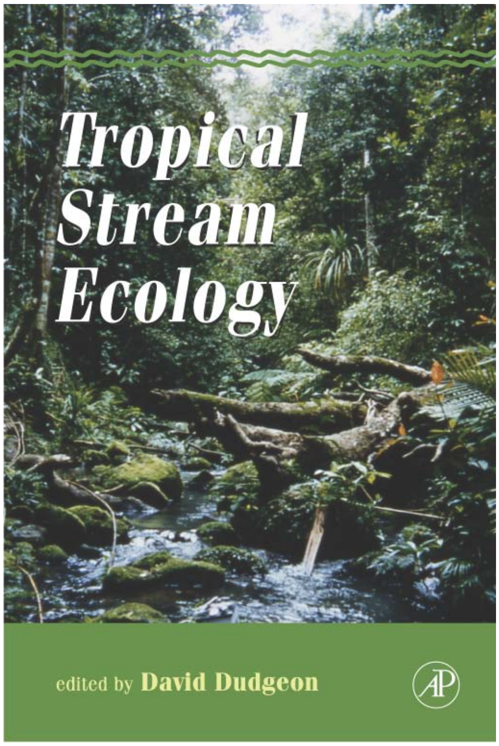

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# 1

# Physical and Chemical Features of Tropical Flowing Waters

William M. Lewis, Jr

Tropical latitudes offer an abundance of well watered landscapes because the Hadley circulation favors heavy seasonal rainfall, particularly within the migration area of the Intertropical Convergence Zone. Hydrographic seasonality typifies tropical streams and rivers, and to a large extent is predictable on the basis of latitude within the tropics. Because thunderstorms play an important role in the delivery of precipitation, hydrographs for small streams often show numerous intra-annual spikes in discharge, but these patterns are obscured through hydrographic averaging at the regional scale. Tropical flowing waters typically show well-defined seasonality in depth and velocity of flow, water chemistry, and metabolic rates, but seasonality is based primarily on hydrology alone rather than hydrology in conjunction with temperature, as would be more typical of temperate latitudes.

Total annual irradiance at tropical latitudes does not differ greatly from that of latitudes as high as 40° because of the high moisture content of tropical air. Because of high mean water temperature, the oxygen reserve at saturation is substantially lower for tropical waters at low elevations than for temperate waters averaged over the growing season. Metabolic rates of rivers within the tropics are affected by thermal variation related to elevation and percent moisture in the atmosphere.

Topography is the dominant control on suspended and dissolved solids of tropical streams and rivers. Concentrations of dissolved solids range from a few mg $L^{-1}$ in wet areas of low gradient and resistant lithology to 1000 mg $L^{-1}$ or more on high gradients with readily eroded lithologies, especially in the presence of disturbance. Seasonality in discharge is accompanied by seasonality in concentrations of dissolved and suspended solids, organic matter, and nutrients; seasonal ranges in concentration often reach an order of magnitude.

Dissolved forms of phosphorus and nitrogen in tropical streams and rivers are present in quantities sufficient to support moderate to high biomass of autotrophs even under pristine conditions. Concentrations of phosphorus (P), nitrogen (N), and dissolved organic carbon (DOC) show no obvious categorical contrast with those of higher latitude at similar elevations, but mechanisms for the delivery of P, N, and DOC from tropical watersheds to streams and rivers, and their subsequent processing within the aquatic environment, may differ in important ways that are not yet well understood.

*Tropical Stream Ecology*

## I. INTRODUCTION

Generalizations about tropical streams and rivers are most easily approached through the influences of climate. A climatic perspective on tropical flowing waters also establishes a useful framework for comparisons between tropical waters and more familiar temperate waters and highlights the differences that are related to latitude by way of climate. Therefore, this chapter begins with an overview of tropical climatology and follows the climatic connections through hydrology and water temperature. Next is a presentation of water chemistry with a focus on suspended and dissolved solids as well as P, N, and C, which sets the stage for later chapters that deal with ecosystem functions and biotic communities.

Tropical climatology is a subject for books rather than chapters. Only a sketch of tropical climates can be given here, but a substantial narrowing of scope is justified by special relevance of the connections between climate and flowing waters, which are a subset of connections between climate and all ecosystem types combined.

Table I shows a list of climatic variables that are most directly connected to the ecosystem functions of tropical flowing waters. The list differs from one that would be applicable to lakes or to terrestrial ecosystems. For example, lakes are much affected by wind, whereas flowing waters are much less so. The same can be said for heat budgets, which have striking effects on lakes but are less important for flowing waters except insofar as they control the seasonal and diel ranges of temperature.

