model is inappropriate for detritivorous and herbivorous fish which consume plant materials directly. A model with two trophic levels would be more appropriate and would indicate a higher potential contribution to fish from phytoplankton. Further, measurements of carbon isotopic ratios for phytoplankton (B. R. Forsberg, unpublished data) suggest that phytoplankton may also be a major carbon source for detritivores and other higher aquatic organisms.

Overall, these results suggest a general pattern of carbon flow in lakes on the central Amazon floodplain. Nutritious plant materials, primarily derived from C-3 plants (phytoplankton, periphyton, C-3 macrophyte leaves, tree fruits, and seeds) are selectively consumed by aquatic herbivores and detritivores and dominate the organic carbon flow to higher trophic levels. Some C-3 plant materials and the bulk of C-4 plants decompose and release their organic carbon, predominantly in the dissolved form, to the water column. The labile component of this DOC, dominated by C-4 plant carbon, is rapidly consumed by heterotrophic bacterial communities and released as either CO₂ or CH₄ to the atmosphere. The more refractory DOC component has a much slower turnover rate and tends to persist in the system where it is eventually exported to the main river channel.

Net carbon losses

Organic carbon is lost from Amazon floodplain lakes by permanent burial, emission as CO₂ and CH₄ to the atmosphere or export to the river. Sufficient data are now available to estimate most of these losses. Methane production is predominately in anoxic environments associated with flooded habitats. Methane emission rates have been estimated in a variety of habitats and sites along the central Amazon floodplain (Devol et al. 1988, 1990, 1994, Grill et al. 1988, Bartlett et al. 1988, 1990, Wassmann et al. 1992, Wassmann and Thein 1994, Engle and Melack 2000). The average emission rates encountered in aquatic macrophyte beds, flooded forest and open water, including data from both seasonal and regional studies, were 0.233, 0.103, and 0.050 t C km⁻² d⁻¹, respectively. Using these values, together with average flooding periods of 182.5, 135, and 365 days and maximum flooded areas of 29,300, 28,200, and 10,370 km², we estimated the total annual CO₂ emissions from macrophyte beds, floodplain forests and open water areas in lakes to be 11.7, 3.6, and 7.5 Tg C yr⁻¹, respectively, resulting in a total floodplain CO₂ loss of 22.8 Tg C yr⁻¹. This value does not include active respiration of above ground and above water vegetation, and, therefore, underestimates the total regional CO₂ flux.

Particulate organic carbon which is incorporated into lake sediments and not oxidized by detritivore and bacterial communities is lost through permanent burial. In an analysis of carbon diagenesis in the pelagic sediments of Lake Jacaretinga, Devol et al. (1984a) estimated the permanent burial rate of particulate organic carbon to be 43 t C km⁻² yr⁻¹. Lake Jacaretinga is a small (about 5 ha) floodplain lake connected to the Amazon River by a 500 m long channel during 6 months of the year. Smith-Morrill (1987) determined burial of organic carbon based on cores collected from three sites in Lake Calado, a moderately sized (2 to 8 km²) lake connected year round to the Amazon River. Lake-wide, burial rates were estimated to be 42 t C km⁻² yr⁻¹. Assuming that burial in these two lakes is representative of the entire floodplain area of 67,900 km², we estimated the total regional loss of particulate organic carbon to permanent burial to be about 2.9 Tg C yr⁻¹.

