

RIVERS OF NORTHERN SOUTH AMERICA

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INTRODUCTION

More water reaches the sea from the northern half of South America than from any other land area of similar size. This region, which for present purposes is defined as all river basins of South America that lie predominantly north of 15°S latitude (Fig. 8.1), has an area of 12×10^6 km², mean precipitation of 1700 mm yr⁻¹, and mean runoff of 850 mm yr⁻¹, for a combined average discharge to the sea of 330 000 m³ s⁻¹ [unreferenced geographic statistics are original from a treatment by a geographical information system (GIS) of map-derived data]. Northern South America contains both the Amazon, which defines a class by itself among world rivers, and the Orinoco, which carries the world's third-largest discharge (Table 8.1).

Large amounts of precipitation over much of northern South America support not only rivers of great width, depth and discharge, but also a dense network of small streams, particularly in the extensive wet areas of low relief in the Amazon and Orinoco basins. Junk and Furch (1985) have estimated that the jungle near Manaus supports approximately 2 km of stream per square kilometer of land. If this figure is typical of wet areas of low relief that occupy large portions of northern South America, the whole of northern South America must contain at least 10⁷ km of low-order streams.

Ecological studies of running water in Europe and North America have focused on streams rather than rivers (Hynes, 1989). In contrast, work on running waters in South America and in the tropics generally has emphasized large rivers. A good preliminary understanding of the main-stems of the Amazon and Orinoco rivers and a few of their major

tributaries has emerged over the last decade, but small rivers and streams have scarcely been studied. Ironically, some of the intensive studies of main-stems and large tributaries of the Amazon and Orinoco rivers have few parallels for rivers of higher latitudes because appropriate funding for the ecological study of large rivers has seldom been available, and because rivers of higher latitudes have been so altered as to discourage study by those in search of baseline characteristics for large rivers.

This chapter is based primarily on internationally accessible literature. Summary papers are cited where possible; numerous additional important sources can be found in the bibliographies of the summary papers. Regional studies are not fully represented because small or short-term projects often find their final resting place in student theses or government reports rather than the open literature. However, portions of sustained regional projects are usually published in the open literature. The importance of symposium volumes in this regard will be especially evident.

The perspective of this chapter is restricted insofar as possible to running waters; terrestrial environments and flood plains are treated exclusively from the viewpoint of their influence on running waters. This arbitrary means of limiting scope is not intended to obscure the reciprocal nature of interactions among flood plain, river and forest.

PHYSIOGRAPHY AND GEOLOGY

The physiography and surface geology of northern South America can be understood at the most fundamental level in terms of four structural elements (Fig. 8.2): (1) the crystalline basement; (2) the

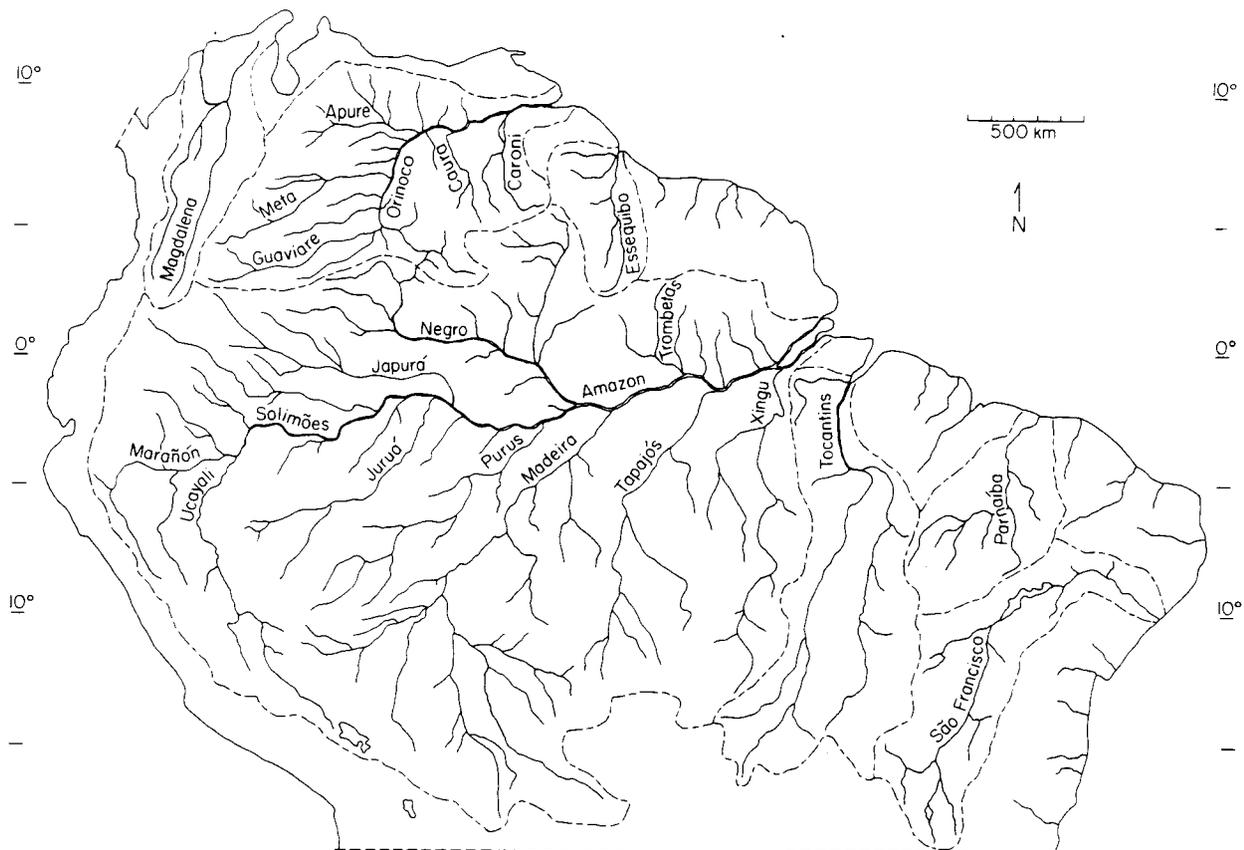


Fig. 8.1. Major drainage basins of northern South America.

TABLE 8.1

Physical characteristics of three large rivers of northern South America

Characteristics	Amazon	Orinoco	Magdalena	Sources ¹
Fringing flood plain ($\text{km}^2 \text{km}^{-1}$)	32	9.3	35	a, b, c
Deltaic flood plain (km^2)	25 000	20 000	—	a, b
Flood-plain coverage by lakes (%)	11	7	13	a, b, c
Human population density (indiv km^{-2})	1	1	90	c
Channel width (lower reaches, km)	5	2	—	d, e
Mean channel depth (lower reaches, m)	20–50	10–25	—	d, e
Maximum depth (lower reaches, m)	100	50	—	d, e
Annual amplitude of water level (m)	9	12	7	c, f, g

¹ Sources:

- a: Sippel et al. (1992), Melack and Fisher (1990).
- b: Hamilton and Lewis (1990a).
- c: García Lozano and Dister (1990).
- d: Sioli (1975, 1984).
- e: Lewis and Saunders (1984, 1993)
- f: Meade et al. (1991).
- g: Saunders and Lewis (1989b).

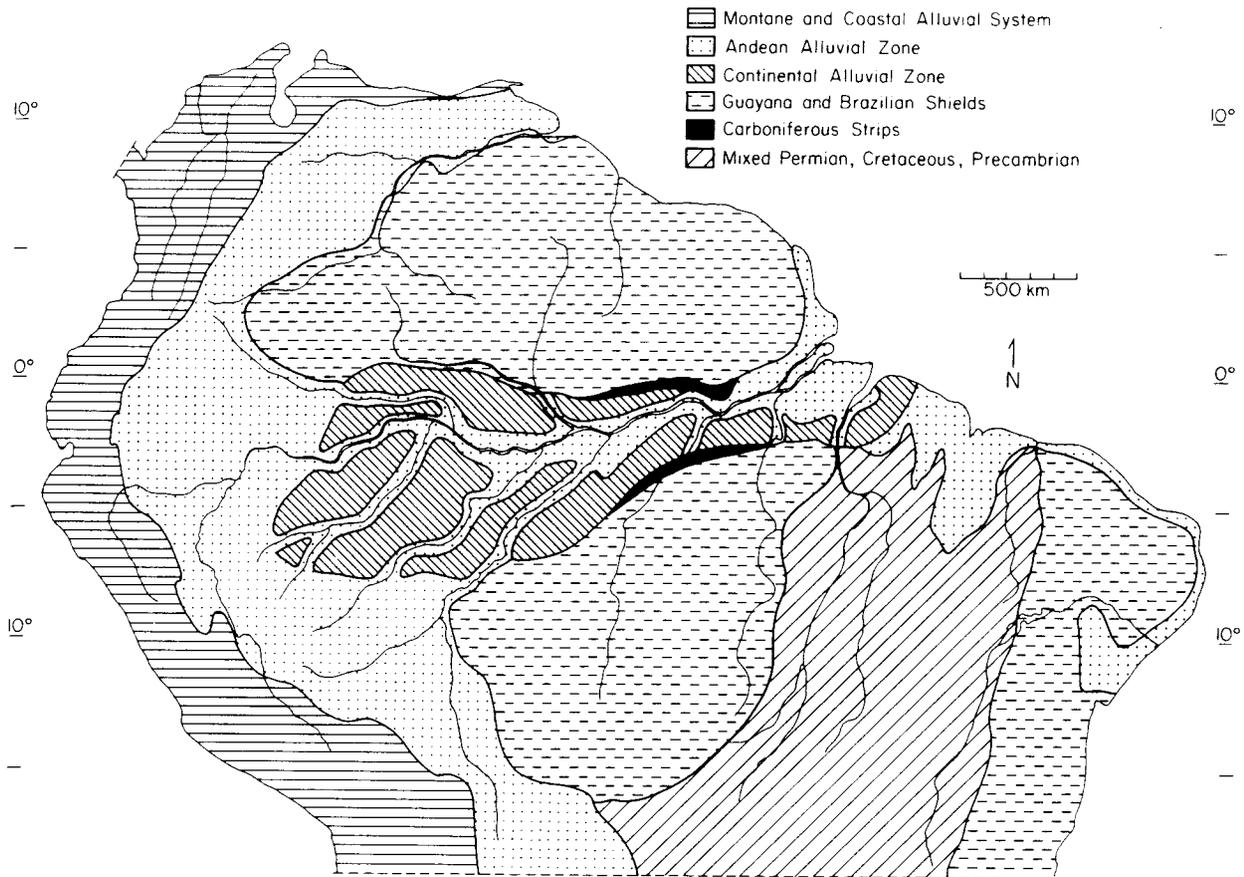


Fig. 8.2. Major geologic surface features of northern South America (simplified from many sources).

Andes; (3) alluvial deposits; and (4) deposits from inland seas and large lakes. The following brief account of these features is taken primarily from Fittkau et al. (1975), Klammer (1984), Putzer (1984), and Stallard (1985).

The crystalline basement rock underwent metamorphic transformation over the interval between 3500 and 600 million years B.P. The basement lies near the surface in two large areas, which are designated the Guayana Shield (north of the Amazon) and the Brazilian Shield (south of the Amazon). The Amazon flows through a deep, sediment-filled graben in the basement rock separating the Brazilian and the Guayana Shields, and the Orinoco flows along the northern margin of the Guayana Shield. Three arches (Iquitos, Purús, Gurupá) across the graben divide the underlying sediments but do not appear at the surface.

The shields account for one-third of the area of northern South America (Fig. 8.2). Some portions

of the two shields are covered by thick layers of consolidated or unconsolidated sediments of pre-Tertiary origin. Unconsolidated sediments often take the form of mesas; an example is the Roraima Group of southern Venezuela and northern Brazil, which is identifiable in Fig. 8.3 as an elevated area on the shields. Unconsolidated sediments are the erosion products of surfaces that were once similar to those of the remaining mesas. Near the regions of high relief on the shields, and in depressions created by the most recent erosion of the shields, the unconsolidated deposits are of recent origin.

The shields and their overlying consolidated and unconsolidated sediments are the intact and the eroded and redeposited remnants of the crystalline basement. For this reason, waters draining from the two shields have in common a geochemical profile primarily reflecting highly weathered crystalline basement. In some regions, igneous intrusions and volcanic deposits add topographic and geochemical

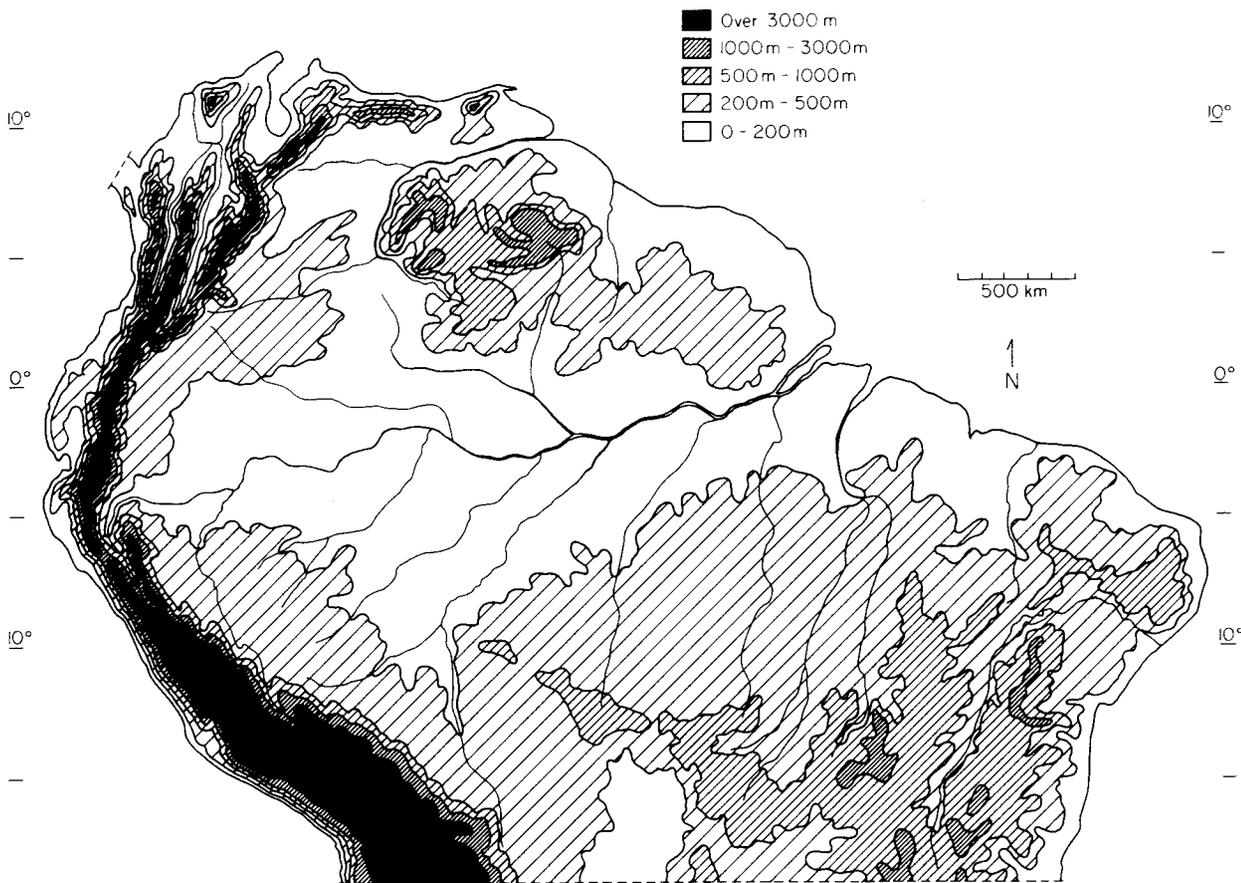


Fig. 8.3. Topography of northern South America [original prepared with data from Anon. (1969)].

irregularities, but the shield region is without limestones or evaporites.

Where the shields are not covered by sediments, the land-surface elevation is seldom more than 150 m above sea level. The pre-Tertiary consolidated sediments that form large blocks on top of the shields have created some steep relief, especially in the southern portion of the Orinoco drainage, where the highest peaks exceed 3000 m above sea level (Fig. 8.3). Relief on the Brazilian Shield is less extreme (typically below 500 m). The low-elevation portions of the shields also show some relief.

At the south margin of the Guayana Shield and the north margin of the Brazilian Shield adjacent to the channel of the Amazon, carboniferous strips, which are solute-rich remnants of an extensive marine transgression, are exposed at the surface. These strips, although small relative to the whole basin, create geochemical and biological peculiarities in the streams and rivers that flow through them.