## II. CLIMATIC ORGANIZING PRINCIPLES

Tropical climates are heterogeneous spatially, but they show a certain amount of order that can be understood in terms of the global distribution and movement of heat and moisture through the atmosphere. For present purposes, tropical latitudes are construed as spanning the tropics of Cancer and Capricorn, although in a climatic sense tropical phenomena may spill beyond or withdraw from these margins at certain times and places.

### A. Hadley Circulation

Within the tropics, one organizing feature is Hadley circulation, which can be depicted as an immensely wide rotation of air roughly spanning each of the hemispheric ranges of tropical latitudes (Fig. 1). The rotation is generated by rising air at the lowest latitudes in response to a combination of heating and convergence of air flows from the two hemispheres. Rising air near the equator carries moisture that was transferred to it as it passed over the ocean surface en route higher to lower latitudes. The rising air releases moisture as precipitation, which falls in copious amounts beneath the convergence of north and south Hadley cells, but not necessarily

*TABLE I* Climatic Features of the Tropics Most Relevant to Ecosystem Functions of Tropical Streams and Rivers, along with their Direct Ecosystem Connections

| *Climatic variable* | *Ecosystem connection for flowing waters* |
|---|---|
| Insolation | Control of photosynthesis |
| Temperature | Regulation of all metabolic rates |
| Precipitation | Control of mass transport and physical habitat through depth and velocity of water |

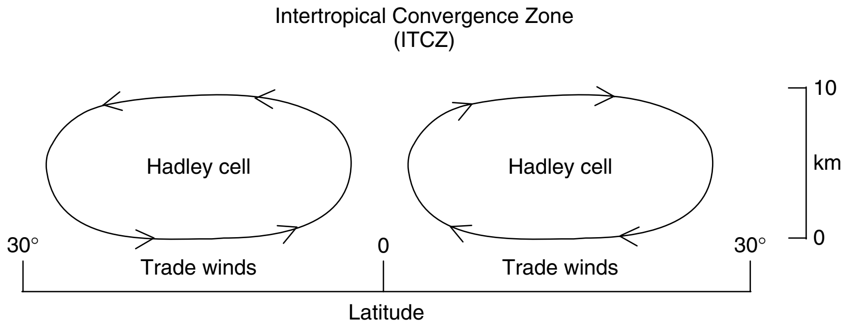

*FIGURE 1* Cross-sectional diagrammatic view of the adjoining Hadley cells from the northern and southern hemispheres. Note the vertical exaggeration of the diagram (the cells in reality are approximately 1200 times as wide as they are high). The position of the convergence between the two adjoining (north and south) Hadley cells, although shown here as being on the equator, typically is displaced somewhat from the equator and moves seasonally.

directly over the margins of the cells. The constant push of air from below moves the formerly ascending air mass, now drier, laterally, toward higher latitudes, where it sinks to the earth's surface, causing a constant flow of dry air, or trade winds, back toward the equator, thus completing the cycle.

Hadley circulation is disrupted by other atmospheric forcing factors and through the interruption of its mainly oceanic drivers by land masses. Even so, Hadley circulation causes a band of arid landscapes near the margins of the tropics and abundant precipitation over much of the equatorial zone.

### B. The Intertropical Convergence Zone

Another organizing feature of tropical climate related to Hadley circulation is the intertropical convergence zone (ITCZ). Hadley cells on either side of the equator come together as a convergence of upward-moving, moisture-laden flows (Fig. 1). The convergence between Hadley cells from the two hemispheres is marked by constantly low pressure corresponding to the constant rise of air within the zone of convergence. Either this low-pressure zone (the 'equatorial trough') or the underlying convergence and uplift of air masses marks the ITCZ, which also has been called the 'meteorological equator' (McGregor and Nieuwolt, 1998).

The ITCZ is not aligned with the geographical equator (Fig. 2). It shows seasonal variation that is loosely correlated with the path of the sun, which facilitates the constant rise of air where and when irradiance is most direct. Often there is a notable lag (a few weeks: McGregor and Nieuwolt, 1998) between seasonal movement of the sun and change in position of the ITCZ, presumably reflecting time over which solar heat must accumulate.

The position of the ITCZ, while generalized in Fig. 2 for the entire earth, varies in width and spatial distribution from one continent to the next. In addition, the ITCZ varies from one year to the next in its location and its rate of cross-latitudinal progress. Cloud cover and rainfall associated with the ITCZ therefore are to some extent irregular on a river-basin scale.