As part of an analysis of exchanges of sediment between the floodplain and channel of the Amazon River in Brazil, Dunne et al. (1998) calculated the amount of suspended sediments accumulating on a decadal time scale on the floodplain along the reach of the Amazon River from about 52° to 69°W. They used two different approaches and estimated a net transfer of 209 Mt yr⁻¹ and 500 Mt yr⁻¹ of sediments from the river to the floodplain.
Hedges et al. (1986) reported organic carbon to be about 1% of the coarse, sand-size fraction (> 65 μm) of suspended sediments and about 1.2% of the fine, silt-clay fraction (< 65 μm) of suspended sediments. Using the average of these values (about 1.1%), we calculate organic carbon deposited on the floodplain from the river to be between 2.3 Tg C yr⁻¹ and 5.5 Tg C yr⁻¹. The estimate of burial in the floodplain based on cores from lakes should incorporate inputs of suspended sediments from the river, production occurring on the floodplain and inputs from the local catchments. Hence, the value of 2.9 Tg C yr⁻¹ may be low. Given the range of values and the uncertainties in each, we will estimate the burial of organic carbon in the floodplain to be 3 Tg C yr⁻¹. Organic carbon losses due to export to the river were estimated by the difference in the overall carbon balance (see next section).

**Total organic carbon balance**

The total organic carbon balance for lakes on the central Amazon floodplain can be examined by comparing total inputs due to primary production and external loading with total losses (Table 14.4). The combined input of organic carbon due to primary production, river import and local runoff was estimated as 117.3 Tg C yr⁻¹. Combined losses due to biogenic gas emission and permanent burial were estimated to be 27.6 Tg C yr⁻¹. The residual loss term of 89.7 Tg C yr⁻¹ is high, but the majority of the residual probably corresponds to organic carbon export to the Amazon River.

Richiey et al. (1990) used flow-weighted estimates of organic carbon flux and microbial respiration measurements to evaluate the organic carbon balance along 1800 km of the Amazon River. Organic carbon inputs estimated from tributaries were half those required to support in situ oxidation. They hypothesized that the residual oxidation was sustained by diffuse inputs of labile organic carbon from floodplains with a total flux at least as large as the final TOC flux of the mainstem, 36.1 Tg C yr⁻¹. The large organic carbon residual that we calculated suggests that the flux from the floodplain may be significantly greater.

### Biogeochemical Processes and Fluxes: Nitrogen and Phosphorus Dynamics

Understanding the biogeochemistry of nitrogen and phosphorus in floodplain lakes requires measurements of numerous processes, pools, and fluxes. Key processes include nitrogen fixation, denitrification, nitrification, and nitrogen and phosphorus uptake and regeneration. Fluxes within lakes include sedimentation, sediment-water exchange and burial. Further, measuring fluxes between lakes and the atmosphere and neighboring rivers requires merging frequent measurements of solutes or gases with hydrological, hydrodynamic, and meteorological analyses. We emphasize the importance of multiyear, multisite data on these processes and fluxes to determine adequately their spatial and temporal differences and variations. Because most of these processes and fluxes have been examined at Lake Calado, we focus our discussion on it.

Lake Calado (3°15'S, 60°34'W) varies in depth depending on the stage of the Solimões River. This dendritic, ria lake is connected year round to the river via a well-defined channel. All major aquatic habitats and interfaces (as described in our conceptual framework of a floodplain lake) are represented in the lake. As is typical of floodplain lakes, Lake Calado receives solutes and particulates from the Solimões River and local sources that include direct rainfall and dry deposition, upland runoff, groundwater seepage, exchanges with neighboring lakes, and nitrogen fixation within the lake. All these fluxes have been measured at Lake Calado (Table 14.5; Lesack 1988, Lesack 1993a, Lesack and Melack 1991, Doyle and Fisher 1994). While the river was the major supplier of P, inputs of N predominantly were from local sources. Nitrogen fixation provided about 8% of the total annual N inputs (Doyle and Fisher 1994).

Measurements of atmospheric deposition spanning at least one full year, based on event collections with timely assays and including inorganic and organic fractions of N and P are very rare for the Amazon basin. The only two studies available (Lesack and Melack 1991, Williams et al. 1997a) were done at Lake Calado in 1983–1984 and 1986–1990, respectively. Solute concentrations were not statistically different between these two studies, and both studies attributed most of the solutes to biogenic rather than anthropogenic sources. To detect temporal trends and spatial differences in atmospheric deposition to the Amazon as development proceeds will require multi-year monitoring programs at several sites.