Fringing the Amazon and Orinoco basins, and separating these basins from the Magdalena and from the many small drainages reaching the west and north coasts of northern South America, are the Andes. The uplift of the Andes was complete by the end of the Miocene, and probably resulted in reversal of drainage from the upper basin, which is believed to have drained previously to the Pacific. For the last 60 million years, the Andes have provided abundant alluvial materials to the basins of the Amazon, Orinoco and Magdalena. The greatest extent of these alluvial materials is the Andean foreland, a band about 500 km wide along the eastern front of the Andes ("Andean alluvium"). The Andes are of great geochemical significance to the waters of northern South America because they have exposed the thick sedimentary beds and volcanic deposits that had accumulated over the basement in this region, and are producing from this source much greater amounts of dissolved and

suspended solids than the flatter, more thoroughly weathered, and more resistant shields. In addition, the elevational gradient of the Andes has created gradients of temperature, vegetation, current velocity and mean incident irradiance for running waters.

In the immediate vicinity of the Amazon main-stem, between the Guayana and Brazilian Shields, are extensive unconsolidated deposits derived from the shields. This "continental alluvium" differs physically and chemically from the Andean alluvium (Fig. 8.2); it is rich in the mineral end-products of weathering, and has a geochemical affinity with the shields rather than the Andes. The Andean alluvium penetrates the continental alluvium along the main-stems of rivers that originate from the Andes or the Andean foreland; surface sediments in the flood zone of these rivers are more similar to the Andean alluvium than to the surrounding continental alluvium.

Because the largest rivers are as yet unregulated, they show great annual amplitudes of change in water level (Sioli 1975, 1984; Saunders and Lewis 1989b; Meade et al. 1991); great amplitudes produce the extensive flooding that maintains fringing flood plains along the river margins. Large expanses of fringing flood plain are found along the main stems of the Amazon, Orinoco and Magdalena (Table 8.1). The fringing flood plain of the Orinoco is concentrated on the northern margin, whereas those of the Amazon and Magdalena occupy both margins. Above the Amazon fringing flood plain, which is designated "várzea", are multiple depositional terraces that probably reflect changes in sea level (Klammer, 1984).

The fringing flood plains of the Amazon, Orinoco and Magdalena are occupied by uncanopied permanent water bodies that include both broad, flat depressions and channels that were formed by flowing water (Table 8.1). The Amazon and Orinoco have extensive amounts of seasonally flooded forest, whereas the Magdalena flood plain is intensively farmed. The Orinoco and the Amazon also have extensive deltaic flood plains (Table 8.1). The highly productive flood plains influence the biogeochemistry of the rivers, and are woven into the life cycles of many organisms that move between the river and the flood plain. The main-stems of the rivers also flow around numerous islands, portions of which may flood annually. Some islands are quite

large and appear to be very stable, whereas others are ephemeral (Klammer, 1984).

The most recent rise in sea level has drowned the lower ends of the Amazon tributaries that flow from the shields on either side of the river. The drowned valleys, which extend from the tributary confluences with the Amazon back to the points of descent from the shields, are called "mouthbays". They are lacustrine in character, and typically deposit their sediment loads (Sioli, 1984). The Orinoco, which does not have mouthbays, forms a large (7000 km²) internal deltaic flood plain near the mouth of the Río Apure, where the rivers of the Llanos are blocked by rising water as they join the Orinoco main-stem. In general, tributaries of the Amazon and Orinoco that drain from Andean alluvium form more extensive flood plains than tributaries draining from the shields, because rivers of the shield carry much smaller sediment loads and therefore do not readily create depositional features leading to flood-plain formation. Some rivers on Andean alluvium meander extensively, and thus leave oxbows (e.g., the Purús and the Juruá: Sioli, 1984).

The catchments and flood plains of the Amazon and Orinoco are mostly undeveloped. Although flood plains have served as settlement sites since pre-European times, their vegetation and hydrology are still largely natural, and population density is generally low, despite the growth of a few population centers (Table 8.1). In contrast, the Magdalena catchment supports a substantial population density, and the flood plain has been extensively converted to agricultural use.

CLIMATE

Annual precipitation in the northern half of South America spans most of the global range, from less than 500 mm yr⁻¹ on the west coast below the equator and in eastern Brazil near Recife, to more than 5000 mm yr⁻¹ in some portions of the shields (Fig. 8.4). Precipitation may be as great as 8000 mm yr⁻¹ in the wettest places (Salati and Marques, 1984). The area-weighted mean precipitation is high (1700 mm yr⁻¹: Orinoco 2000 mm yr⁻¹, Amazon 2000 mm yr⁻¹, other catchments 1300 mm yr⁻¹). Annual precipitation can be understood at the most general level in terms of five interacting factors (Salati, 1985; Molion, 1990): (1) a tendency toward

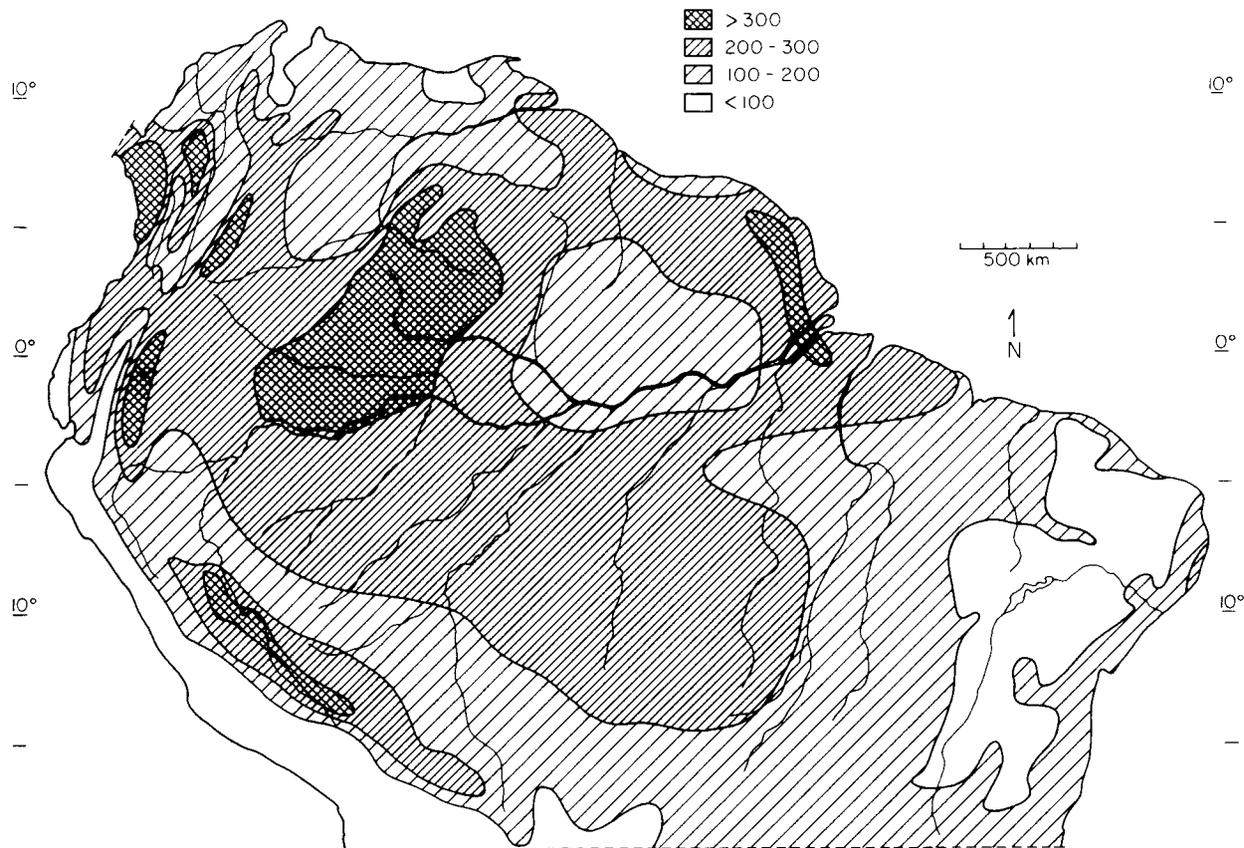


Fig. 8.4. Rainfall of northern South America [original prepared with data from Baumgartner and Reichel (1975); cm yr^{-1}].

greatest precipitation near the equator, and declining amounts toward the margins of the region considered here (15°N or S latitude), where the subtropical high-pressure zones begin to exert their suppressive effect on precipitation; (2) large amounts of precipitation in the upper Amazon and Orinoco basins because of a persistent high-pressure cell, the Bolivian High, that moves between the central and northwest Amazon basin; (3) sustained heavy precipitation over much of the Amazon and southern Orinoco basins because of the recycling of moisture; (4) the intertropical convergence zone (ITCZ), which brings moisture inland from the Atlantic; and (5) especially small amounts of precipitation to the west of the Andes below the equator because of a rain-shadow effect.

The seasonality of precipitation is determined primarily by the position of the Bolivian High, a persistent upper-atmosphere thermal circulation cell (Molion, 1990), and by the seasonal oscillation of the intertropical convergence zone. The circulation

cell is best developed during the late and early months of the calendar year, when it is centered over the Amazon basin. Toward the middle of the calendar year, the cell moves north and west, creating a dry season to the south and east, thus reducing the mean annual rainfall of that region. In the last quarter of the calendar year, the high moves back to the south. The strength of the circulation cell varies with a period of 10 to 15 days, probably reflecting negative feedback cycles resulting from cloudiness (Molion, 1990). Despite substantial variation among years and among regions, there is a trend toward minimal seasonality in the vicinity of the equator, particularly over the northwestern part of the Amazon basin where the Bolivian High is most persistent. At some locations very near the equator there may be two rainfall maxima, but in most locations there is a single maximum and a distinct dry season. The dry season becomes progressively more pronounced at greater distances from the equator, and especially so in the extreme southeast. The dry season is

centered on the middle of the calendar year in the southern portion of the region, and shows a phase shift of approximately six months in the northern extreme of the region.

Northern South America is also affected by frontal systems originating either from the north or south (Molion, 1985, 1990). Frontal systems, which sometimes become stationary, may bring heavy rainfall and low air temperature (15–20°C) over periods of a few days or more.

The range of mean solar irradiances at the top of the atmosphere between 15°S and 15°N is only 3% (List, 1951). This variation is trivial by comparison with regional variations in mean atmospheric attenuation coefficients over northern South America. Although direct information on solar irradiance over this region is still very poor, estimates of the mean annual irradiance pattern over northern South America demonstrate that global radiation within approximately 5° of the equator is below 120 kcal cm⁻² yr⁻¹ (160 W m⁻²), and that irradiance shows an outward gradient to values above 160 kcal cm⁻² yr⁻¹ (210 W m⁻²) in the driest portions of northern South America (Landsberg, 1961). Salati and Marques (1984) have shown a median value of approximately 400 cal cm⁻² d⁻¹ (190 W m⁻²) at Manaus, which would be consistent with Landsberg's earlier estimates. Annual irradiance as far north as southwestern North America and Mexico exceeds 160 kcal cm⁻² yr⁻¹, which is substantially above that of the equatorial moist-forest zones of South America. Because of high attenuation caused by moisture, irradiance in the wettest portions of Amazonia is no greater than that of the southwestern portions of Canada. In the Andes, incident irradiance is as much as 50% higher than at sea level for a given atmospheric moisture regime, because of the reduced optical airmass at high elevation.

Tropical moist forest occupies 51% of the total area of northern South America (Fig. 8.5: note that more accurate maps of finer scale are now available for selected regions and may differ in some instances from the source used for Fig. 8.5). Tropical moist forest forms the canopies over streams of low order, and reduces irradiance at the floor of the forest to about 1% of the value at the top of the canopy (Brinkman, 1985), but rivers are often sufficiently wide to be uncanopied in the tropical moist-forest zone. The seasonal dry forest (covering 13% of the area) and some of the montane forest (13% of the

area) are not sufficiently dense to shade streams fully. Streams of the savanna (22% of the area) and the driest and highest portions of the Andean region are primarily uncanopied at all stream orders, although first-order streams may be canopied by herbaceous plants in some places. Variations in moisture, elevation and vegetative cover cause the mean annual irradiance reaching the surface of streams and rivers of northern South America to vary by a factor of 300 or more.

Day length is almost constant near the equator, but grades toward a day-length range of approximately two hours at the latitudinal margins of northern South America (Brylinsky, 1980). Irradiance is much less variable seasonally than at temperate latitudes, although seasonal variation of two-fold or more, and even greater short-term variation, is caused by changes in atmospheric moisture.

Mean air temperature varies little with latitude for northern South America, but mean moisture content of the atmosphere and elevation have significant effects superimposed on latitude. For a series of low-elevation stations ranging between 16°S and 2°N, Salati and Marques (1984) showed annual means ranging from 24 to 28°C. Temperature in relation to elevation can be expected to follow the mean normal lapse rate, which is 5 to 10°C per 1000 m of elevation. Lewis (1973) obtained an average of 6.7°C per 1000 m of elevation for a selection of tropical locations. Given that the Andes extend above 4000 m, mean air temperatures must be as low as 0°C at the highest elevations (e.g., -0.3°C, Pico Espejo, Venezuela, 4765 m a.s.l.: Monasterio, 1980). However, the lowest temperatures are seldom reflected in running waters: if irradiance is sufficient to supply the latent heat of melting, rapid warming of water is likely. Ward's literature survey shows that the lowest mean water temperatures on record for the tropics at high elevations are about 10°C (Ward, 1985). At low elevations, absolute air temperature minima over a long span of years are surprisingly low (10°C, low-elevation Amazon: Salati and Marques, 1984). Brief periods of low temperature correspond to penetration of frontal systems from high latitudes, and presumably are reflected to some extent in small streams, but less so in large rivers that would respond less quickly.

Annual amplitudes of temperature in equatorial rivers and rain-forest streams are only a few degrees

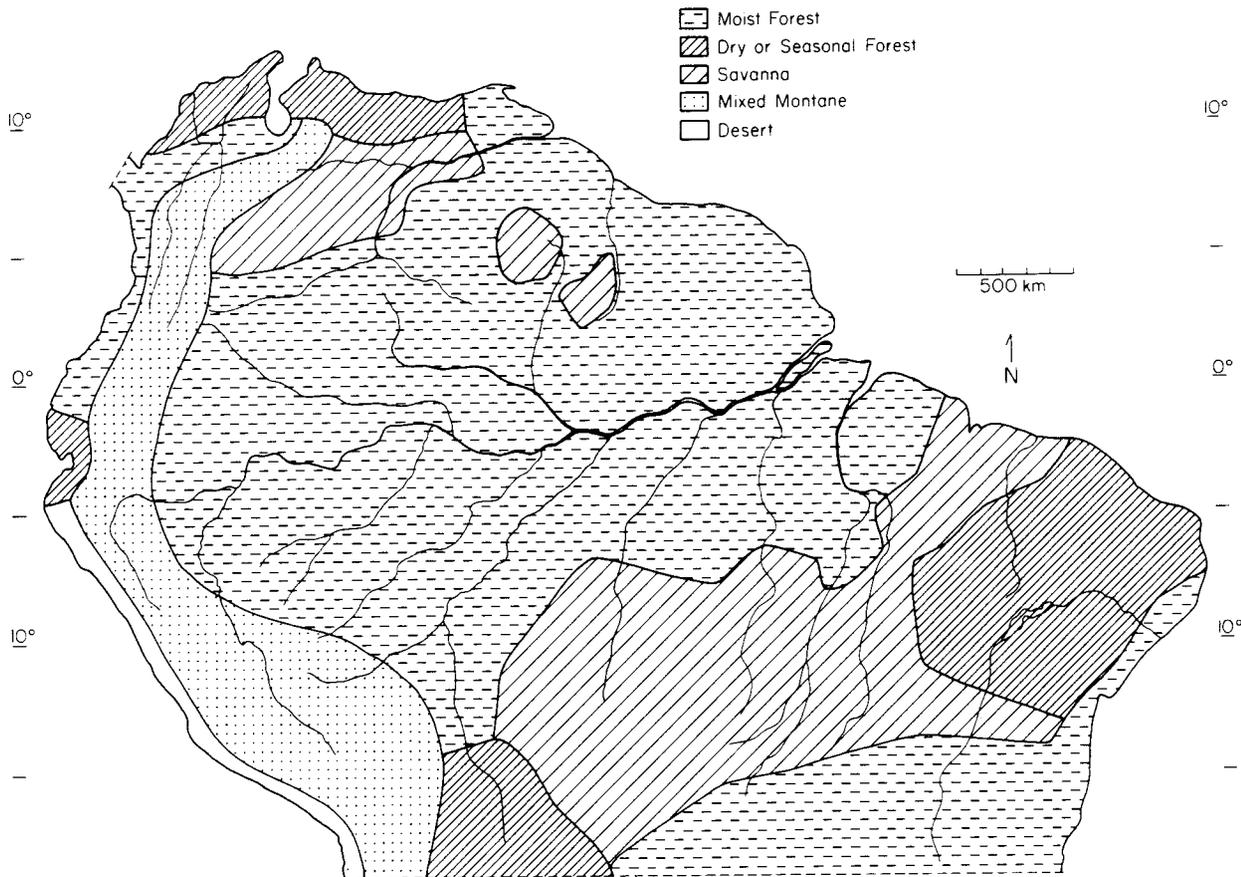


Fig. 8.5. Vegetation types of northern South America [original based on data of Udvardy (1975); simplified and slightly modified].

centigrade (Ward, 1985), although no record is available for the effects of frontal systems, which may greatly amplify the maximum possible range for small rain-forest streams. Temperatures of the largest rivers are especially stable. The lowland Amazon is usually within 1°C and always within a few degrees of 29°C (Sioli, 1975), and the Orinoco is similarly stable.