### C. Solar Irradiance

Another organizing feature of tropical climates is the seasonal pattern of solar irradiance, which shows latitudinal gradients in total annual amount and seasonality over the tropics (Fig. 3). The gradient in total annual solar irradiance at ground level is the reverse of the expected gradient at the top of the atmosphere because of the high moisture content of air near

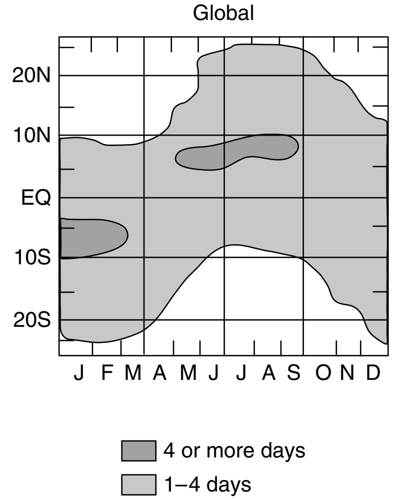

*FIGURE 2* Composite global monthly movement of the ITCZ within the tropics. Heavy shading indicates four days or more of strong cloudiness, and light shading indicates one to four days of strong cloudiness. Although virtually all specific locations around the earth reflect the composite pattern, the details differ from one location to another. Redrawn from McGregor and Nieuwolt (1998) after Waliser and Gautier (1993). Copyright John Wiley & Sons Limited. Reproduced with permission.

the equator. In fact, average annual irradiance for land masses within 10° of the equator is little different than it would be at 45° latitude because of the strong suppression of total irradiance at the earth's surface due to high moisture content of the air near the equator (Fig. 3).

Latitude has a strong effect on annual range in solar irradiance per day, as shown in Fig. 3. Annual maximum daily irradiance at the top of the atmosphere varies little with latitude, even beyond the tropics. In contrast, annual minimum irradiance, uncorrected for cloudiness, decreases steeply with latitude; at the equator, it is almost 50% higher than at the margin of the tropics. Latitudinal variation in cloudiness obscures these trends to some degree, however, by suppressing the annual maximum wherever moisture is abundant in the hemispheric summer months.

## D. Monsoons

Movement of the ITCZ and its associated atmospheric moisture is one cause of annual monsoon cycles. Monsoons, which have in common a persistent seasonal reversal of wind direction, are found throughout tropical and southeast Asia as well as northern Australia. They also affect most of tropical Africa north of the equator, but are not pronounced in South America. In general, the northern movement of the ITCZ and its associated low-pressure zone leads to a movement of air from the southern to the northern hemisphere across the equator. If this air is moisture laden, as is often the case, it brings heavy rainfall during the northern hemispheric summer. At a given location, monsoons tend to be oscillatory in intensity, and also show considerable variation from one year to the next (McGregor and Nieuwolt, 1998). East Asia also has a winter monsoon caused by a persistent high-pressure center over the Tibetan plateau.

## E. El Niño Southern Oscillation

Organizing features that are temporally irregular include variations in the pressure gradient of the equatorial Pacific. Fluctuation in the status of this gradient is called 'the southern