Througfall and litterfall from flooded forests represent a complex aspect of nutrient dynamics in floodplain lakes that has received little attention. Filoso (1996) measured wet deposition and throughfall from igapó forest of the Anavilhanas archipelago in the lower Negro River, and calculated that about two-thirds of the rain that fell on floodplain lakes in the Anavilhanas was influenced by flooded forest canopy. The deposition of dissolved P increased about seven times after rain was

---

**Table 14.4 Organic carbon balance for floodplain of Amazon River between 52.5⁰W and 70.5⁰W.**

<table>
<thead>
<tr>
<th>Input or Output</th>
<th>Regional Total (Tg C yr⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aquatic net primary productivity</td>
<td>113.0</td>
</tr>
<tr>
<td>Amazon River input</td>
<td>1.6</td>
</tr>
<tr>
<td>Local runoff input</td>
<td>2.7</td>
</tr>
<tr>
<td>Methane emission</td>
<td>-1.8</td>
</tr>
<tr>
<td>CO₂ emission</td>
<td>22.8</td>
</tr>
<tr>
<td>Burial</td>
<td>-3.0</td>
</tr>
<tr>
<td>Export to river and residual errors</td>
<td>-89.7</td>
</tr>
</tbody>
</table>

* See text for derivation of values.

---

**Table 14.5 Inputs of total nitrogen (TN) and total phosphorus (TP) to Lake Calado in 1984–1985.**

<table>
<thead>
<tr>
<th>Source</th>
<th>TN (Tg C yr⁻¹)</th>
<th>%</th>
<th>TP (Tg C yr⁻¹)</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Direct rainfall</td>
<td>0.24</td>
<td>9</td>
<td>0.006</td>
<td>6</td>
</tr>
<tr>
<td>Surface runoff</td>
<td>1.29</td>
<td>43</td>
<td>0.011</td>
<td>11</td>
</tr>
<tr>
<td>Groundwater</td>
<td>0.14</td>
<td>5</td>
<td>0.018</td>
<td>19</td>
</tr>
<tr>
<td>Adjacent lakes</td>
<td>0.24</td>
<td>8</td>
<td>0.013</td>
<td>13</td>
</tr>
<tr>
<td>Amazon River</td>
<td>1.03</td>
<td>35</td>
<td>0.049</td>
<td>51</td>
</tr>
</tbody>
</table>

* Source: Data are from Lesack (1988), and calculations modified from Fisher et al. (1991).

* Units are 10⁶ moles of N or P yr⁻¹, and % is the percentage of the total contributed by each source.*
intercepted by the canopy, and the N to P ratio in throughfall was 3. In contrast, the N to P ratio in Negro River waters was 20, and these waters supplied only about half of the P to the lakes.

While nutrients supplied by throughfall are immediately available to the algae, forest litter must first decompose to supply nutrients to the overlying water. For example, based on measurements of decomposition of *Pseudobombax munguba* leaves in a stagnant tank and a litterfall of 4 tons ha\(^{-1}\) yr\(^{-1}\) decomposing underwater, Parch et al. (1984) estimated that after 4 weeks of decomposition concentrations of P would increase about 50% in a 4 m water column. However, given that flooded forests can be composed of 50 to 80 tree species per ha, each with different foliar composition (Klinge et al. 1983) and decay rates, and that decomposition varies as a function of the in situ physicochemical conditions, considerably more study (e.g., Parch et al. 1989) is required to determine the quantitative role of decomposition of litterfall in floodplain biogeochemistry.

Floodplain lakes lose N and P via outflow to rivers and neighboring lakes, burial in sediments and groundwater seepage. Nitrogen can also be lost via denitrification. During the period of study at Lake Calado, outflow to the river was the major loss (Table 14.6, Lesack 1988). Burial in lacustrine sediments was of secondary importance (Smith-Morrill 1987), and groundwater seepage was small. Although annual losses to the river exceeded annual inputs from the river, interannual variations in these fluxes are to be expected, and it is premature to state that the floodplain is a net source of N or P to the river.