The climate of northern South America has changed substantially in the past, even within the last 10 000 to 20 000 years (Dickinson and Virji, 1985; Colinvaux, 1989). The climate was probably drier and cooler during the last glaciation, and had entered its present warmer and wetter condition by 10 000 B.P. However, substantial fluctuations in moisture have also occurred in the last 10 000 years. Evidence from soils and from forest lakes indicates that even the Amazon rain forest has dried enough to burn at times in the last several thousand years, and that river hydrographs may have been much

different at times over the last few thousand years from what they are at present (Colinvaux et al., 1985; Colinvaux, 1989).

HYDROLOGY

Multi-year hydrologic records are available for a few locations along the main-stems of large rivers (Table 8.2); little information is available on the hydrology of smaller rivers and streams. Table 8.2 gives estimates based on field measurements of discharge where possible, but the field data are often not fully validated. Some of the field data result in estimates that are notably lower than GIS estimates based on runoff coefficients (GIS: Juruá 9100, Japurá 22 000, Tapajós 23 000, Içá 10 000). With reference to a model developed by Vörösmarty et al. (1989), discharge values of Table 8.2 deviate by more than 25% for the Juruá (—), the Purús (—) and the Xingú

TABLE 8.2

Discharge and suspended load for rivers of northern South America and their largest tributaries

River name	Drainage area (10 ³ km ²)	Discharge (m ³ s ⁻¹)	Specific discharge (mm yr ⁻¹)	Suspended solids (mg l ⁻¹)	Sources ¹
Amazon	6000	220 000 ⁴	1200	220 ³	d, h
Solimões ²	1200	43 000	1200	380	d, h
Içá	120	7500	1900	90	g, h
Juruá	220	6500	930	194	g, h
Japurá	300	18 000	2000	55	g, h
Purús	370	11 000	1000	74	d, g, h
Negro	620	30 000	1600	7	d, g, h
Madeira	1300	30 000	740	540	d, g, h
Trombetas	130	1900	540	–	d
Tapajós	500	14 000	910	–	g
Xingú	510	17 000	1200	–	d, h
Orinoco	950	38 000	1300	80	a, i
Guaviare ⁵	150	8700	1800	118	c, j
Meta	110	5600	1600	362	c, j
Apure	170	2300	300	235	b, i
Caura	48	3000	2000	12	b, i
Caroní	95	5000	1700	5	f, i
Magdalena	270	7000	830	780	e
Essequibo	90	2300	800	–	d
Tocantins	820	18 000	680	–	d
Parnaíba	320	2300	220	–	d
São Francisco	640	2800	140	60	d, k

¹Sources:

(for hydrology)

a: D. Pérez-Hernández, recent (1993) unpublished estimate.

b: J. Saunders (unpubl., 1993), mostly 1984 data.

c: Weibezahn (1990).

d: Estimated from maps by GIS methods.

e: García Lozano and Dister (1990).

f: Morales and Gorzula (1986).

g: R. Meade (pers. comm., 1993), approximated from raw gauge data.

(for sediment)

h: Richey et al. (1986), discharge weighted as calculated from their table 3 plus Meade (1985).

i: Lewis and Saunders (1990), multi-year discharge-weighted means: Meade et al. (1990) gave a higher estimate for the Orinoco.

j: Weibezahn (1990), one-year arithmetic means.

k: Milliman and Meade (1983).

²Above Juruá.³At Óbidos.⁴About 15% higher than the estimate from Richey et al. (1989a); excludes Tocantins.⁵Below the Inirida.

(+). Most means for discharge in Table 8.2 are consistent with the graphical data of Richey et al. (1989a), but some are not.

Although the rain-forest environment that makes

up much of northern South America is often viewed as physically stable, hydrographs for small rain-forest streams show high short-term variation in discharge (Fig. 8.6), because irregularity of precip-

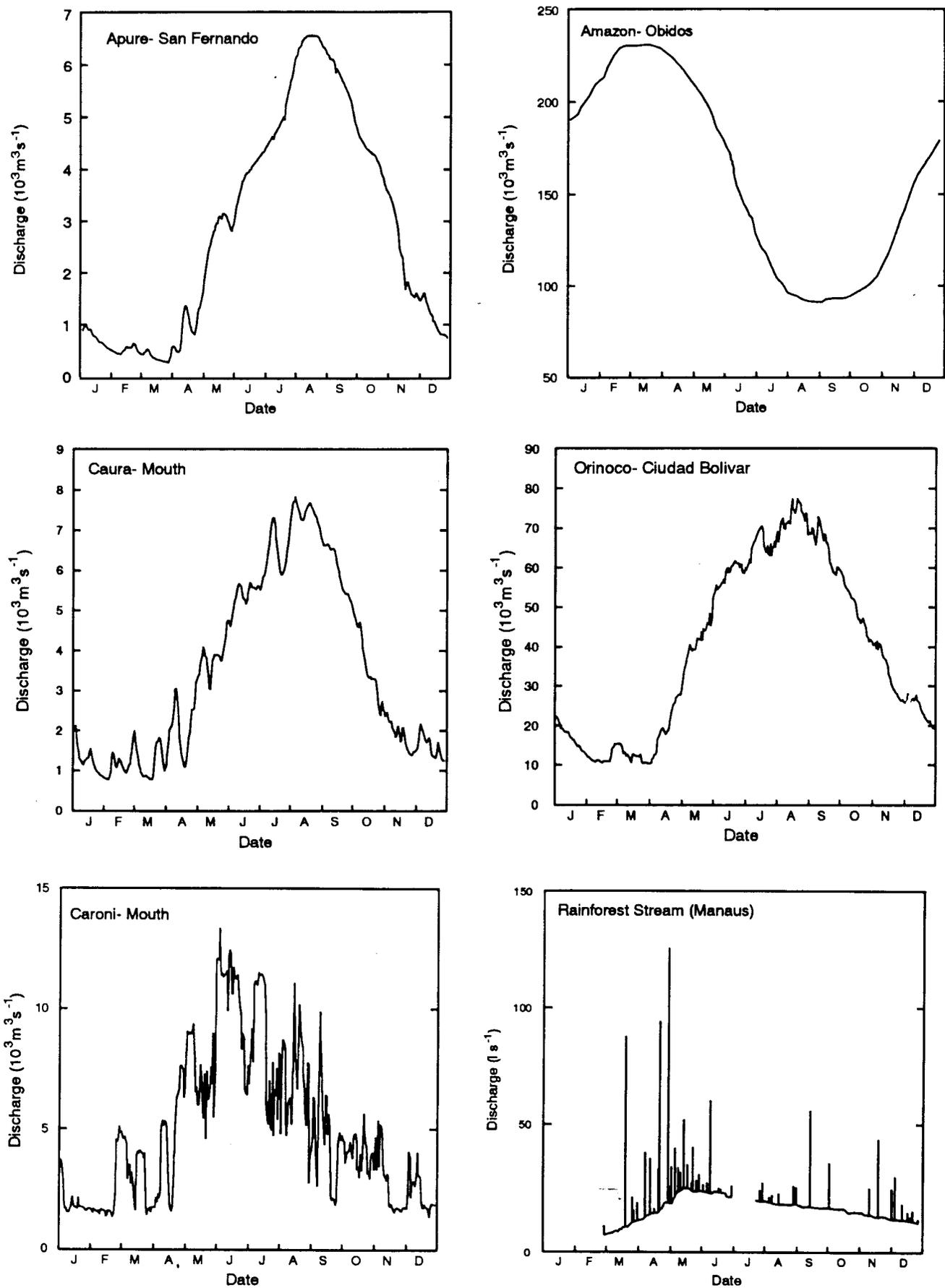


Fig. 8.6. Hydrographs for running waters of northern South America [redrawn from Lesack, 1988; Lewis, 1988; Richey et al., 1990].

itation is quickly reflected in the discharge of small streams (Franken and Leopoldo, 1984; Junk and Furch, 1985; Lesack, 1988). Even large rivers draining rain forest show substantial short-term variation in discharge, although relative variation is less as a percentage of mean discharge for large rivers (Fig. 8.6). In the Amazon tributaries, short-term rises in discharge are sufficiently noticeable to have a specific designation (“*repiquete*”) among fishermen, who correlate these rises with changes in the behavior of migrating fishes in rain-forest rivers (Goulding 1980). In addition, short-term variations in the hydrograph have important effects on the plankton transport of rain-forest rivers (Saunders and Lewis, 1988c, 1989b). Short-term variation appears to be less pronounced for rivers that drain savanna and dry forest than for rivers that drain rain forest (for instance, compare the Apure with the Caura in Fig. 8.6), but interpretations are complex because of morphometric contrasts among rivers and their flood plains.

The main-stems of the Amazon and Orinoco show only small amounts of short-term variation because short-term variation in runoff from tributary catchments is hydrologically unsynchronized. Some short-term variation in the Orinoco main-stem at Barrancas has been induced artificially by the Guri Dam on the Caroní (Fig. 8.6).

All large rivers of northern South America show marked seasonality in the hydrograph. To the south, the lowest discharge occurs near the beginning of the calendar year. Reflecting the latitudinal phase shift in precipitation, discharge shifts latitudinally toward a minimum as late as early May north of the equator. Most of the large rivers show a unimodal seasonal discharge pattern, but the Magdalena has a more complex pattern including dual minima (February, October). For most rivers with a unimodal pattern, maximum discharge lags four to six months behind the minimum discharge, and the hydrograph rises more steeply than it falls.

The mean ratio of annual maximum to annual minimum discharge for large rivers of northern South America is related to mean annual runoff (Fig. 8.7), which in turn reflects the degree of seasonality in precipitation and accounts for a loose association between degree of seasonal variation in hydrograph and catchment vegetation types (Fig. 8.5). For rivers that drain savanna and dry forest, the mean ratio can be well over 20. For rivers that

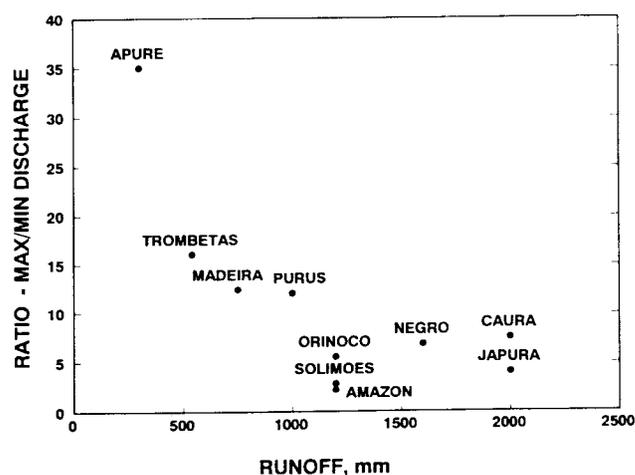


Fig. 8.7. Approximate median ratio of annual maximum to minimum discharge in relation to runoff for large rivers of northern South America (data from (Lesack, 1988; Lewis, 1988; Richey et al., 1989a).

drain only moist forest, the ratio is below 10. Mixed catchments have intermediate ratios. The ratios for the main-stem of the Amazon and the Orinoco are especially low because they receive tributaries that differ in amplitude and phasing of discharge, and because storage of water in the flood plain flattens the hydrograph (Meade et al., 1991).

Interannual variation affects maximum and minimum discharge, the timing of the flood wave, the duration of extremes of high and low water, and many other more subtle features of discharge. This is illustrated by Fig. 8.8, which shows the composite variation of discharge for the Orinoco at all times of the year. Composite variation, which is quantified

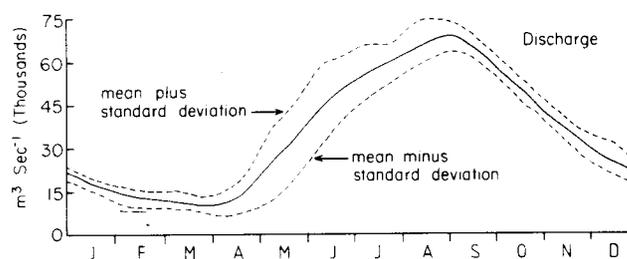


Fig. 8.8. Composite variation in the hydrograph of the Orinoco at Barrancas, illustrated as standard deviation around the mean discharge (from Lewis and Saunders, 1989).

as standard deviation around the mean for any day of the year, is caused by variation in the wetness of individual years and by variation in the timing of the flood wave and other seasonal features. Inter-annual differences in timing of major events can be as much as 30 to 60 days for the large rivers (e.g., Lewis, 1988; Richey, et al., 1989b; Meade et al., 1991).

Richey et al. (1989b) reconstructed an 83-year record of discharge for the Solimões at Manacapuru. The coefficient of variation for peak flow, estimated for present purposes from their graphical data, is 7%; the coefficient of variation for minimum flow is 13%. In the driest year, the peak flow was below the long-term annual average flow. The maximum discharge showed a degree of pattern connected with the El Niño Southern Oscillation; spectral analysis revealed a strong component of variance with a period of about three years (Richey et al., 1989b).

The large hydrologic systems of northern South America are still almost unperturbed by human activity. Gentry and Lopez-Parodi (1980) concluded from discharge records that the Amazon had been affected hydrologically by catchment deforestation. Although reanalysis by Nordin and Meade (1982), Sternberg (1987) and Richey et al. (1989a) refuted the conclusions of Gentry and Lopez-Parodi, future hydrologic effects resulting from conversion of tropical moist forest are likely. An even more immediate cause of change is hydroelectric development, which will break the functional continuity of the rivers (Ward and Stanford, 1983). The hydrograph of the Caroní, a major tributary of the Orinoco, illustrates the degree to which the discharges of rivers can be expected to change in response to the construction of large dams (Fig. 8.6).

Only 10% of the hydropower potential in northern South America is presently developed (Petts, 1990). Lower main-stem dams (complete or under construction) are found on the São Francisco, the Tocantins and the Caroní (Vásquez, 1989; Petts, 1990). Large dams on upper tributaries are found on the Tocantins, two upper western tributaries of the Orinoco, the Magdalena, and two small coastal Andean rivers. Many more large dams are planned (Bunyard, 1985). Dams cause suspended solids to be deposited, drastically alter the hydrograph, change the area and pattern of down-stream inundation, and interrupt the migration of fishes. De Merona (1990) has documented serious decline in fisheries

on the Tocantins associated with impoundment; Bayley (1989) explained why similar reductions could follow from construction of impoundments in the Amazon basin.

OVERVIEW OF GEOCHEMISTRY

The shields and continental alluvium of northern South America are so thoroughly weathered that their yield of dissolved inorganic solids approaches the minimum possible for extended contact of water with rock. To the west, the Andes have exposed a heterogeneous collection of sources, most of which are far more readily weathered because of their relative youth and sedimentary origin. These sources include in selected locations even some evaporites that give up large amounts of dissolved solids. Thus, northern South America as a whole produces running waters that are exceedingly diverse chemically (Stallard and Edmond, 1983, 1987; Stallard, 1985).