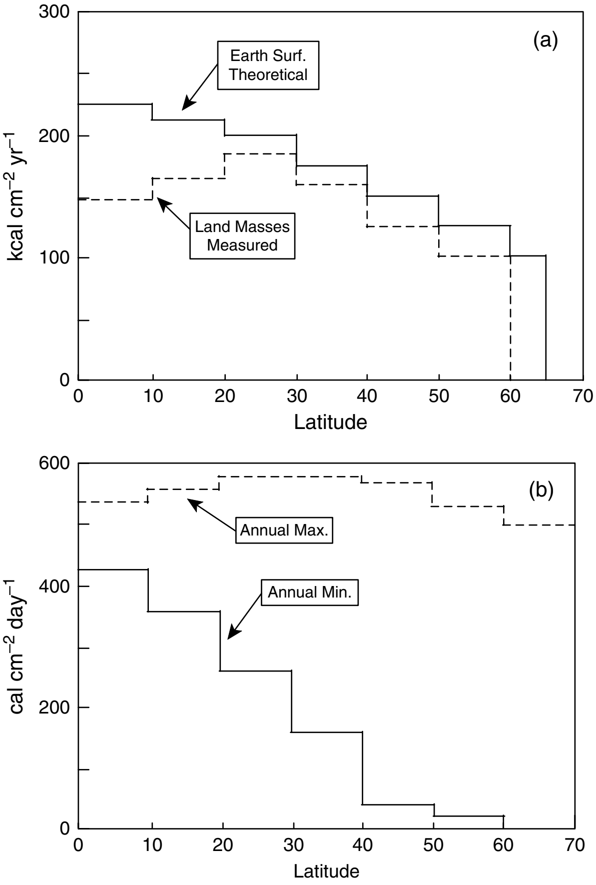

*FIGURE 3* (a) Comparison of the amount of irradiance that would reach the surface of the earth at a fixed uniform attenuation coefficient of 0.8, as compared with the actual amount of irradiance observed over the tropical land masses. (b) Gradients in the annual maximum daily irradiance and the annual minimum daily irradiance as a function of latitude, assuming a uniform attenuation coefficient of 0.8. Redrawn from Lewis (1987), based on data from List (1951). Reproduced from Lewis Jr (1987), with permission from the *Annual Review of Ecology and Systematics*. Copyright 1987, Annual Reviews (www.annualreviews.org).

oscillation'; extremes are referred to as 'El Niño Southern Oscillation' (ENSO) conditions. Most often pressure is notably higher in the eastern than in the western Pacific; this condition is termed a 'positive oscillation gradient.' Unusual strengthening of this gradient, which is called 'El Niño,' is associated with an unusual degree of warmth in or around December in marine waters along the western coast of South America. The opposite extreme is designated 'La Niña.' Upwelling caused by extreme thermocline (density gradient) tilt brings up cold, deep ocean water in La Niña years, as contrasted with a Kelvin wave (a large pool of warm water moving across the upper ocean: Kessler *et al.*, 1995) return flow of warm surface waters under El Niño conditions, when the thermocline tilt is relaxed. Most years (about 70%) belong to neither category, but interannual clustering of extreme conditions (El Niño at a frequency of about 20% or La Niña at a frequency of about 10%: website of the National Oceanic and Atmospheric Administration, 2004) is typical (Barry and Chorley, 2003).

The extreme conditions of El Niño and La Niña in the western Pacific are associated with specific climatic variations in various parts of the tropics (see maps given by McGregor and Nieuwolt, 1998). El Niño events correspond to unusually dry conditions (even severe drought) from December through February in Southeast Asia, northern Australia, the eastern Amazon basin, and southeastern Africa; equatorial western Africa is unusually wet. Conditions in these months under La Niña for the most part are opposite (including flooding in some locations) and, in addition, tropical western Africa tends to be cooler than usual. From June to August, El Niño years bring drought to much of India, and southern Southeast Asia as well as northern Australia, warmth to western South America, and warmth plus drought to lower central America and upper South America. La Niña in these months is nearly the opposite, with the addition of a cool tendency in western tropical Africa.

### F. Spatially Irregular Phenomena

A number of other climatic phenomena of the tropics, including tropical thunderstorms, cyclones, jets, and orographic effects, deserve consideration in the analysis of climate at any particular location. For example, the frequency and severity of thunderstorms determines the frequency and magnitude of significant non-seasonal irregularities in the hydrograph, which in turn have ecological effects through mobilization of sediment, movement of biofilms, and facilitation of transport from land surfaces to streams and rivers. Such phenomena do not lend themselves well to generalization because they are spatially even more heterogeneous than the above-mentioned organizing features of tropical climate.

## III. TEMPERATURE

Mean daily air temperatures in the tropics are affected primarily by moisture content of the atmosphere and elevation. The timing of the annual thermal maximum, however, is determined primarily by latitude. Within 10° of the equator, most of the tropical land mass at sea level has a daily mean temperature of 25–30°C in July (northern hemispheric summer). Mean air temperatures near the equator in December–January also are 25–30°C, although there is a seasonal shift in the isotherms that reflects cooling of a few degrees north of the equator and warming of a few degrees south of the equator in the northern hemispheric winter (Fig. 4). Toward the margin of the tropics, temperatures are much higher (30–35° at sea level) in July for the northern hemisphere and in January for the southern hemisphere. The higher maxima at the margins of the tropics reflect the much lower moisture content of air there, as explained mostly by the Hadley circulation (McGregor and Nieuwolt, 1998).

### A. Air Temperature

Near the equator, the annual range of mean daily air temperature is 1–4°C (mean near 2°C). At the margin of the tropics, the annual amplitude reaches 12–16°C. In coastal zones, the annual amplitude is reduced by as much as 50% through oceanic influences. Diel air-temperature variations are approximately 10°C near the equator, where they are moderated by suppression of back radiation due to humidity. At the tropical margins, where humidity is low, they are 15–20°C. Close proximity to the coast reduces diel variations by as much as 50%.