Conditions conducive to denitrification seem to occur only intermittently in selected sites in Amazon floodplain lakes. Melack and Fisher (1988) were unable to detect denitrification in water or sediments of Lake Calado during periods of rising and falling water. However, undersaturated concentrations of nitrous oxide observed in lake water could indicate denitrification is occurring. In Lake Camaleão, Kern et al. (1996) measured denitrification, without substrate amendment, during low water when nitrate in overlying water reached about 5 μM, but not at other times during their seven month study. Denitrification was highest in sediments exposed to air at low water, and N\(_2\)O was evolved from these exposed sediments, but not from flooded sediments. Sediment slurries amended with 100 μM nitrate exhibited detectable denitrification, a result indicating limitation by nitrate of denitrifiers.

Recycling of N and P occurs in the water column and at interfaces between the water and substrata such as profundal sediments. In Lake Calado, regeneration of ammonium and phosphorus is dominated by planktonic heterotrophs less than 55 μm in size (Table 14.7, Lenz et al. 1986, Fisher et al. 1988a, Fisher et al. 1989b, Morisset and Fisher 1988). Sediment—water exchange is smaller than planktonic processes, but is substantial.

### Table 14.6 Losses of total nitrogen (TN) and total phosphorus (TP) from Lake Calado.

<table>
<thead>
<tr>
<th>Term</th>
<th>TN</th>
<th>%</th>
<th>TP</th>
<th>%</th>
</tr>
</thead>
<tbody>
<tr>
<td>Groundwater</td>
<td>0.18</td>
<td>4</td>
<td>0.012</td>
<td>5</td>
</tr>
<tr>
<td>Burial</td>
<td>1.36</td>
<td>28</td>
<td>0.072</td>
<td>31</td>
</tr>
<tr>
<td>Outflow</td>
<td>3.26</td>
<td>68</td>
<td>0.152</td>
<td>64</td>
</tr>
</tbody>
</table>

Source: Data are from Lesack (1988) and Smith-Morrill (1987), and calculations are from Fisher et al. (1991).

### Table 14.7 Summary of nitrogen (as NH\(_4\)) and phosphorus (as PO\(_4\)) regeneration in Lake Calado.

<table>
<thead>
<tr>
<th>Term</th>
<th>N</th>
<th>P</th>
<th>N:P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Zooplankton (&gt; 55 μm)</td>
<td>1.0 (5%)</td>
<td>0.11 (2%)</td>
<td>9</td>
</tr>
<tr>
<td>Total plankton</td>
<td>13.8 (65%)</td>
<td>3.36 (78%)</td>
<td>4</td>
</tr>
<tr>
<td>Sediments</td>
<td>6.5 (30%)</td>
<td>0.89 (20%)</td>
<td>7</td>
</tr>
</tbody>
</table>

Source: Calculations are from Fisher et al. (1991), and data are from references cited in text.

* Units are 10\(^6\) moles of N or P yr\(^{-1}\), and % is the percentage of the total contributed by each term.

* Total plankton and zooplankton data are assigned over a 3 m epilimnion. Units are nmol m\(^{-3}\) d\(^{-1}\). Percentages (in parenthesis) are the percent of total recycling represented by each process. N:P is the atomic ratio of the rate.
indicated limitation by phosphorus; physiological assays implied that the phytoplankton were impoverished in both N and P (Setaro and Melack 1984). In contrast, during falling and low water, N and P or nitrogen alone were required to stimulate algal growth; physiological measurements detected nitrogen deficiency or N or P sufficiency. Bioassays done in another floodplain lake adjacent to the Amazon River during low water also indicated responses to N or to N plus P (Zaret et al. 1981, Devol et al. 1984b). Measurements of sestonic N to P ratios and bioassay experiments done in a small lake bordering the Negro River indicated phosphorus limitation (Forsberg 1984).