Although no simple organizational scheme can capture the full geochemical diversity of northern South America, three general schemes have been used beneficially for Amazon waters and can be extended to the adjoining drainages of northern South America. The first of these is an optical classification initially proposed by Wallace (1853) and subsequently developed extensively by Sioli in his pioneering studies of the Amazon (summarized by Sioli, 1975). The optical classification recognizes black waters, white waters and clear waters. These classes reflect the combined influences of geochemistry, geomorphology, soils and vegetative cover (Sioli, 1984). Blackwater rivers are very poor in dissolved inorganic solids and suspended solids and have a reddish-brown color caused by dissolved organic matter; they typically have low pH, are found in areas of low relief, and are identified exclusively with podzols canopied by tropical moist forest. In contrast, white waters carry large amounts of suspended solids that give a characteristically muddy or silty appearance, have substantial amounts of dissolved inorganic solids, and are slightly alkaline or circumneutral. Most white waters derive their suspended load from the Andean montane or Andean alluvial zones. The thoroughly weathered slopes of the shields, although rising to more than 3000 m, do not produce white waters unless they are disturbed

by mining or construction. Clear waters are chemically most diverse; they range from acidic to slightly alkaline, lack significant amounts of suspended material, and have high transparency without brown color. The concentrations and ratios of dissolved inorganic substances in these waters vary widely. Clear waters are found primarily in areas of low relief, are associated with latosols rather than podzols, and drain regions that support tropical moist forest, dry forest, or savanna.

The Amazon and Orinoco are properly classified as mixed waters because they receive large amounts of all three water types. Most of the major tributaries of the Amazon and Orinoco, as well as the other large rivers of northern South America, can be classified reasonably well as belonging predominantly to one of the three optical types. However, in streams of lower order, the water types are more varied within a specific region than might be evident from a classification of the major rivers. On the shields, for example, blackwater and clearwater streams, reflecting irregularities in the distribution of podzols, may lie adjacent to each other.

A second scheme of organization was proposed for the non-Andean Amazon by Fittkau on the basis of major geochemical provinces. Fittkau (1970, 1971) divided the Amazon basin into three large units that show a sequence of increasing richness in inorganic solids: (1) the central Amazon (exclusive of the várzea immediately adjacent to large rivers), where the substrate has been derived from the shields and has been redeposited several times, thus becoming the most thoroughly weathered of all substrates in the Amazon, (2) the exposed shields, which Fittkau classed as slightly richer in ionic solids than the central Amazon, and (3) the Andean foreland, which is richer in ionic solids because of the lower degree of weathering of the substrate. The distinction between zones (1) and (2) would be small on an arithmetic scale of concentrations but, if verified, could be important because some important physiological thresholds for organisms may fall within this range.

Fittkau's scheme can be extended beyond the central Amazon to other areas. Fittkau's zone (1) (continental alluvium, 7% of the area of northern South America: Fig. 8.2) is uniquely Amazonian, except to the extent that some of this substrate may be mixed with alluvium of Andean origin near the western margin of the Guayana Shield in the Orinoco

drainage. Large portions of the Orinoco and the Amazon are in Fittkau's zone (2) (the shields, 32% of northern South America). The Essequibo, although unstudied, should be geochemically aligned with zone (2) (shields). Extension of Fittkau's scheme beyond the central Amazon requires that zone (3) (Andean alluvium, 29%) be supplemented with a fourth major zone, the Andean montane zone (15%). The Andean alluvium and the Andean montane zone account for the Magdalena drainage as well as the northern tributaries of the Orinoco and the headwaters of the Amazon (Fig. 8.2). East of the Xingú, the system breaks down because the geology is mixed (Tocantins) or because the amount of precipitation is so small that waters are altered geochemically by evapoconcentration of dissolved solids (São Francisco). Within the Amazon drainage, Fittkau recognized the Carboniferous strips along the Amazon as geochemically distinctive because of their high carbonate content (Sioli, 1963).

A third organizational scheme, from Carson and Kirkby (1972), has been applied to the Amazon by Stallard (1985). This scheme is based on a continuum connecting two contrasting denudation regimes: (1) weathering-limited denudation, which is identified with steep relief and thin soils; and (2) transport-limited denudation, which is identified with low relief and thick soils. In weathering-limited regions, denudation rates are almost entirely related to rock composition, which determines the rate of chemical weathering; transport is so efficient that solids are quickly removed as they become detached from the parent material, and waters tend to be rich in dissolved solids because the exposed surfaces are removed before they have been fully weathered chemically. Particulate material accumulates in transport-limited regions. This promotes chemical weathering by maximizing reactive surface area and contact time with water, and tends to produce ion-depleted solid phases. Although the continuum between these types is complex, ionic solids will usually be more concentrated toward the weathering-limited end of the spectrum and less so toward the transport-limited end of the spectrum, as long as water is sufficiently abundant that evapoconcentration is not a factor. In the Amazon basin, Stallard (1985) identified the shields and the continental alluvium near the shields as transport-limited regions that approach the limits of ion depletion from crystalline parent material.

SUSPENDED SOLIDS

For many years, occasional samples have been taken of suspended solids in rivers of northern South America. However, accurate measurement of suspended load in large rivers has proven to be difficult, and for this reason early measurements based on dip samples taken at the surface cannot be considered reliable. For example, Gibbs (1967) estimated the suspended load of the Amazon as $90 \text{ mg } \ell^{-1}$ based on surface samples, whereas re-estimates based on depth-integrated sampling produced an estimate of $220 \text{ mg } \ell^{-1}$ (Table 8.2). The main methodological problem is the very uneven distribution of suspended sediments over cross-sections of rivers. Cross-sectional sediment distributions have been mapped for the Amazon and Orinoco main-stems (Lewis and Saunders, 1984; Meade, 1985; Weibezahn, 1990). Causes of uneven distribution include sedimentation in a non-uniform current-velocity field and lateral mixing of large tributaries, which may require as much as 150 km to blend fully with the main-stem.

Table 8.2 gives the mean concentrations of total suspended solids, typically as obtained within the last few years by depth-integrating methods (see the following sections for information on the partitioning of total solids into inorganic and organic components). None of the concentrations of suspended solids are extraordinarily high, given that world-average load of suspended solids in rivers is between 400 and $500 \text{ mg } \ell^{-1}$ (Meybeck, 1976). Both the Amazon and the Orinoco are among the world's least-turbid large rivers (Meade, 1992). Among the world's largest rivers, the Orinoco carries an exceptionally small load of suspended solids, primarily because most of the water originates from the Guayana Shield.

Rivers draining the Andean montane zone have the highest suspended load (typically $> 200 \text{ mg } \ell^{-1}$), reflecting the vulnerability of the Andean region to erosion, and are classified as white waters (Table 8.2). Black waters and clear waters draining from the shields and the continental alluvium have the lowest concentrations ($< 20 \text{ mg } \ell^{-1}$; e.g., Rio Negro, Caura and Caroní; the low load of the Caroní is reduced even further by impoundment). Rivers that primarily drain Andean alluvium, and that have only small headwater exposures at higher elevations, carry intermediate suspended loads ($50\text{--}100 \text{ mg } \ell^{-1}$; Içá,

Purús, Japurá); they are typically classed as white waters. Waters spanning the range between 50 and $100 \text{ mg } \ell^{-1}$ can also develop through mixture of water types or deposition from more turbid waters on flat terrain.

Little is known about the suspended loads of streams and small rivers [see Weibezahn (1990) and DePetris and Paolini (1991) for selected data on small Orinoco tributaries]. The lowest loads are undoubtedly for blackwater or clearwater rivers of low velocity on flat terrain. An example is the Atabapo, a tributary of the upper Orinoco, which has a suspended load of $1.7 \text{ mg } \ell^{-1}$ (Weibezahn, 1990). The suspended loads of small whitewater rivers may demonstrate some interesting complexities that have not yet been worked out. Sioli (1975) noted that the suspended loads of these rivers are irregular because they depend to some extent on mass wasting of sediments rather than steady erosion. If so, Andean streams may show a much wider range of suspended loads than might be evident from the loads of the main rivers into which they flow. These factors will affect transparency and bioenergetics of low-order Andean streams and rivers.

As is typical of rivers generally, concentrations of suspended solids in rivers of northern South America reach their maximum on the rising limb of the hydrograph. For example, the Orinoco, which has a four-fold annual range in suspended load (Meade et al., 1990), entrains as the water rises fine sediments that were deposited the previous year on the falling limb of the hydrograph (Lewis and Saunders, 1989). The Orinoco is unusual in having a secondary peak in suspended solids near the bottom of the falling limb of the hydrograph. This possibly represents detachment of the river from the flood plain, where the river deposits sediment during periods of high discharge. Other large rivers of the region may have a secondary peak, but more frequent sampling would be necessary to show it. The suspended load of the Amazon is extraordinarily aseasonal, even by comparison with the Orinoco or other large rivers, because of the storage and remobilization of sediments and the differential phasing among the tributaries within this large system (Meade et al., 1985; Richey et al., 1986). In both the Orinoco and the Amazon, individual fractions of suspended solids, including particulate carbon, nitrogen and phosphorus, follow the same pattern as total suspended solids (Lewis and Saunders, 1989; Richey et al., 1991).

DISSOLVED INORGANIC SOLIDS

Tables 8.3 and 8.4 summarize the concentrations of dissolved inorganic solids in surface waters and precipitation of northern South America. Surface waters are grouped by a scheme that reflects the concepts of Fittkau and Stallard. The differences among regions are best indicated by total ionic solids (i.e., omitting silica). The concentrations of ionic solids in waters draining moist shield and continental alluvium typically fall below 10 mg l^{-1} (Table 8.4). In drier regions of the shields where evapoconcentration is important, the concentrations will undoubtedly be higher, but these are not yet documented. Waters originating from Andean alluvium have concentrations of ionic solids between 10 and 20 mg l^{-1} , except where evapoconcentration is important (Apure: 100 mg l^{-1}). The Andean montane drainages produce concentrations typically $> 50 \text{ mg l}^{-1}$, but with high variance that reflects a lithologic range from siliceous rocks to evaporites. Groupings may also be possible from soil types (Bruijnzeel, 1991).

Although geologic sources generally determine the ionic composition of surface waters, the shields and continental alluvium of northern South America are so thoroughly weathered that atmospheric sources potentially have an important influence on concentrations of some substances. Disregarding precipitation data for the relatively dry catchments of the Río Apure and Lago de Valencia, where precipitation chemistry is strongly influenced by locally derived salts, the precipitation chemistry data of Table 8.3 show that the content of inorganic solids in precipitation is very similar to that of a selection of small forest streams around Manaus (Furch, 1984; Junk and Furch, 1985; Lesack, 1992), except for silica, which is not mobilized through the atmosphere in significant amounts relative to geologic sources. Data on more rain-forest locations would be desirable. Table 8.3 excludes extensive precipitation data for three major ions in the well-known Venezuelan Amazon rain-forest site at San Carlos de Río Negro, because published concentrations are an order of magnitude above those for other rain-forest sites (see summary by Bruijnzeel, 1991).

On the shields and continental alluvium, chloride is the most reliable index of the atmospheric source of ions because there are no geologic sources of

chloride in these regions. The correspondence between chloride concentrations in precipitation and in large rivers draining from the shields, with allowance for moderate concentration of chloride by evapoconcentration, shows the expected direct influence of precipitation on concentrations of chloride. The relative influence of the atmospheric source is weaker for sodium which, unlike chloride, is released in significant amounts by the weathering of granite. Sulfate concentrations reflect strong atmospheric influences that may be partly oceanic and partly associated with volatile sulfur species released from anaerobic coastal or inland environments.

The exceedingly low concentrations of major cations in precipitation and in forest streams are not characteristic of the large rivers that flow from the shields. Although the large rivers have very low concentrations on an absolute scale, they carry substantially higher concentrations of all of the major cations than precipitation or forest streams (Table 8.3). One possible explanation is that the catchments of the large rivers are sufficiently diverse geologically to include element sources that are not evident from the small selection of forest streams for which data are presently available. It may also be significant that the continental alluvium, where small streams have been sampled, is more thoroughly weathered in general than the shields, where larger rivers have been sampled (Fittkau, 1971). Yet another explanation has been proposed by Bruijnzeel (1990, 1991), who noted that the incision of rivers, in contrast with that of streams, is so great as to create a zone of groundwater flow that is on a fresh weathering front below the zone of root uptake. This would cause enrichment of rivers in solutes. These possibilities are difficult to resolve, because scarcely any data are available for small streams on the shield, and because no large rivers flow entirely through continental alluvium.

Stallard and Edmond (1981) estimated the percentages of ions originating from the atmosphere for the Amazon basin at Óbidos during peak discharge: calcium 0.1%, chlorine 17.6%, magnesium 1.3%, potassium 0.4%, sodium 6.9% and sulfur 3.6%. The percentage contributions would be higher if calculated specifically for the shields and continental alluvium, given that the Amazon as a whole receives a substantial part of its ion load from the Andean montane and Andean alluvial regions, where atmospheric sources do not play a major role because of

TABLE 8.3

Summary of water chemistry data from northern South America (mg l^{-1} , except pH; data are for lower reaches unless indicated otherwise)

Water Type	Cations					Anions				Totals		Sources ¹
	pH	Ca ⁺⁺	Mg ⁺⁺	Na ⁺	K ⁺	HCO ₃ ⁻	SO ₄ ⁼	Cl ⁻	SiO ₂	All	Ionic	
Reference												
World Rivers	–	13.4	3.4	5.1	1.3	52	8.3	5.7	10.4	99	89	a
Amazon at Óbidos	6.6	5.5	1.1	1.5	0.9	22	1.8	1.1	7.5	41	33	b
Lower Orinoco	6.8	2.6	0.7	1.5	0.7	10	2.3	0.9	6.4	25	19	h
Andean montane												
Amazon at Iquitos	7.4	19.8	2.4	6.3	1.1	69	7.9	6.6	10.8	120	110	b
Solimões at Juruá	6.9	13.0	1.7	3.2	1.2	47	3.4	2.9	9.7	82	73	b
Magdalena	7.1	20.0	–	–	–	26	49	–	–	–	–	k
Andean alluvium												
Apure	7.2	16.2	3.0	4.1	2.2	61.8	10.7	1.7	11.3	111	100	f
Meta	7.4	9.0	1.7	2.7	0.9	10.4	11.3	2.1	4.4	43	38	e
Japurá	6.5	6.8	1.0	1.8	0.8	25.8	1.9	1.5	7.7	47	40	b
Juruá	6.7	7.3	1.2	1.7	1.1	31.0	0.7	0.4	9.8	54	44	b
Continental alluvium												
Forest streams	4.5	0.04	0.04	0.22	0.15	1.1 ²	–	2.2 ²	4.5	–	–	i
Forest stream	4.6	0.03	0.02	0.14	0.03	–	0.19	0.46	–	–	–	m
Shields												
Orinoco above Guaviare	6.4	0.44	0.18	0.78	0.78	2.1	0.22	0.35	4.7	9.6	5	e
Caura	6.5	0.60	0.23	1.2	0.63	4.8	0.34	0.39	7.9	16	8	f
Caroni	6.4	0.50	0.21	0.71	0.43	2.5	0.24	0.32	5.1	9.9	5	f
Negro	5.1	0.38	0.16	0.40	0.39	0.55	0.23	0.26	4.2	6.5	2	b
Mixed waters: complex sources												
Guaviare	6.6	2.5	0.5	0.7	0.5	5.5	1.0	0.36	4.3	15	11	e
Madeira	6.7	4.0	1.5	1.6	1.2	17.6	3.5	0.46	8.6	38	30	b
Mixed waters: from Shields through Carboniferous strips												
Tapajós	6.8	1.1	0.4	0.7	0.8	5.8	0.2	0.3	8.9	18	9	b
Trombetas	6.2	1.9	0.4	1.0	0.7	6.8	0.6	0.6	6.9	19	12	b
Xingú	6.8	1.9	0.6	1.7	1.0	11.2	0.2	0.8	10.9	28	17	b
Precipitation												
Amazon	5.0	0.044	0.029	0.28	0.039	–	0.49	0.48	0.0	1.4	1.4	c
Caura	–	0.033	0.007	0.20	0.026	–	0.21	0.29	0.0	0.8	0.8	g
Amazonia, Manaus	4.6	0.07	0.02	0.12	0.10	–	–	1.9 ²	–	–	–	i
Amazonia, Manaus	4.9	0.042	0.018	0.058	0.027	–	0.22	0.17	–	–	–	j
Amazonia, Manaus	4.7	–	0.005	0.007	0.008	–	–	0.30	0.1	–	–	n
Apure	–	0.29	0.92	0.49	0.30	–	0.22	–	–	–	–	d
Lago de Valencia	5.9	1.15	0.73	2.21	0.57	6.66	2.17	2.56	0.1	16	16	l

¹Sources:

a: Meybeck (1979).

b: Stallard and Edmond (1983), mostly two-sample means.

c: Stallard and Edmond (1981), 10 events at different locations; wet only, a few samples each at many stations.

d: Montes and San Jose (1989), median bulk precipitation, 1200 mm yr^{-1} .

e: Weibezahn (1990), one-year arithmetic means.

f: Lewis and Saunders (1990), four-years discharge-weighted means.

g: Lewis et al. (1987), 3000 to 4000 mm yr^{-1} , bulk precipitation.

h: Lewis and Saunders (1989).

i: Furch (1984), Junk and Furch (1985); wet precipitation near Manaus.