Setaro and Melack (1984) hypothesized that the seasonal changes in nutrient limitation in Lake Calado were related to differences in stratification and mixing. At high water, when the lake was deep and stratified, phosphorus-rich particulates derived from the river tended to sink from the water column, increasing the potential for P-limitation. At low water, these sediments were resuspended, increasing P availability and driving the system toward N-limitation. However, the presence of anoxic-anoxic interface in the water column when floodplain lakes are stratified, as commonly observed in Lake Calado (MacIntyre and Melack 1988) and other floodplain lakes, could create a sink for dissolved inorganic nitrogen because of enhanced denitrification at the interface but have little influence on the upward flux of P.

B. R. Forsberg (unpublished data) provides further evidence for nutrient limitation (Table 14.2). Light saturated rates of photosynthesis (Pmax) were found to vary as a linear function of either total nitrogen (TN) or total phosphorus (TP) concentration. TP was mostly the main source of variation in Pmax in black- and clearwater lakes at both high and low water. This indicates a consistent pattern of P-limitation in these systems, which was linked to the high TN to TP ratios. In whitewater lakes, Pmax varied as a function of TP at high water and TN at low water. This reflects a shift from P-limitation to N-limitation and was accompanied by a decrease in average TN to TP ratios.

The N and P adsorbed to suspended sediments in Amazon floodplain lakes are available to phytoplankton (Grobbelaar 1982). Up to 30% of available P may be adsorbed to clay particles (Engle and Sarnelle 1990). Further, rapid exchange can occur among the pools of particulate, dissolved inorganic P (DIP) and dissolved organic P (DOP). Carrier-free 32P (as PO4) additions to surface waters of Lake Camaleão, collected during low stage, were fractionated over 12 hours into four compartments: particulate (>0.2 μm, 83%), dissolved inorganic P (9.4%), high molecular weight DOP (about 66,000 Da, 7.3%) and very high molecular weight DOP (>200,000 Da, 0.3%). Turnover times of DIP were 8 to 11 hours (Pinheiro 1996). In addition, enzymatic hydrolysis of DOP occurs in white- and blackwaters with low molecular weight fractions (<1,000 Da) being the most susceptible (Pinheiro 1996).

Because attached algae retain their position close to the water surface, they may be better placed to exploit nutrients in turbid riverine floodwaters. Further, because particulate-bound nutrients are retained among the floating macrophytes, epiphytic algae have access to these nutrients, as well. Engle and Melack (1995) investigated the interactions between suspended sediments, dissolved nutrients, and epiphytic algal growth in floating meadows in a series of in situ experiments in Lake Calado. During rising and high water, chlorophyll per gram of macrophyte roots was less than controls in experimental treatments bathed in river water. Addition of N and P without sediments increased chlorophyll above controls. Further, when epiphytic algae were treated with dilutions of river water (9%, 10%, 25%, and 100%), only the 10% treatment resulted in significantly more algal chlorophyll. Hence, the influence of nutrient-rich, turbid water on epiphytic algal abundance will depend on subtle differences in suspended sediment concentrations. Nutrients for macrophyte growth in lakes can be derived from sediments, soils, rivers, and local streams. Nutrient availability in lake sediments or soils tends to be higher on whitewater floodplains and lower in black- and clearwater environments (Purch 1997). Nutrient availability for floating species tends to be highest during low and rising water and lowest during falling water when river inputs are reduced. Junk and Piedade (1997) found little evidence for short-term nutrient limitation in macrophyte communities growing in whitewater environments. Nutrient limitation was more common in acidic blackwaters and appeared to restrict the growth.

**Figure 14.8** Input and output of nitrogen (tons per 650 ha) at Lake Camaleão during the period from 2 June, 1992 to 14 March, 1993; from Kern and Darwich (1997).
and occurrence of aquatic and semiaquatic macrophytes in these environments. Biota
assays with Salvinia auriculata, Eichhornia crassipes and Pistia stratiotes transferred from
whitewater to acidic blackwaters indicated short-term growth limitation (Junk and
Pingale 1997).