TABLE 8.4

Distribution of geochemical influences, vegetation and moisture across large rivers.

	Dominant vegetation and moisture (mm)		
	1000–3000	Precipitation (mm) 2000–4000	1000–2000
Main geochemical influence	Montane mixed	Lowland moist forest	Savanna and seasonal forest
Andean montane	Solimões (4, w) ¹ →		
Andean alluvium	Magdalena (4, w) →	Japurá (3, w) Juruá (3, w) Purús (3, w) Içá (2, w)	Apure (4, w) ² Meta (3, w)
Continental alluvium		Small Amazon Tributaries (1, b, c) ³	
Shields		Essequibo Negro (1, b) Caroní (1, b) Caura (1, b) Upper Orinoco (1, b)	Trombetas (2, c)
Geologically mixed		Tocantins Xingú (1, c) Tapajós (2, c)	São Francisco Parnaíba
	Madeira (3, w) →		

¹The parentheses give for each river the concentration of ionic solids:

- 1: 1–10 mg l⁻¹,
- 2: 10–20 mg l⁻¹,
- 3: 20–50 mg l⁻¹,
- 4: > 50 mg l⁻¹,

and the water type:

- w: white water,
- b: black water,
- c: clear water.

Rivers that are not coded have unknown classifications.

²Low precipitation concentrates total dissolved solids.³Dissolved ionic solids ca. 1 mg l⁻¹.Table 8.3 (*footnote continued*)

j: Lesack and Melack (1991), wet precipitation, Central Amazon.

k: García Lozano and Dister (1990); solids estimated from conductance, calcium from hardness, middle zone.

l: Lewis (1981); bulk precipitation, weekly for 2 years, 750 mm yr⁻¹.

m: Lesack (1992).

n: Brinkman (1985); no methodological documentation.

²Probably erroneous

the high ionic loads derived from weathering. However, a recent study of deposition chemistry in the central Amazon indicates that at most 16% of the major ions reaching that region originate from the sea (Lesack and Melack, 1991).

In a two-year study of the Río Caura catchment on the Guayana Shield, Lewis et al. (1987) estimated the contributions from the atmosphere for calcium (7%), chlorine (100%), magnesium (4%), potassium (5%), sodium (20%) and sulfur (82%). Of the atmospheric contribution, very high percentages were accounted for by marine sources for chlorine (100%), magnesium (100%) and sodium (80%). Only one-fifth to one-quarter of the calcium, potassium and sulfur coming from the atmosphere was estimated to originate from marine sources; the balance presumably is derived from terrestrial or coastal sources.

Waters of the Andean montane and Andean alluvial zones are approximately one order of magnitude richer in ionic solids than those of the shields and continental alluvium, show predominance of calcium and magnesium among the cations and bicarbonate among the anions, and contain approximately twice as much silica. For the shields and the continental alluvium, sodium and potassium typi-

cally predominate over calcium and magnesium, and bicarbonate is present only in very small amounts. The relative proportions of bicarbonate, chloride and sulfate remain in doubt because of analytical difficulties for these ions at very low concentrations. The shields and continental alluvium of northern South America may be the largest region in the world for severely ion-depleted waters in which potassium and sodium dominate (Furch, 1984, 1987).

Organic acids also play a significant role in ion balance for the ionically depleted waters of the shields and continental alluvium (Lewis et al., 1987), and they suppress pH in these weakly buffered waters. Among the large rivers, the Río Negro, which ranges in pH from 3.6 to 5.8 (Goulding et al., 1988), is the most extreme example of pH suppression by organic acids.

NITROGEN AND PHOSPHORUS

Information on phosphorus in precipitation is scarce, even though the atmospheric component of the phosphorus cycle may be quite important for the phosphorus-poor regions of the shields and continental alluvium (Table 8.5). The data of Montes

TABLE 8.5

Summary of information on nitrogen, phosphorus and carbon transport for rivers of northern South America

Water type	Phosphorus ($\mu\text{g l}^{-1}$)				Nitrogen ($\mu\text{g l}^{-1}$)					Carbon (mg l^{-1})		Sources ²
	SRP ¹	TDP ¹	PP ¹	TP ¹	NO ₃ -N	TIN ¹	DON ¹	PN ¹	TN ¹	DOC ¹	POC ¹	
Reference												
World Rivers	10	25	530	550	100	120	260	560	940	5.8	4.8	a
Amazon at Óbidos	22	37	202	239	140	140	162	202	505	4.1	2.5	k, o, p
Lower Orinoco	10	20	44	65	80	115	160	185	460	4.4	1.5	h
Andean montane												
Solimões at Iquitos	21	—	—	—	170	180	—	—	—	—	—	b
Solimões above Iça	28	47	375	422	200	200	113	325	638	3.2	4.2	k
Andean alluvium												
Apure	44	60	128	188	135	178	266	512	957	6.2	3.6	f
Meta	—	15	75	90	111	134	—	—	—	3.1	7.0	e
Japurá	9	28	47	74	102	102	204	122	430	3.4	1.7	k
Juruá	22	43	146	189	202	202	134	160	494	4.1	1.7	k
Limon	40	—	11	51	560	600	220	40	850	—	19	n
Continental alluvium												
Forest streams	—	—	—	10	—	—	—	—	300	—	—	i
Forest stream	1	3	2	5	160	170	40	40	250	—	—	q

(continued)

TABLE 8.5. (Continued)

Water type	Phosphorus ($\mu\text{g l}^{-1}$)				Nitrogen ($\mu\text{g l}^{-1}$)					Carbon (mg l^{-1})		Sources ²
	SRP ¹	TDP ¹	PP ¹	TP ¹	NO ₃ -N	TIN ¹	DON ¹	PN ¹	TN ¹	DOC ¹	POC ¹	
Shield												
Caura	2.6	8.5	9.9	18	70	107	172	127	406	4.5	1.0	f
Upper Orinoco	–	4.4	12	17	57	79	–	–	–	3.8	1.6	e
Caroni	2.1	5.7	5.6	11	86	122	138	44	304	5.4	0.4	f
Negro	3.0	19.0	9.0	28	42	42	155	1	199	8.5	0.4	k
Fixed waters: from Shield through Carboniferous strips												
Tapajós	0.6	–	–	–	28	–	–	–	–	–	–	b
Trombetas	2.0	–	–	21	52	99	–	–	407	–	–	b, k, l
Xingú	0.9	–	–	–	24	–	–	–	–	–	–	b
Mixed waters: complex sources												
Guaviare	–	13	31	44	52	69	–	–	–	4.8	2.9	e
Madeira	19	43	304	347	176	176	175	274	626	2.9	2.7	k
Precipitation												
Amazon	–	–	–	–	29	–	–	–	–	–	–	c
Caura	–	–	–	3.5	–	–	–	–	–	–	–	g
Amazonia, Manaus	2	3	2	5	49	141	98	26	226	–	–	i
Amazonia, Manaus	2	–	–	–	50	140	–	–	410	–	–	j
Amazonia, Manaus	–	–	–	15	19	97	–	–	243	–	–	r
Apure	36	–	–	–	18	190	–	–	–	–	–	d
Lago de Valencia	40	53	170	220	170	490	180	810	990	1.8	2.6	m

¹SRP: Soluble reactive phosphorus,

TDP: Total dissolved phosphorus,

PP: Particulate phosphorus,

TP: Total phosphorus,

TIN: Total inorganic nitrogen

DON: Dissolved organic nitrogen,

PN: Particulate nitrogen,

TN: Total nitrogen,

DOC: Dissolved organic carbon,

POC: Particulate organic carbon.

²Source:

a: Meybeck (1982).

b: Stallard and Edmond (1983), mostly two-sample means.

c: Stallard and Edmond (1981), wet only, 10 events sampled at different locations.

d: Montes and San Jose (1989), median bulk precipitation, 1200 mm yr⁻¹.

e: Weibezahn (1990), one-year arithmetic means.

f: Lewis and Saunders (1990), four-years discharge-weighted means.

g: Lewis et al. (1987), 4000 mm yr⁻¹, bulk precipitation.

h: Lewis and Saunders (1989).

i: Junk and Furch (1985), wet precipitation and streams near Manaus.

j: Lesack and Melack (1991), wet precipitation, Central Amazon.

k: Richey et al. (1990) and J. Richey (pers. comm., 1993).

l: Forsberg et al. (1988), some numbers differ substantially from (p) or (g).

m: Lewis (1981), Lewis and Weibezahn (1981); bulk precipitation, weekly for 2 years, 750 mm yr⁻¹.

n: Lewis and Weibezahn (1983).

o: Richey et al. (1991).

p: Devol et al. (1989).

q: Lesack (1992).

r: Brinkman (1985); no methodological documentation.

and San Jose (1989) for the Apure region indicate high concentrations of soluble phosphorus in bulk precipitation, but these estimates are probably influenced by local mobilization of phosphorus in dust. Near Lago de Valencia, large amounts of phosphorus are found in the atmosphere during extended dry intervals (Lewis, 1981; Lewis and Weibezahn, 1981). Of greater interest are the phosphorus deposition rates for precipitation over regions that are depauperate in phosphorus. Lewis et al. (1987) reported $3.5 \mu\text{g l}^{-1}$ volume-weighted total phosphorus over a two-year interval in the Caura basin, and estimated that this accounted for approximately 30% of the total phosphorus in runoff; the remainder is accounted for by weathering. Concentrations obtained by Furch (Junk and Furch, 1985) for rain in the vicinity of Manaus are about three times as high. Much higher values are reported for the Venezuelan Amazon, but these may not be accurate (Bruijnzeel, 1991). The practical distinction between concentrations of 3 and $11 \mu\text{g l}^{-1}$ is potentially quite great: at $11 \mu\text{g l}^{-1}$, atmospheric phosphorus could account for virtually all of the phosphorus transport of streams; at lower concentrations, weathering must be a substantial additional source of phosphorus in streams. Also at issue is the transport distance for atmospheric phosphorus; some phosphorus may originate from local rather than distant sources. Transport of phosphorus from dry areas, where phosphorus is more mobile, to tropical moist forest may be a significant component of the phosphorus cycle for the shields and continental alluvium of northern South America (Lewis et al., 1987). However, both the transport distance and the characteristic concentrations of phosphorus in precipitation within tropical moist forest are uncertain at present.

The concentrations of phosphorus in rivers of the shields and continental alluvium are not nearly so low as might be expected from the poverty of these waters in major cations and anions. Phosphorus concentrations in the large rivers fall in the range 10 to $20 \mu\text{g l}^{-1}$, of which 30 to 60% is dissolved. These concentrations are substantially higher than the concentrations of phosphorus found in some of the most oligotrophic running waters of temperate areas (Lewis, 1986). If these waters were impounded, which would lead to loss of most of the particulate fraction, they could be expected to have phosphorus concentrations between 5 and $10 \mu\text{g l}^{-1}$, which

would overlap the phosphorus range for mesotrophic lakes. Thus, while the waters of the shields and continental alluvium have been repeatedly characterized as extreme in their nutrient impoverishment, their phosphorus concentrations are well above the lowest concentrations for surface waters, even though phosphorus is likely to limit the rain-forest plant communities that occupy the catchments (Vitousek and Sanford, 1986).

An analysis of phosphorus sources and sinks of the Caura basin showed that weathering rates (1.8 cm in 1000 yr) are sufficient to account for total phosphorus concentrations as high as $12 \mu\text{g l}^{-1}$ (Lewis et al., 1987). Continuously high temperatures, and the presence of soil-vegetation complexes that promote contact between precipitation and rock, maintain weathering rates sufficient to cause the release of significant phosphorus to running waters, even though the parent material is very poor in phosphorus and resistant to weathering. Given the critical importance of phosphorus for both terrestrial and aquatic systems, and the probable significance of both atmospheric and geologic sources, further studies of phosphorus mass balance are a high priority for catchments of the shields and the continental alluvium. Waters originating from the Andean montane and alluvial zones have a higher mean and greater variance of phosphorus concentrations, and correspond as expected to global averages for unpolluted rivers (Meybeck, 1982).

Fixed nitrogen is even less reflective than phosphorus of major ionic solids. As expected, the waters of the Andean montane zone and the Andean alluvium have the highest concentrations of total nitrogen (median *c.* $500 \mu\text{g l}^{-1}$) and inorganic nitrogen (median *c.* $200 \mu\text{g l}^{-1}$). However, the concentrations of inorganic nitrogen species in the water of the shields and continental alluvium (median *c.* $100 \mu\text{g l}^{-1}$) and of total nitrogen (median *c.* $300 \mu\text{g l}^{-1}$) are not radically lower than those of the ion-rich Andean areas, i.e., waters that differ by one to two orders of magnitude in dissolved ionic solids differ only by a factor of two or less with respect to fixed nitrogen. Low concentrations of inorganic nitrogen in the flowing waters of all parts of South America that have been studied thus far are sufficiently high for none to be characterized as depauperate with respect to nitrogen supply for aquatic autotrophs.

Fixed nitrogen, particularly nitrate and ammo-

mium, are present at substantial concentrations in precipitation, as expected from the mobility of ammonia and nitrogen oxides. In contrast with other ions and phosphorus, ammonium and nitrate appear not to be notably scarcer in precipitation falling over tropical moist forest than over other vegetation zones in northern South America (Table 8.5: Apure), except in areas where widespread burning temporarily enriches the atmosphere in fixed nitrogen (Table 8.5: Lago de Valencia).

The transport distances for fixed nitrogen compounds in precipitation are unknown. A large proportion of fixed nitrogen could be recycled through the atmosphere within large tracts of tropical moist forest. Peripheral moist forest in particular may receive substantial fixed nitrogen from adjoining dry regions as a result of seasonal burning, the significance of which is presently unknown.

Yields of fixed nitrogen from catchments probably exceed deposition rates in lowland moist forest (see, for instance, Lewis, 1986), although information is very scarce. If so, the net nitrogen source is accounted for by an excess of fixation over denitrification in the forested areas. Lewis (1986) estimated by mass-balance methods that nitrogen fixation of at least $10 \text{ kg ha}^{-1} \text{ yr}^{-1}$ would be required to account for the difference between nitrogen deposition and nitrogen export in stream water. Fixation of this magnitude could only be terrestrial, not aquatic.

According to the data of Schmidt (1972), as reported by Junk and Furch (1985), the inorganic nitrogen concentrations of small forest streams in Amazonia are exceedingly low, indicating that forests surrounding the small streams can strip inorganic nitrogen from precipitation and from pore waters of soils before the waters collect in first-order streams. However, this impression is contradicted by the data for the larger rivers that collect water from many small streams, and by the data of Lesack (1992) on a forest stream near Manaus (Table 8.5). Resolution of the contradiction is important to the interpretation of the nutrient economy of running waters in forested areas.

ORGANIC CARBON

Organic carbon has been studied primarily in the large rivers of northern South America; little is known about organic carbon in small rivers or

streams. Rivers draining from the Andean montane and alluvial zones have the lowest concentrations of dissolved organic carbon (DOC) of the rivers that have been studied in the region (as low as $3\text{--}4 \text{ mg l}^{-1}$; Table 8.5), presumably because of the flocculation of dissolved organic carbon by divalent cations (Thurman, 1985). Rivers draining from the shields have DOC concentrations most often in the range of 4 to 6 mg l^{-1} . Variation among these rivers is probably accounted for by differences in soil and vegetation types. The highest concentrations are found in the Rio Negro drainage [*c.* 9 mg l^{-1} ; there is also a single value of 15 mg l^{-1} from the Atabapo on the right bank of the Orinoco (DePetris and Paolini, 1991)], which probably has tributaries with even higher concentrations. This reflects the combination of podzolic soils, extreme depletion of inorganic ions, and an associated specialized vegetation known to yield high amounts of dissolved organic carbon.

The DOC content of clear waters has not yet been studied. Possibly they will establish a lower range of concentrations, in the vicinity of 1 mg l^{-1} , as suggested by some limited data from small clear-water rivers (Vegas-Vilarrúbia and Rull, 1988; Vegas-Vilarrúbia et al., 1988). If so, the range of DOC concentrations in northern South America for rivers of moderate to large size would span approximately an order of magnitude ($1\text{--}10 \text{ mg l}^{-1}$). The range of variation in small streams will probably be broader at the upper end, but this remains to be documented.

It has been repeatedly stated in the literature that blackwater rivers of northern South America contain large amounts of dissolved organic carbon. This impression, which derives from the appearance of the waters, is misleading. In fact, the range of dissolved organic carbon concentrations for major rivers in northern South America is remarkably narrow (Table 8.5: $3\text{--}6 \text{ mg l}^{-1}$ for large rivers except the Rio Negro), despite the widely varying appearance of these rivers. The contrasting optical properties of the rivers are accounted for partly by the potency of forest-derived DOC in absorbing photosynthetically active radiation (PAR), which causes variations of only a few mg l^{-1} to be visible in a deep water column free of particles, and also by wide variation in suspended load. Suspended load masks color by backscatter, which reduces the mean distance of travel for light returning through the water column to the eye of the observer (Kirk, 1980).

Concentrations of particulate organic carbon (POC) in large rivers vary over a range very similar to the range for dissolved organic carbon [$1-7 \text{ mg l}^{-1}$; see Table 8.5 and Paolini (1990)]. There is no close relationship between DOC and POC. Rivers that carry a large suspended load typically have the highest absolute concentrations of POC and the highest ratio of POC to DOC. This is at least partially accounted for by the adsorption of some DOC onto inorganic particulate material, which facilitates transport of organic matter either by carrying it in the adsorbed phase from the point of origin, or by adsorbing DOC from solution and thus changing the DOC/POC partitioning in transit.

The relationship between total suspended solids and the percentage of organic carbon in suspended solids for rivers generally takes the form of a hyperbola. There is a rapid initial decline in percentage of organic carbon as total suspended solids increase; the decrease levels to an asymptotic plateau at high concentrations of total suspended solids (Meybeck, 1982). The waters of northern South America follow this general relationship. The whitewater rivers, which have high suspended loads, carry the lowest percentages of particulate organic matter (e.g., 1.5% organic carbon for the Apure; Saunders and Lewis, 1988a). The rivers of the shields carry far higher percentages (e.g., 16% organic matter or 8% organic carbon for particulate matter in the Río Caura; Lewis et al., 1986; Lewis and Saunders, 1989), but also have a much lower suspended load. For rivers in general, there is an inverse relationship between ionic solids and the ratio of dissolved organic carbon to total organic carbon (Meybeck, 1982; Thurman, 1985); this relationship also applies well to the waters of northern South America.

The discharge-weighted total organic carbon load of the lower main-stem of both the Amazon and the Orinoco is close to 6 mg l^{-1} . For the Orinoco, 75% of the load is dissolved and 25% particulate. For the Amazon, the load is slightly more heavily weighted toward the particulate (62% dissolved, 38% particulate; Richey et al. 1990), as would be expected from the higher suspended load of the Amazon.

Seasonal phasing of concentration and transport of dissolved and suspended organic material has been studied in detail for the Orinoco and for some of its tributaries (Lewis et al., 1986; Saunders and Lewis, 1988a; Lewis and Saunders, 1989), and for the Amazon (Richey et al., 1990). For the Orinoco,

organic matter is unique among the major fractions of dissolved solids in showing a concentration pattern that can be described as purging (Lewis and Saunders, 1989): concentrations rise rather than fall on the ascending limb of the hydrograph, in contrast to the concentration of inorganic dissolved constituents, which show dilution. The mechanism is unknown; it may involve removal of soluble organic carbon from concentrated terrestrial sources that have accumulated during the dry season. Seasonal variation of dissolved organic carbon concentration is remarkably small because the purging effect offsets dilution, which is otherwise the main cause of seasonal variation in concentrations of dissolved substances. Low seasonal variation in concentrations is also characteristic of the Amazon (Richey et al., 1990). In the Orinoco main-stem, the mean annual variation is between 3 and 5 mg l^{-1} DOC (coefficient of variation 27%). Variation across years is smaller (coefficient of variation 5%). For tributaries, the seasonal variation in concentration may be even lower (Lewis et al., 1986); seasonal variation in the Orinoco main-stem is partly magnified by seasonal heterogeneity in tributary contributions of DOC.

Particulate organic carbon shows seasonality paralleling that of total particulate matter: there is a steep increase on the rising limb of the hydrograph. Variation in concentration of particulate organic carbon is typically greater than for dissolved organic carbon. Particulate organic matter is primarily detrital in the large rivers. For the Orinoco, suspended organisms (bacteria, phytoplankton, zooplankton) account for only about 1% of particulate carbon (Lewis et al., 1990a, b).

The nitrogen content of organic matter has been studied only for a few rivers. In the Orinoco main-stem, dissolved organic nitrogen accounts for 58% of the total dissolved fixed nitrogen (Lewis and Saunders, 1989); in the Amazon the percentage is very similar (54%; Richey et al., 1991). The ratio of inorganic to organic dissolved nitrogen does not vary a great deal across tributaries in the Orinoco system (Lewis and Saunders, 1990). Particulate nitrogen varies more widely than dissolved nitrogen in both the Orinoco and Amazon. In the Orinoco main-stem, 40% of the total fixed nitrogen is particulate (47% for the Amazon; Richey et al., 1991). In the whitewater Apure, the percentage is 54%, and the absolute concentrations of particulate nitrogen

are several times higher than in the main-stem. In the blackwater Caura, 31% of fixed nitrogen is particulate and concentrations of particulate nitrogen are lower. The molar ratio of organic carbon to organic nitrogen (C:N) is 24 in soluble material in the Orinoco, and the C:N molar ratio for particulate material is 9.5. Thus both of these organic-matter pools are nitrogen-depleted with respect to protoplasm (the Redfield molar ratio is 6.6: Redfield, 1958). The C:N ratios are not highly variable for tributaries of different type, and are consistently greater than the Redfield ratio. However, many of the source materials of organic matter have even greater C:N molar ratios (wood = 209, leaf = 28, macrophyte = 46 and grass = 72: Hedges et al., 1986a). For the Amazon, the C:N ratios average 20 for coarse particulate organic matter (1.4% of total suspended solids) and considerably less (9) for fine particulate organic matter (2.5% of suspended solids). Low C:N ratios for fine particles are attributed by Hedges et al. (1986a) to adsorption of nitrogen-rich humic substances by particles.

The particle size for suspended organic material in the large rivers is predominantly very small. Richey et al. (1990) found for cruise data covering the Amazon main-stem and a number of its major tributaries that fine particulate organic matter (<63 μm) accounted for 70 to 85% of total particulate organic matter. Lasi (1984), who studied a blackwater and a clearwater tributary of the upper Orinoco, found that 1% or less of the particulate organic matter transported by these rivers was greater than 500 μm , and that >97% of coarse particulate organic matter was allochthonous (mostly leaves).

Hedges et al. (1986a, b) showed that coarse particulate organic matter in the Amazon main-stem is primarily well-preserved tree-leaf debris and some wood. In the fine fraction, the organic matter appears to be considerably older, and probably originates from soils. The analysis by Hedges et al. indicates that the common C_4 grasses on the flood plain of the Amazon do not contribute significantly to the coarse or fine particulate organic matter in the main-stem. Mass-balance studies of the Orinoco main-stem also indicate minimal flux of organic carbon from flood plain to river, despite the large amounts of grass and macrophyte production on the flood plain (Hamilton and Lewis, 1987; Lewis et al., 1990a). The rate of transport for very large

woody debris is not known for rivers of northern South America.

Ertel et al. (1986) analyzed the humic substances of the Amazon and its tributaries. In the main-stem, humic and fulvic acids, which are largely derived from terrestrial vegetation, account for 60% of dissolved organic carbon; the carbon mass ratio of fulvic to humic acids is approximately 4.7. Fulvic and humic acids show conservative properties over most of the main-stem, but appear to be removed from solution by adsorption onto fine particulate material downstream of the Rio Negro, which adds large quantities of these organic acids to the main-stem. For the Orinoco system at low water, humic substances were estimated as 25% of DOC in the main-stem and 40% of DOC in the blackwater Río Caroní (Lewis and Saunders, 1990). These preliminary data for the Orinoco, which indicate unexpectedly low percentages of humic substances by comparison with the Amazon, need to be verified by additional analyses.

For the Orinoco main-stem, 50% of soluble phosphorus is organic ($10 \mu\text{g l}^{-1}$ organic: Lewis and Saunders, 1989). For the tributaries of the shield, the proportion of organic phosphorus is closer to 75%, whereas the whitewater tributaries carry a much lower proportion (25%). The Amazon has a somewhat higher total of dissolved organic phosphorus ($16 \mu\text{g l}^{-1}$) and a higher ratio of inorganic to organic dissolved phosphorus (Richey et al., 1991).

BACTERIA

Bacterioplankton of rivers in northern South America have scarcely been studied. A single set of samples was taken of the Amazon main-stem and major tributaries in 1977 by Wissmar et al. (1981). A one-year series is available for the Orinoco and its major tributaries (Lewis et al., 1990b). The Amazon samples taken by Wissmar et al. show bacterial densities ranging from $0.9 \times 10^6 \text{ m}^{-1}$ to almost $4 \times 10^6 \text{ m}^{-1}$ in the main-stem of the Amazon and its major tributaries. The bacterial densities in this series show no pattern with respect to geochemistry, suspended load or organic carbon among the tributaries and main-stem of the Amazon. For the Orinoco samples, Lewis et al. found bacterial densities between 0.2 and $0.6 \times 10^6 \text{ m}^{-1}$. The counting of bacteria for rivers is subject to much error

because of the presence of large amounts of suspended sediment; it remains to be seen if the Amazon and Orinoco systems are truly different in bacterial densities. Lewis et al., like Wissmar et al., found very little difference among tributaries. This is a surprising result given the wide variation in chemistry and suspended load of rivers.

Seasonal variation in bacterial densities in the Orinoco main-stem and tributaries is quite small (approximately two-fold: Lewis et al., 1990b). The densities are highest on the rising limb of the hydrograph, probably because of the especially strong terrestrial and benthic influences on the river at that time. Falling densities at peak discharge probably reflect the dilution effect of large amounts of water. Declining discharge, which is accompanied by drainage of the flood plain into the main-stem, is not accompanied by any notable peak in bacteria. The factors controlling bacterial densities are fundamentally different from those controlling the densities of other suspended organisms in the river: whereas zooplankton and phytoplankton originate primarily from stagnant incubation areas, bacteria may also originate from terrestrial and benthic surfaces.

RIVER PHYTOPLANKTON

Samples of phytoplankton in the major rivers have been collected numerous times by systematists, who have described species composition and have searched for new taxa. Studies of algal systematics are cited by Uherkovich (1984) for the Amazon and by Chitty (1989) for the Orinoco. Although a number of new forms have been found, all of the dominant and abundant forms are cosmopolitan or at least circumtropical; the algae do not show any evidence of the remarkable endemism and geographic isolation that is characteristic of the vertebrates and even the large invertebrates of these drainages. Endemics are most numerous among the Zygnematales, which are very diverse but never dominant components of the biomass.

For the upper Orinoco and its major tributaries, Chitty (1989) tabulated 952 species from his own studies and those of others (376 chlorophytes, 14 chrysophytes, 7 cryptophytes, 96 cyanophytes, 331 diatoms, 8 dinoflagellates and 122 euglenophytes). The predominance of green algae and diatoms in the

species lists is characteristic of both the Orinoco and the Amazon system. The low diversity of chrysophytes is remarkable, given the importance of chrysophytes in oligotrophic waters of high latitude, but this may be a general characteristic of tropical waters (Lewis, 1978).

Table 8.6 lists the most important taxa for a selection of rivers in the Orinoco basin; information for the Amazon is more fragmentary. Although many of the taxa represented on the comprehensive species lists of taxonomists are not euplanktonic, all of the quantitatively important taxa appear to be euplanktonic (Lewis et al., 1990b). This suggests that the algal biomass of these waters is derived almost entirely from stagnant areas that support the growth

TABLE 8.6

Dominant taxa of phytoplankton and zooplankton in the Orinoco system¹

River	Phytoplankton	Zooplankton
Caura (black water)		
	<i>Melosira</i>	Cyclopoid nauplii (1.1) ²
	<i>Rhizosolenia</i>	<i>Bosminopsis</i> (0.9)
	<i>Eunotia</i>	<i>Trichocerca</i> (0.7)
	<i>Nitzschia</i>	<i>Keratella</i> spp. (2.0)
	<i>Eutetramorus</i>	<i>Brachionus</i> (0.4).
	<i>Coccomyxa</i>	<i>Filinia</i> (0.5)
	<i>Chlamydomonas</i>	<i>Lecane</i> (0.3)
Apure (white water)		
	<i>Melosira</i>	Cyclopoid copepods ³
	<i>Cyclotella</i>	(2.8)
	<i>Nitzschia</i>	<i>Brachionus</i> spp. (16)
	<i>Synedra</i>	<i>Keratella</i> spp. (14)
	<i>Lyngbya</i>	<i>Lecane</i> (8)
	<i>Microcystis</i>	<i>Trichocerca</i> (8)
	<i>Oscillatoria</i>	<i>Filinia</i> spp. (4)
	<i>Actinastrum</i>	
	<i>Tetrastrum</i>	
	<i>Eutetramorus</i>	
Lower Orinoco (mixed)		
	<i>Melosira</i>	Cyclopoid nauplii (1.0)
	<i>Merismopedia</i>	<i>Bosmina</i> (0.5)
	<i>Oscillatoria</i>	<i>Trichocerca</i> (2.7)
	<i>Actinastrum</i>	<i>Keratella</i> (2.1)
		<i>Lecane</i> (1.0)
		<i>Brachionus</i> (0.5)
		<i>Filinia</i> (0.4)

¹ Saunders and Lewis (1988b, c, 1989a), Lewis et al. (1990b).

² Mean individuals per liter for one or more annual cycles shown in parentheses.

³ About half nauplii, half copepodids and adults.

of euplanktonic taxa, rather than from algal mats, periphyton or other sources of nonplanktonic forms.

The genus *Melosira*, and particularly *Melosira granulata*, is uniquely important in the Orinoco and Amazon systems. Some of the special adaptations of this genus, which include perennation and ability to survive on substrates as well as in suspension, may explain its success (Lewis et al., 1990b). Although *Melosira* is often identified with ion-rich waters, it is also found in the Rio Negro (Uherkovich, 1981, 1984), and therefore may not be distributed according to simple geochemical rules. Other especially important diatom genera include *Eunotia* and *Rhizosolenia*. Regional differences in dominant taxa

of both the Amazon and Orinoco drainages are substantial and suggest a diversity of mechanisms for the entry of algae into flowing water, even among geochemically similar rivers.

Phytoplankton biomass, as indicated by cell counts or chlorophyll *a* concentrations, is typically very low in the Orinoco and Amazon main-stems and major tributaries. Exceptions are the mouthbays of the shield rivers entering the Amazon and a few other areas where water moves very slowly. Table 8.7 summarizes the existing information on phytoplankton biomass for the Amazon, the Orinoco and their major tributaries. The Table contains both direct and indirect estimates of chlorophyll *a* con-

TABLE 8.7

Chlorophyll, transparency and primary production in the Orinoco and Amazon systems

	Chlorophyll <i>a</i> ($\mu\text{g l}^{-1}$)		Transparency (1% light, m)	Gross production ¹ $\text{mg C m}^{-2} \text{d}^{-1}$	Potential chl <i>a</i> ² ($\mu\text{g l}^{-1}$)	Source ³
	Direct	Indirect				
Largest rivers						
Amazon, Óbidos	8.9 (4)	–	0.77 ¹	22	38	a, c
Middle Orinoco	–	0.12	0.95	19	–	b
Lower Orinoco	–	0.11	1.23	23	16	b
Andean montane						
Amazon, Iquitos	1.0 (0)	0.01	0.35 ¹	8	28	a, c
Solimões, Juruá	0.7 (6)	–	0.40 ¹	18	44	a, c
Andean alluvial						
Apure	–	0.35	0.46	26	49	b
Meta	–	–	0.40	–	12	d
Japurá	3.2 (11)	–	1.60 ¹	36	13	a, c
Juruá	1.4 (6)	–	0.37 ¹	12	38	a, c
Shield						
Upper Orinoco	–	–	2.72	–	4	d
Caura	–	0.04	2.63	13	7	b
Coroni	–	0.01	2.88	4	5	b
Negro	4.3 (1)	0.04	3.02 ¹	141	12	a, c
Mixed waters						
Guaviare	–	–	1.15	–	11	d
Trombetas	0.7	–	2.42	–	5	c
Madeira	1.1 (2)	–	0.80 ¹	–	31	a, c

¹Multi-year series for source b, calculated from one sample for source a.