The N to P ratio in the sources and sinks of N and P provides an ecosystem level
indication of the likelihood of limitation by N or P (Howarth 1988). Based on the
measurements at Lake Calado summarized above, it is possible to determine the N to P
ratios for inputs, losses and recycling within the lake. Overall, inputs to Lake Calado
from rain, upland runoff, groundwater seepage, adjacent lakes, and riverine inflows had
an aggregate molar N to P ratio of 32; inclusion of nitrogen fixation would increase
the ratio. Losses via burial as sediments and outflow to the river, but not including
gaseous losses of N, had an N to P ratio of 20; denitrification would decrease the ratio.
Internal recycling by bacteria and zooplankton within the water column and by regen-
eration from sediments had molar N to P ratios of 4 and 7, respectively. Typically,
molar N to P ratios below 10 are indicative of N-limitation, and molar N to P ratios
above 20 are indicative of P-limitation in primary producers. Therefore, the likelihood
of N or P-limitation will vary as a function of spatial and temporal differences in the
relative importance of inputs or recycling.

Impacts of Human Disturbances

Floodplain lakes can be perturbed by direct alterations to the lakes and fringing
wetlands, by changes to the river with which they are associated, and by modifications to
the uplands surrounding their local catchments and to their aisheds. To date, human-
induced impacts on floodplain lakes are not

ments of the Amazon, including Curú-Uma, Samuel, Tucuruí, and Balbina in Brazil (Junk
1994). Many more are planned. Melack (2001) reviewed published studies of condi-
tions within the reservoirs, a topic outside the scope of this chapter. Altrations of flows
downstream of dams have major implications for floodplain ecosystems adapted to
and dependent on a natural flood regime. While detailed studies are not available for
any of the major Amazonian dams, numer-
ous interactions between the biota and the
flood pulse documented elsewhere in the
Amazon (Junk 1997) are fair warning that
myriad impacts are likely. The regulated
flows will reduce flood levels and maintain
higher low flows with a net effect of decreasing the area of floodplain enriched with
riverine sediments each year and hence
available for agriculture and use by fishes
and other organisms (Barrow 1988).

Mercury pollution

Mercury contamination is a significant problem in many Amazon lakes. While
commonly linked to the indiscriminant use of azougue (liquid mercury) in gold mining
areas, a portion of the mercury in lakes appears to be derived from natural sources.
The relative importance of these sources and their influence on the biota and human
inhabitants of lakes can only be understood in context of the larger regional and global
mercury cycles. The primary source of mercury in most lacustrine environments is
the atmosphere (Watras et al. 1995). Atmospheric mercury concentrations have
tripled globally during the last hundred
years due to increased emissions from
anthropogenic sources (Mason et al. 1994). Emissions of mercury vapor from Amazon gold fields have contributed to this rise, accelerating significantly during the last 25 years (Forseberg 1992). Natural sources (i.e., volcanism, weathering, and air-ocean exchange) also contribute significantly to the atmospheric mercury load and have contributed to atmospheric deposition. Atmospheric mercury reaches lakes directly through atmospheric deposition and indirectly through inputs of atmospherically derived mercury from the terrestrial catchment (Swain et al. 1992). B. R. Forseberg (unpublished data) has found evidence of a gradual increase in mercury inputs to Lago Cristalino, a floodplain lake associated with the Negro River, during the last 60 years (Fig. 14.9). This finding suggests that atmospheric deposition from global and regional anthropogenic sources have had a significant impact in central Amazon basin.

Exceptionally high levels of mercury, apparently derived from natural sources, have been encountered in Amazonian soils (Roulet et al. 1998, Silva-Gorsberg et al. 1998). These soils represent an important natural source of mercury to lacustrine ecosystems. Mercury is released from soils by both physical and chemical weathering, and generally complexed to particulate or dissolved organic matter (Roulet et al. 1998). The highest levels of mercury are consequently encountered in blackwater rivers and lakes which receive large inputs of terrestrially derived organic matter. The low pH and high DOC in these systems also favors the methylation and bioaccumulations of mercury resulting in high levels of contamination in predatory fish and fish-eating human populations (Forseberg et al. 1995). Strong, basin-wide correlations have been found between human mercury contamination and both river pH and DOC.