²Estimated from TDP and the Redfield ratio (see text).

³Source:

Calculated as $2.5 \times$ Secchi depth.

a: Wissmar et al. (1981), a few values per site.

b: Lewis (1988), multi-layer means.

c: Forsberg et al. (1988), single values shown in parentheses.

d: Weibezahn (1985), one annual cycle.

centrations. The direct estimates are based upon standard spectrophotometric methods for measurement of chlorophyll. The indirect estimates are based on the ratio between chlorophyll and photosynthetic efficiency (Lewis, 1988), or on the conversion of cell volumes to chlorophyll *a*, assuming 20% as the ratio of dry to wet mass and 1% as the chlorophyll content of phytoplankton dry mass [calculated for present purposes from cell volume data given by Wissmar et al. (1981) for the Amazon].

The direct measurements of chlorophyll *a* shown in Table 8.7 are probably incorrect. Spectrophotometric methods are very difficult to apply at low chlorophyll concentrations in the Orinoco and Amazon systems because of complications associated with large amounts of very fine particulate solids and the presence of substantial amounts of highly colored humic substances or phaeopigments (W. Lewis and S. Hamilton, unpubl., 1993). The direct estimates are inconsistent with any probable sources of algae, and cannot be explained by growth of algae *in situ* because of low transparency and great channel depth of these rivers. For example, the probability seems exceedingly low that the Amazon at Óbidos carries chlorophyll concentrations between 4 and 9 $\mu\text{g l}^{-1}$, given that these concentrations of chlorophyll span the mesotrophic range for lakes and represent quite a substantial amount of phytoplankton biomass. The concentrations reported for the Rio Negro, which are as high as 4 $\mu\text{g l}^{-1}$, seem even less likely. Finally, there is gross disagreement between indirect methods of estimating phytoplankton biomass and the direct methods for the same samples. The data of Wissmar et al. (1981), when used to calculate chlorophyll from cell volume, indicate for the Rio Negro a concentration of 0.04 $\mu\text{g l}^{-1}$ chlorophyll rather than 4 $\mu\text{g l}^{-1}$, as shown by direct measurement.

The two kinds of indirect estimates of chlorophyll *a* produce results within similar ranges for waters of comparable type. If these estimates prove to be correct, the chlorophyll concentrations of the main-stems of the Orinoco and Amazon and of the flowing waters of the major tributaries are consistently below 1 $\mu\text{g l}^{-1}$ chlorophyll *a*. The chlorophyll concentrations represent dry mass of phytoplankton ranging from approximately 1 to 100 $\mu\text{g l}^{-1}$ organic matter, or 0.5 to 50 $\mu\text{g l}^{-1}$ organic carbon. This is 1% or less of the particulate carbon load of the rivers.

The annual cycles of phytoplankton biomass

have been studied only in the Orinoco and its major tributaries (Lewis, 1988). For the Orinoco system, chlorophyll concentrations fall to undetectable levels (less than 0.01 $\mu\text{g l}^{-1}$) on the rising limb of the hydrograph. The spread between the mean and the maximum for any given year is approximately three- to five-fold for these rivers. Blackwater and whitewater tributaries, as well as the main-stem, show a significant rise in transport of algal biomass on the falling limb of the hydrograph, which corresponds to the return of water from the flood plain to the main-stem. The entire season of low water is also a period of high transport of algal biomass, and is the season of highest phytoplankton densities. Algae in the river at this time cannot be originating on the flood plain, from which the river is disconnected at low water.

The origins of phytoplankton in the large rivers of northern South America have not been well determined. For the lower Amazon, the tributary mouthbays must be important, although transport rates of algae from mouthbays to the Amazon have not been estimated. The clearwater mouthbays develop high phytoplankton biomass, whereas the blackwater ones do not, even though both drain from the shields (Sioli, 1975). For the Orinoco, a mass-balance analysis shows that at most 37% of the algae in the main stem can originate from the flood plain (Lewis, 1988). This is also evident from algal composition; the algae in the river are typically very different in species mix from those in the flood plain.

Given that most algae in transit, at least within the Orinoco system, do not originate from the flood plain, there must be other sources upstream. Phytoplankton apparently originate primarily from pools and anabranches that are connected directly to the flowing waters throughout the system (Lewis, 1988; Lewis et al., 1990b). For this reason, minor variations in the hydrograph regulate algal supply to the flowing waters: algae grow for short intervals in stagnant areas, and are flushed from these areas by the unpredictable small hydrograph spikes that are characteristic of these unregulated rivers.

RIVER ZOOPLANKTON

Zooplankton have also been sampled sporadically throughout northern South America, but almost

exclusively for purposes of establishing species composition rather than absolute abundance or even relative abundance. Much of the taxonomic literature is cited by Robertson and Hardy (1984) for the Amazon system and by Vásquez (1984a, b) and Vásquez and Sánchez (1984) for the Orinoco system. Vásquez (1989) recorded 116 taxa of rotifers, 58 of Cladocera, and an unknown number of copepod taxa in the lower half of the Orinoco region. As with the phytoplankton, most of the taxa are cosmopolitan, and only a few of the many taxa are quantitatively important. The rotifer fauna is distinctively tropical in that it shows high diversity of *Brachionus* and *Lecane*, although these taxa are only occasionally numerically dominant. Among the Cladocera, the Bosminidae are especially prominent quantitatively in both the Amazon and the Orinoco system.

The dominant taxa in the main-stem of the Orinoco and in its whitewater and blackwater tributaries are euplanktonic, which would indicate that they originate from stagnant waters connected to the flowing waters. Numerically, rotifers predominate in all of these waters over either cladocerans or copepods. Cladocerans and copepods show a nearly even balance numerically overall, although one or the other may predominate at any given location. Cladocerans are most often important in terms of biomass because the rotifers are extremely small; the copepods are typically represented as nauplii rather than as copepodids or adults.

Tributaries may differ greatly in species composition. For example, the blackwater tributaries of the Orinoco consistently carry *Bosminopsis*, but have negligible densities of copepods; the Apure carries almost no *Bosminopsis*, but does carry nauplii (Saunders and Lewis, 1988b, c, 1989b). Both river types carry rotifers. The mechanisms underlying these differences in composition still require explanation.

There is much similarity in species composition between the Orinoco and Amazon systems. In the Tocantins and in the Rio Negro, Schaden (1978) and Koste (1972) found *Brachionus*, *Keratella* and *Polyarthra* to be most abundant (cf. Orinoco: Table 8.6).

Absolute densities of zooplankton in the Orinoco and its whitewater and blackwater tributaries are quite low (Orinoco: rotifers 7.6 indiv. ℓ^{-1} , cladocerans 0.9 indiv. ℓ^{-1} , copepods 1.2 indiv. ℓ^{-1}). The seasonal patterns of total transport and numerical abundance of zooplankton are nearly identical to

those of the phytoplankton, indicating common origins for the two groups. The absolute densities are highest at the time of low water. This is a counterintuitive pattern, given that the flood plain, which is not in contact with the river at low water, might be expected to serve as a major source for zooplankton. Transport shows two peaks: one sustained peak at low water, and a second peak on the falling limb of the hydrograph.

As is the case with phytoplankton, the composition of zooplankton in the Orinoco system overlaps only partly with zooplankton composition in the flood plain (Twombly and Lewis, 1987; Hamilton et al., 1990). For example, adult copepods, which become very abundant in many flood-plain habitats, are scarcely represented in the Orinoco main-stem. The dissimilarity in composition, when taken in combination with the phasing of transport for zooplankton in relation to flood-plain inundation, indicates that only a small proportion of the total zooplankton transport in the main-stem can be accounted for by flood-plain sources. Zooplankton appears to be added to the river by a mechanism similar to that of phytoplankton – that is, through the alternating flushing and stagnation of pockets of water found near the river at any time of the year, but particularly during the low-water stage (Saunders and Lewis, 1988c).

Zooplankton in transit seldom show evidence of either reproduction or mortality. Reproduction is probably inhibited by high current velocities, but the current velocities are not sufficient to kill the organisms, and the number of zooplankton predators is too low to have much effect once the organisms reach large rivers (Saunders and Lewis, 1989a).

PHOTOSYNTHESIS IN LARGE RIVERS

Although gross photosynthesis occurs at measurable rates in high-order rivers of the Orinoco and Amazon systems, the low transparency of these waters precludes positive net photosynthesis in the water column unless the waters become stagnant to such a degree that the water column ceases to mix vertically from top to bottom. Stagnation does occur in the Amazon mouthbays during some seasons (Sioli, 1984), but for the most part the water in the channels is moving so rapidly that the water

column is unstable. Table 8.7 summarizes the transparency data in terms of the 1% surface irradiance, which would mark the approximate depth limit for positive net photosynthesis. Even for the most transparent of the large rivers, significant photosynthesis could not be expected throughout the water column unless water depths were less than approximately 3 m. The blackwater rivers typically have considerably greater transparency than the whitewater rivers, even though they are highly colored.

Primary production has seldom been measured for the rivers of northern South America (Table 8.7). Wissmar et al. (1981) reported the results of single measurements for the Amazon main-stem and some of its major tributaries. Although the data are given as production per unit volume, they have been converted in Table 8.7 to estimates of gross production per unit area on the basis of transparency and day length. An extensive series of measurements is available for the Orinoco main-stem and its lower tributaries (Lewis, 1988). Gross primary production in the main-stems and the major tributaries of the Orinoco and Amazon systems is exceedingly low, and net production is essentially zero, except where the water is impounded for significant periods of time, as in the case of the Amazon mouthbays. Significant benthic production by algae in these large rivers is not possible because of low transparency and great depth. Some production occurs on the river margin by macrophytes and periphyton but has not been measured.

Table 8.7 includes an approximation of the potential chlorophyll *a* that would be in equilibrium with the phosphorus concentrations of the rivers. This approximation is based on the simplifying assumption that the total soluble phosphorus inventory could be converted to phytoplankton biomass in amounts reflected by the Redfield ratio (106:16:1, C:N:P, molar). Where direct measurements were unavailable, total soluble phosphorus was estimated from other phosphorus fractions. Although these are rough approximations, it is clear that the phytoplankton in these rivers is not suppressed by lack of inorganic nutrients, and that as much as 99% of the potential for biomass accumulation remains unrealized as long as the waters are in transit. These conclusions are confirmed by the much higher chlorophyll concentrations for stagnant waters on flood plains or in lakes that receive their water from

the river during inundation (e.g., Rai and Hill, 1984; Hamilton and Lewis, 1990b).

RESPIRATION IN LARGE RIVERS

Respiration has seldom been measured in the flowing waters of northern South America. The Orinoco main-stem has a mean annual respiration rate of approximately $80 \mu\text{g C l}^{-1} \text{d}^{-1}$, the major part of which is accounted for by bacteria (Lewis et al., 1990b). The respiration rates for the Caura (black water) are lower, and the respiration rates for the Apure (white water) are slightly higher. The minimum respiration rate in the Orinoco system occurs at highest discharge, as would be expected from the reduced numbers of suspended organisms at this stage of the hydrograph.

For the Amazon main-stem, Devol et al. (1987) measured respiration rates between 200 and $560 \mu\text{g C l}^{-1} \text{d}^{-1}$ (main-stem stations and major tributaries, measured as O_2 but converted to carbon for present purposes at a respiratory quotient of 1.0). These measurements confirmed earlier measurements made by Richey et al. (1981) for early rising water, but contrasted markedly with much lower rates measured by Richey et al. (1981) for a period of high water ($5 \mu\text{g C l}^{-1} \text{d}^{-1}$) as well as one set of measurements by Wissmar et al. (1981: $14 \mu\text{g C l}^{-1} \text{d}^{-1}$). These could be seasonal variations, but are probably explained by differences in methods (Devol et al., 1987). The data of Devol et al. (1987) show no systematic pattern for water types; the Rio Negro falls within the middle range of values for other types of tributaries and for the main-stem. Similarly, the information for the Orinoco (Lewis et al., 1990b) shows a relatively small difference in respiration rates between blackwater tributaries and whitewater tributaries or the main-stem. Although the Amazon and Orinoco data still allow only provisional conclusions, it appears that the presumptions of sterility and low metabolic rates for blackwater rivers may have been unjustified. The respiration rates, although low on an absolute scale, are significant in relation to travel times; they are consistent with substantial degradation of organic carbon in transit.

A more comprehensive data set for the main-stem of the Amazon, but without the tributaries, has been reported by Richey et al. (1990). This study showed

a mean respiration rate of either 320 or 400 $\mu\text{g C l}^{-1} \text{d}^{-1}$, depending on method. There was a seven-fold variation in the mean rates, possibly representing seasonal trends. An accompanying mass-balance analysis indicated that organic carbon input was substantially lower than the estimated consumption of carbon by respiration. There is indirect evidence for two pools of carbon, one of which is refractory and not subject to rapid decomposition, and a second pool that is highly labile and subject to rapid degradation after it enters the river; the presence of two carbon pools may help explain the inconsistencies between respiration and carbon mass balance.

On the basis of cruise data, Richey et al. (1988) concluded that waters of the Amazon main-stem are consistently supersaturated with carbon dioxide, which would confirm their consistently heterotrophic status, and are also supersaturated with methane, possibly as a result of water reaching the main-stem from the flood plain. Supersaturation of waters with carbon dioxide can be partly explained by flood-plain sources, but also can be explained by respiration in the moving waters.

METABOLISM OF SMALL STREAMS

Metabolism of small streams has scarcely been studied anywhere in the tropics. Northern South America is as poorly known in this respect as other tropical locations. The present information is confined to a few simple but possibly important generalities and some fragmentary data.

In the rain forest of the Amazon and Orinoco basins, the light reaching the forest floor is 1% or less of the light reaching the canopy (Sioli, 1975; Brinkman, 1985). From this observation and the lack of obvious algal growth, it appears that autotrophy in these streams is negligible, although this conclusion should not be accepted uncritically without field measurements. The rain-forest streams receive organic matter from allochthonous sources, but the rates of supply, the sources (e.g., litter versus groundwater DOC), and the accompanying rates of metabolism are undocumented.

In the dry forests and savannas, more light reaches the streams, which may show significant autotrophy. Lewis and Weibezahn (1976) studied the Rio Limon, a second-order, undisturbed stream near Lago de Valencia, during the dry season.

Although the canopy extended over the stream in most areas, the average percentage of light reaching the stream surface was 6.2% of the light reaching the canopy during sunny weather and as high as 25% during cloudy weather because of the higher proportion of diffuse light. Because the stream was shallow (25 cm), the bottom of the stream was covered to the extent of 61% with a mat of diatoms and bluegreens. Measurements of production showed that the rate of photosynthesis in the flowing water was low ($2.5 \text{ mg C m}^{-2} \text{ d}^{-1}$). The mat of diatoms and bluegreens had high net production ($1.2 \text{ g C m}^{-2} \text{ d}^{-1}$), and high community respiration ($1.4 \text{ g C m}^{-2} \text{ d}^{-1}$). A composite picture of the metabolism of the stream indicated close balance between net production ($0.73 \text{ cal cm}^{-2} \text{ d}^{-1}$) and total respiration ($0.73 \text{ cal cm}^{-2} \text{ d}^{-1}$). Extensive algal mats are also characteristic of some rivers in the Gran Sabana of Venezuela, but these have not been studied (S.K. Hamilton, pers. obs., 1993).

Lewis and Weibezahn (1976) also measured photosynthesis in the Rio Santo Domingo and Rio Aracay of the Venezuelan Andes between elevations of 600 and 2500 m. Photosynthesis measurements were limited to the flowing water. The photosynthesis rates were very low (Santo Domingo median $0.28 \text{ mg C m}^{-2} \text{ d}^{-1}$; Aracay $0.25 \text{ mg C m}^{-2} \text{ d}^{-1}$) and showed evidence of photoinhibition.

BENTHOS

The benthic organisms of the large rivers in northern South America have not been studied. This is in part explained by the perception that these rivers lack benthic faunas because of their rapidly shifting, fine-grained substrates. The main channels of the Amazon and the Orinoco have large, slowly moving waves of sandy sediment, or dunes (Sioli, 1975), that leave little doubt about the instability of the substrate, and many large tributaries deposit fine sediments in their lower reaches. However, selected habitats, including rock outcrops, shoreline and debris in the river could support benthos (cf. Benke and Wallace, 1990).

In rain-forest streams of the shields and continental alluvium, benthic organisms appear to depend mainly on allochthonous organic matter, presumably because periphytic algae grow poorly in these habitats (Sioli, 1975; Fittkau, 1983; Walker,

1987). Observing that entire leaves may be found buried in stream sediments, Sioli (1975) speculated that coarse organic matter is degraded very slowly. However, Walker's work indicates that leaves are shredded by chironomids through selective removal of the mesophyll, which sustains the unaltered appearance of the leaf, even after it is extensively shredded.

Primary streams in the forested continental alluvium and shields where ionic solids reach their lowest concentrations are virtually free of molluscs because the cation supplies are insufficient to support skeletal material, except for some highly specialized taxa that have evolved means of minimizing the inorganic matrix of the shell (Sioli, 1975). In waters of higher cation content, molluscs may be abundant, and insect guilds linked to the harvesting of *Aufwuchs* may be present (Río Limón: Lewis and Weibezahn, 1976), but these have been studied even less than the rain-forest organisms.

The rain-forest streams of the shields and continental alluvium are populated by a wide variety of benthic insects, but the mix of guilds and of major taxa probably differs from that of streams at temperate latitudes (Covich, 1988). The chironomids are most diverse: Fittkau (cited by Sioli, 1975) estimated that such regions have as many as 1000 species, but noted that this diversity is not especially high in a comparative sense, given that Europe has approximately 1200 taxa of the same group. The lowland rain-forest streams are depauperate in taxa that have cold-water affinities. Examples include some groups of Diptera and the entire order of Plecoptera, which is represented in the New World tropics primarily by the single genus *Anacroneturia* (Covich, 1988). Some groups may have special warm-water affinities, and thus may be more diverse in the lowland tropics (e.g., riffle beetles: Covich, 1988). Important taxa in the rain-forest streams include, in addition to the chironomids, the Simuliidae and Trichoptera.

Fragmentary observations suggest that the rain-forest stream communities show a high proportion of predaceous taxa, and of generalist feeding capabilities among the nonpredaceous forms. A few special feeding adaptations have been documented among the filter feeders (Sattler, 1963). Walker's work (1985, 1987), which offers the most detail, indicates a dominant role for fungi growing on litter as a base of the food chain. Fungi are harvested

primarily by small chironomids, which nourish the predaceous taxa. The present impressions of the rain-forest streams need to be verified and broadened by intensive studies.

Benthic production and mean densities of organisms for streams of northern South America are not well known. Fittkau (1983) estimated that rain-forest streams contain about 2 gm^{-2} of benthic insects. This estimate, when combined with the evidence of the low quality of benthic food, would suggest very low benthic insect production. The Andean alluvial area, which extends into the várzea, is well known for plagues of black flies and culicids that are not typically present in nuisance proportions within the waters draining from the shields and continental alluvium; Fittkau cites this contrast as evidence of low benthic production. Walker (1987) persuasively presents an alternative explanation: culicids do not thrive because they are filter feeders, and the rain-forest streams are dominated by shredders (chironomids) that depend on fungi. Walker's (1987) demonstration that blackwater streams sustain higher biomass and diversity of benthos contradicts the often-cited hypothesis of blackwater sterility. Walker et al. (1991) have also shown that benthos and fish in a blackwater river of the central Amazon region are spatially very stable; high diversity could be one result of spatial stability.

There is probably a strong zonation of benthic insect fauna extending upward from sea level in northern South America, but gradients of this type have been studied more extensively in Central America than in South America (Covich, 1988). European zonation schemes seem only marginally applicable because high-gradient streams can be much warmer in the tropics than in temperate latitudes (Ward, 1985). However, some recent work in West Africa offers greater promise of unifying zonation schemes for temperate and tropical regions (K. Cummins, pers. comm., 1993).

FISHES AND OTHER VERTEBRATES

The waters of northern South America contain 2000 to 3000 species of fish, of which somewhat over half have been described. This diversity of fishes is probably greater than in any other region of comparable size, and especially so by comparison with temperate regions. For example, North America has

950 fish species (Hocutt and Wiley, 1986). The Amazon basin alone probably contains 2000 species, of which approximately 1200 are described (Gery, 1984). One proximate explanation of the large number of species lies in the large sizes of the Amazon and Orinoco basins; in general, the number of fish species within a drainage bears a reasonably good relationship to the size of the drainage, as described by a power function with an exponent of approximately 0.5 (Welcomme, 1990).

While many essential descriptive details about the fishes and their adaptations have been assembled by taxonomists and natural historians, synoptic information on fish communities encompassing such factors as patterns of diversity, behavior and food webs are still very poorly worked out (Bayley and Petrere, 1989). The characid fishes account for as much as 40% of the total diversity, and the siluriform fishes account for at least another 25%. Other groups are less diverse but may be very important ecologically, even when represented by only a few taxa. Examples include the clupeomorph fishes, which can be extremely abundant zooplanktivores, the osteoglossids, which include the arapaima (*Arapaima*), a top predator in flood-plain waters, and the knife fishes (Gymnotiformes), which include more than 50 highly specialized taxa in northern South America (Gery, 1984).

Commercially important species have been studied most intensively. The total yield of fish from the Orinoco basin is estimated as 16 000 t yr⁻¹ (Novoa, 1990), as compared with a potential yield of 40 000 to 45 000 t yr⁻¹. The total fish yield for the Amazon is estimated as 210 000 t yr⁻¹ (Junk, 1984); potential annual yield is as much as one million tons (Bayley and Petrere, 1989). Fisheries are dependent on a surprisingly small subset of the total fish fauna. Two genera, *Colossoma* and *Prochilodus*, probably constitute more than 50% of the total fish catch in the Amazon and Orinoco basins. Junk (1984) estimated that the ten most important species in the Amazon account for about 93% of the catch; the work of Novoa (1982) on the Orinoco shows a similar pattern. Most commercially important taxa are large fishes that become especially vulnerable during long annual migrations in the river channels.

Contrary to earlier expectations, it appears that the species diversity of blackwater rivers does not differ substantially from that of whitewater rivers (Goulding et al., 1988). Even though diversity is high

in blackwater areas, marketing information on fishes suggests that the fish yield from blackwater areas is far lower than from whitewater areas (e.g., Junk, 1984). However, because commercial fisheries are focused on a few species, some of which are absent from blackwater areas, it should not be assumed that the total fish production of all species in blackwater areas is as much below that of whitewater areas as might appear from the information on fish catch. It is quite likely that the higher nutrient concentrations of white waters are reflected in higher fish production because of the intimate relationship between fish production and flood-plain productivity, but this remains to be proven.

The majority of taxa that inhabit the large rivers spend much or all of the life cycle out of the main channel. Some taxa are essentially confined to the flood plain and make no direct use of the main channel. However, many species use the main channel as a dispersal pathway. The large detritivores in particular undertake long annual migrations. In whitewater areas, detritivores typically migrate upstream at the time of spawning (Bayley, 1973). Following spawning, they may migrate in the reverse direction. Other taxa do not migrate, but use the flowing water as a dispersal mechanism for larvae. A study of fishes in the fringing flood plain of the Orinoco showed that the flood plain lake basins, which were crowded with fish during the period of low water, were almost devoid of fish at high water because the fish had dispersed into the surrounding forest and channels (Rodriguez and Lewis, 1990). Spawning typically occurs once per year on the rising limb of the hydrograph, as indicated in Fig. 8.9 for the Río Metica, a tributary of the upper Meta. A few taxa are fractional spawners and spawn at all times of the year, and some others spawn once per year but are not timed to the rising limb of the hydrograph.

A few taxa are adapted for long-term subsistence in the rapidly flowing waters of the main channel of the large rivers. Lundberg et al. (1987) documented the presence of a guild of electric fishes living in the deep waters of the main channel of the Orinoco, which would appear to offer almost nothing in the way of protective structures that would shelter fish from high current velocities. These taxa are specifically adapted to feed on zooplankton and insect drift. In small rivers, where firm substrates and structures are available, fish communities of the

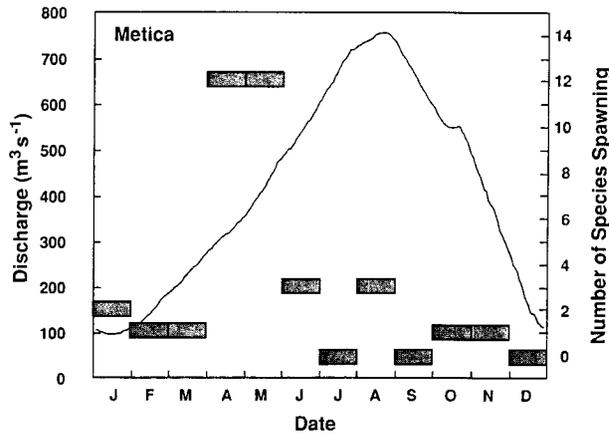


Fig. 8.9. Relationship of discharge to number of fish species spawning (horizontal bars) for the Río Metica, a tributary of the Río Meta in Colombia (Galvis et al., 1989).

channel are more diverse, but their ecological roles are not well known (Lowe-McConnell, 1987).

In rain-forest streams of low order, it is typical to find 50 to 80 species of fish (Fittkau, 1983), which is a considerably greater number than would be expected under similar conditions in a temperate forest. Most of the species appear to be adapted to use allochthonous food sources, and have either flexible or nonspecialized feeding characteristics. Many of these fishes are very small by comparison with fishes of the temperate zone living under similar conditions. A recent study of a small rain-forest stream entering the Caribbean from northern Venezuela indicates fish production of about $37 \text{ kg ha}^{-1} \text{ yr}^{-1}$ (standing stock: 44 kg ha^{-1}), which is far lower than for the main-stem areas of the largest rivers that benefit from large amounts of contiguous flood plain ($2800 \text{ kg ha}^{-1} \text{ yr}^{-1}$, Amazon at Manaus: Bayley, 1989). However, field studies are so few that no generalizations can yet be drawn.

Many fishes are classed as detritivorous, but this classification leaves much doubt about the source of nutrition. Some taxa may ingest detritus incidentally with algae or invertebrates that are the main nutrient source.

On the flood plains of the Amazon and Orinoco, invertebrate feeders and piscivorous taxa are very important, but these are less prominent among the large migratory taxa that are taken commercially in the river channels. The degree of direct or indirect dependence of aquatic food webs on the abundant

detritus from vascular plants of the flood plain is a subject of great importance to the fisheries ecology of the large rivers. Araujo-Lima et al. (1986) showed that the detritivorous characoids of the Amazon system have stable carbon-isotope signatures consistent with diets based on direct or indirect use of carbon from phytoplankton, contrary to the presumed strong nutritional role of vascular plant detritus. In contrast, the siluriform fishes show stable isotope signatures consistent with the direct or indirect use of detritus from higher plants. Hamilton et al. (1991) have demonstrated the importance of both phytoplankton and periphyton as nutrient sources for the Orinoco flood-plain fishes, including migratory taxa. In general, it appears that vascular plants provide a much smaller proportion of energy reaching fishes than might be expected from the high production and high standing stock of vascular plants in flood plains; algae are nutritionally much more important in supporting fishes or invertebrates used by fishes than might have been expected.

Other important aquatic-vertebrate components of the freshwater systems of northern South America include caimans (*Caiman*, *Melanosuchus*, *Paleosuchus*), dolphins (*Inia*, *Sotalia*), manatees (*Trichechus*), otters (*Lutra*, *Pteronura*) and turtles (*Chelonia*) (Best, 1984). Many of these taxa have been drastically reduced in abundance, despite the low population density of humans in much of northern South America. Possibly the most important change from the viewpoint of ecosystem function has been the great reduction in abundance of caimans. The largest taxa of caimans were almost completely eliminated from the central Amazon between 1940 and 1950, when up to 5 000 000 hides per year were removed from the Brazilian Amazon alone. Fittkau (1973) has provided evidence that the original population of caimans in the central Amazon was capable of releasing approximately $1 \mu\text{g l}^{-1} \text{ d}^{-1}$ of phosphorus into flood-plain waters, and has suggested that declines in fish yield in some areas may be explained by the reduction in nutrient mobilization caused by the elimination of caimans. The relative importance of this mechanism in relation to bacterial mineralization of phosphorus has been questioned (J. Melack, pers. comm., 1993), but the potential for cascade of effects from higher to lower trophic levels is clear. In forest streams, small caimans of low commercial value still may be found as the top aquatic carnivores.

OVERVIEW AND SYNTHESIS

The rivers of northern South America offer numerous special opportunities for study, including: (1) latitudinal comparison, which may be essential in demonstrating the regulatory role of such factors as mean temperature or variation in temperature that are difficult to manipulate experimentally on large scales; (2) characterization of very large running-water systems that are not perturbed by hydrologic regulation or by drastic changes in vegetative cover; and (3) study of river and stream systems that have exceedingly low concentrations of ionic and suspended solids. These opportunities have not yet been well exploited.

The current central concepts of running-water systems are as yet difficult to apply to the waters of northern South America because of the fragmentary nature of the underlying information base. In its most general form, the River Continuum Concept, which is based on the principle of biotic equilibrium controlled by a continuum of physical gradients extending from headwaters to large rivers (Vannote et al., 1980; Minshall et al., 1985), is clearly relevant to these large systems. However, it is still unclear how data for large tropical rivers would support, modify or contradict the River Continuum Concept as it has been developed from studies of streams and rivers at higher latitudes. The importance of depth, velocity, flow and temperature are stressed by the River Continuum Concept. Among these, temperature offers the clearest contrast with rivers of higher latitude: the rivers of northern South America do not oscillate seasonally in temperature, but they do present a gradient of mean temperatures paralleling an elevational gradient from zero to almost 6000 m a.s.l.

The information on the Orinoco and Amazon main-stems and their major tributaries may offer some refinement of the River Continuum Concept as applied to rivers of highest order. Contrary to the diagram presented by Minshall et al. (1985), net primary production in the largest rivers of northern South America is negligible. In apparent consistency with the River Continuum Concept, it appears, but is not yet proven, that rain-forest streams are heterotrophic. At intermediate orders, there may be vast numbers of autotrophic streams and small rivers in savanna and dry forest; the possibility of significant autotrophy in rain-forest rivers that

are sufficiently wide to be free of canopy is unstudied.

Organic matter and associated insect-based food webs are still too unfamiliar to be matched to the River Continuum Concept. In the rivers of highest order, the particulate organic matter is overwhelmingly fine, as predicted. Shredding of coarse particulate organic matter for rain-forest streams would seem to be important, but the evidence for it is limited.

The complementary concept of nutrient spiralling is also difficult to apply at the present state of knowledge. Rain-forest catchments show poor retention of inorganic nitrogen. Phosphorus, which is released primarily by weathering, is also surprisingly mobile. The concept of looser spiralling cycles downstream (Minshall et al., 1985) may be contradicted for large rivers because of the retention and remobilization of nutrients and carbon through the annual inundation of large amounts of flood plain (cf. Sedell et al., 1989). Deposition of solids from flood-plain waters must affect phosphorus spiralling, and biotic stripping of nitrogen from flood-plain waters has also been documented. However, the net effect of the flood plain on the river has proven, at least for the Orinoco system, to be far less than might originally have been expected. The flood plain, although receiving a pulse of nutrients each year from the river, shows negligible net export of organic carbon, phosphorus, nitrogen or suspended organisms back to the river, despite very high rates of production and metabolic activity (Hamilton and Lewis, 1987; Lewis et al., 1990a).

The large rivers of northern South America are internally integrated by transport, but, like other large rivers, defy treatment as ecosystems because they do not show the high degree of internal metabolic integration that is expected for ecosystems. These large river systems can be viewed as ecosystem complexes consisting of (1) a cluster of distinct ecosystem types, including savanna, forest and flood plain, each of which shows internal fluxes exceeding boundary fluxes for carbon, nitrogen and phosphorus; and (2) transport pathways, including the atmosphere and the flowing waters, for which the boundary fluxes exceed the internal fluxes (Lewis et al., 1990a).

The great river systems of northern South America present unsurpassed opportunities for the testing of broad concepts applicable to running water. Many

critical opportunities are being lost as the rivers and streams change under the influence of development.

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