Impacts of deforestation on Amazon floodplain lakes

The deforested area in the Amazon basin increased through the 1980s (Skole and Tucker 1993) and has continued to increase in the 1990s. While accessible areas bordering navigable rivers and roads are particularly prone to deforestation, effects of deforestation on the ecology of adjacent streams, rivers and lakes have received limited attention (Brujinzeel 1991). Lake Calado was studied during the 1980s when its catchment was undergoing rapid development (Melack and Fisher 1990, Melack 1996). Downstream lacustrine waters were influenced by increased inputs of water and solutes resulting from deforestation.

The hydrologic characteristics of runoff in the Amazon determine the magnitude of the various hydrologic pathways that transport nutrients and other solutes (see McClain and Eisenbeer, this volume). Given the high frequency of storms in wet equatorial climates, it is important to understand how export of nutrients and solutes is influenced by storm size and frequency, and the volume of generated runoff. However, most hydrological studies in the Amazon basin have been done in areas of intact rain forest (Nordiff and Thomes 1981, Lesack 1993a), and do not address the effects of deforestation.

Intrasystem processes and their effects on solute transport can be evaluated by measuring solution chemistry at different stages of a hydrologic pathway. Studies of nitrogen transformations along hydrologic pathways in Amazon catchments have been conducted by McClain et al. (1994) and Brandes et

solution chemistry for a suite of solutes at different stages of a hydrologic pathway through an upland catchment.

At Lake Calado, Lesack (1993a) measured all the water balance components for a first-order catchment draining a 23 ha stand of undisturbed upland rain forest adjacent to the Amazon floodplain. In parallel studies, Lesack (1993b) measured fluxes of solutes exported by streamflow and subsurface outflow, and Lesack and Melack (1996) calculated mass balances based on input and outputs. Williams and Melack (1997) and Williams et al. (1997b) measured water and solute fluxes from the same catchment after partial deforestation had occurred. Large increases in solute mobilization from the upper soil horizons to groundwater were observed from a 2 ha plot after cutting and burning in a partially deforested catchment. The first water collected from lysimeters in the cut-and-burned plot contained very high nitrate concentrations (about 1800 μM). In groundwater, nitrate increased by a factor of 5 to about 100 μM after cutting and burning. However, mean volume-weighted concentrations of nitrate in the stream water were similar before and after partial deforestation. The high nitrate concentrations evident in groundwater after deforestation may have been dinitrified prior to reaching the stream or sequestered in riparian vegetation or the stream bed. Solute export via streamwater increased and nutrient ratios were altered subsequent to deforestation (Table 14.8). Rainfall was similar during the two periods, but runoff was higher in the catchment after disturbance. While inputs of total N and total P via rain were smaller in 1989–1990 than in 1984–1985, export via streamflow was greater in 1989–1990. In fact, after partial deforestation, more N and P were exported than added via rain. The N to P ratio of fluvial flux from the intact forest was 120:1; following deforestation, the ratio decreased to 33:1. Although the total N yield doubled after disturbance, the total P yield increased by a factor of 7, primarily due to increased particulate P.

Research Frontiers

Regionalization of biogeochemical fluxes

Characterization of the areal extent and temporal changes of the tropical floodplains would extend our understanding of trace gas exchange within these ecosystems and

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Rain quantity</td>
<td>cm yr⁻¹</td>
<td>280.0</td>
<td>275.0</td>
</tr>
<tr>
<td>Rain TN</td>
<td>kg N ha⁻¹ yr⁻¹</td>
<td>6.7</td>
<td>4.5</td>
</tr>
<tr>
<td>Rain TP</td>
<td>kg P ha⁻¹ yr⁻¹</td>
<td>0.34</td>
<td>0.21</td>
</tr>
<tr>
<td>Runoff</td>
<td>cm yr⁻¹</td>
<td>160.0</td>
<td>208.0</td>
</tr>
<tr>
<td>Runoff TN</td>
<td>kg N ha⁻¹ yr⁻¹</td>
<td>4.3</td>
<td>9.1</td>
</tr>
<tr>
<td>Runoff TP</td>
<td>kg P ha⁻¹ yr⁻¹</td>
<td>0.082</td>
<td>0.61</td>
</tr>
</tbody>
</table>
of their significance to regional hydrological and biogeochemical processes. The recent availability of optical and synthetic aperture radar data from satellites can be used to study these processes by providing information on the type and distribution of aquatic plants and temporal distribution of inundation (Melack et al. 1994, Melack and Hess 1998, Mertes et al. 1995). For example, delineation of both flooding status and vegetation, with accuracies greater than 90%, has been demonstrated using multifrequency, polarimetric synthetic aperture radar data for floodplains in the central Amazon (Hess et al. 1995). Application of spectral mixture analysis to Landsat multispectral scanner and thematic mapper imagery has permitted calculation of concentrations of suspended sediments in surface water of the Amazon (Mertes et al. 1993). When combined with models of ecological processes, the synoptic information offered by remote sensing will permit calculation of rates on a larger scale and provide much improved data for resource management.

Comparative limnological studies

As is evident throughout this review, a much wider diversity of lakes and floodplain environments must receive the attention of limnologists. Additional measurements of periphyton productivity, of burial of C, N, and P in sediments, of nitrogen fixation and denitrification, and of carbon dioxide emissions, especially, are needed. A further challenge is to investigate biogeochemical processes in the ATTZ, and to link these processes with the whole floodplain ecosystem.

Hydrological and hydrodynamical analyses

Basic hydrological information is lacking and biogeochemistry on floodplains, it is essential to examine a representative set of lakes in a manner similar to that employed at Lake Calado (e.g., Lesack and Melack 1995). Complementary approaches using naturally occurring and introduced chemical and isotopic tracers should also be tried. Recent advances in measuring and modeling mixing and advective processes in lakes (Maclntyre and Melack 1995) must be applied to floodplain lakes to increase our understanding of processes causing nutrient fluxes. Improved equipment is now available to measure currents (e.g., acoustic Doppler current meters) and mixing (e.g., microstructure profilers). Highly accurate locations can be determined with portable global positioning units.

Experimental approaches

Experimental manipulations of whole lakes or of enclosures within lakes has proven a valuable approach to decipher processes controlling ecological and biogeochemical activity in lakes. The large number of small to moderate-sized lakes on the Amazon floodplain offers an excellent opportunity to employ replicated, whole-system manipulations. Of particular importance would be experimental alterations of flooding periodicity and depth, and of nutrient inputs.

Management issues

The continued construction of hydroelectric dams and expansion of agricultural and urban areas adds urgency to increasing our ability to forecast biogeochemical consequences of such developments in the Amazon basin. Applications of limnological understanding to timber management in flooded forests, to fisheries, to conservation and biogeochemistry of Amazon floodplain lakes and associated wetlands.

Acknowledgments

Our research and perspectives on Amazon floodplain lakes have benefited from collaborations with many individuals in Brazil and the United States, and we especially acknowledge T. R. Fisher, L. F. V. Lesack, M. R. Williams, S. Machnytre, S. K. Hamilton, D. Engle, L. Smith, L. Alves, J. R. Richey, R. L. Victoria, and L. Martinelli. We thank M. McClain, G. Xing, S. Hamilton, D. Engle, T. Homme, Y. LaCapra, J. Sickman, and T. Dunne for thoughtful comments on earlier drafts. Funding from the U.S. National Science Foundation and National Aeronautical and Space Administration has supported much of our research in the Amazon.

Literature Cited