### B. Effects of Elevation on Air and Water Temperature

The mean normal lapse rate (rate of decrease in temperature with elevation) within the tropics is approximately 0.65°C per 100 m of elevation (McGregor and Nieuwolt, 1998). Therefore, the air temperature at high elevations can be quite low (Fig. 5). Elevation-related suppression of air temperature ranging from a few degrees to 20°C or more affects about 20% of the tropical land mass (Fig. 5).

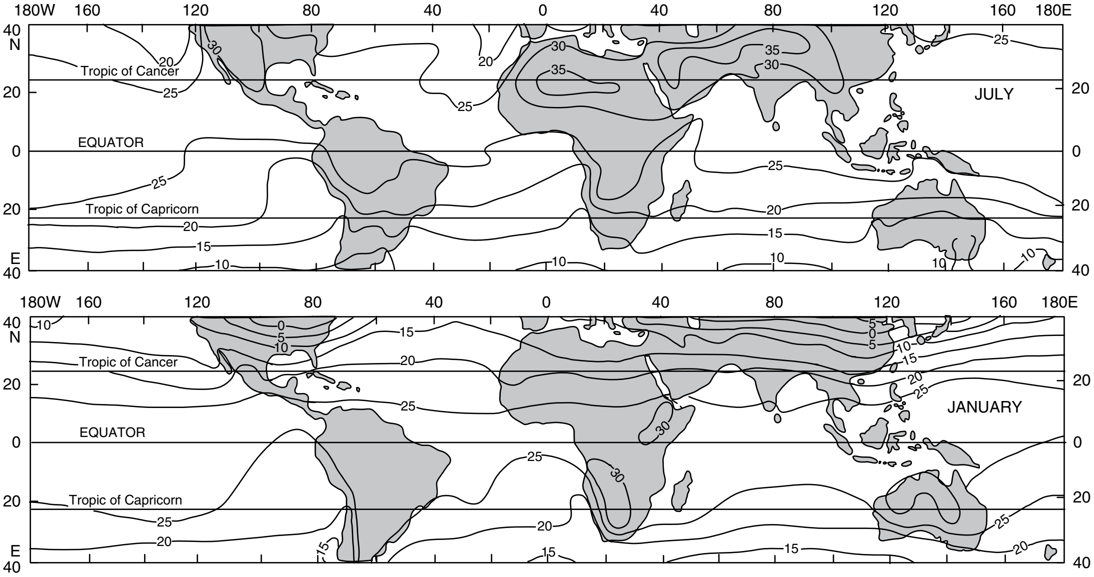

*FIGURE 4* Mean air temperatures during July and January at sea level. Redrawn from McGregor and Nieuwolt (1998), with permission from John Wiley & Sons Limited.

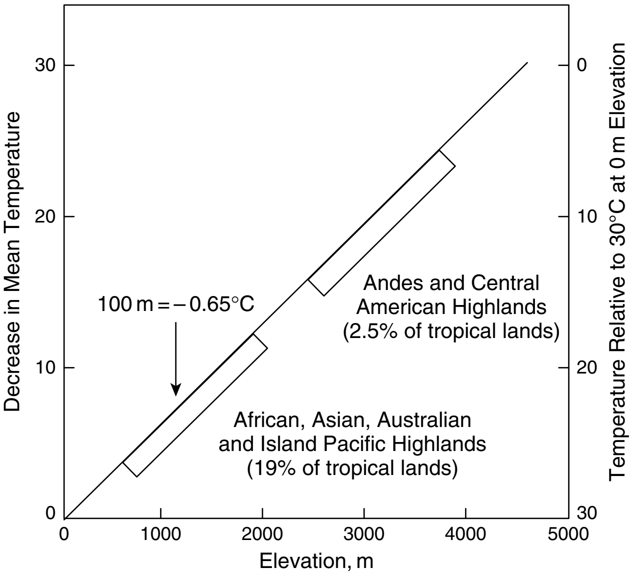

*FIGURE 5* Expected decrease in mean air temperature with elevation at mean normal lapse rate of 0.65°C per 100 m of elevation. The brackets show the elevation range encompassing most tropical lands with elevations above 500 m.

Figure 6 gives information on water temperatures for selected stations covering a range of latitudes and elevations. Maximum water temperatures for stations of low to moderate elevation range between 25 and 35°C, reflecting the range of mean daily air temperatures within the tropics. As expected from air temperatures, the highest maximum water temperatures are associated with low humidity (e.g. Black Alice River, Australia).

At elevations above 750 m, the effect of elevation is distinguishable from other factors that influence maximum temperature. The maximum temperatures at the highest elevations

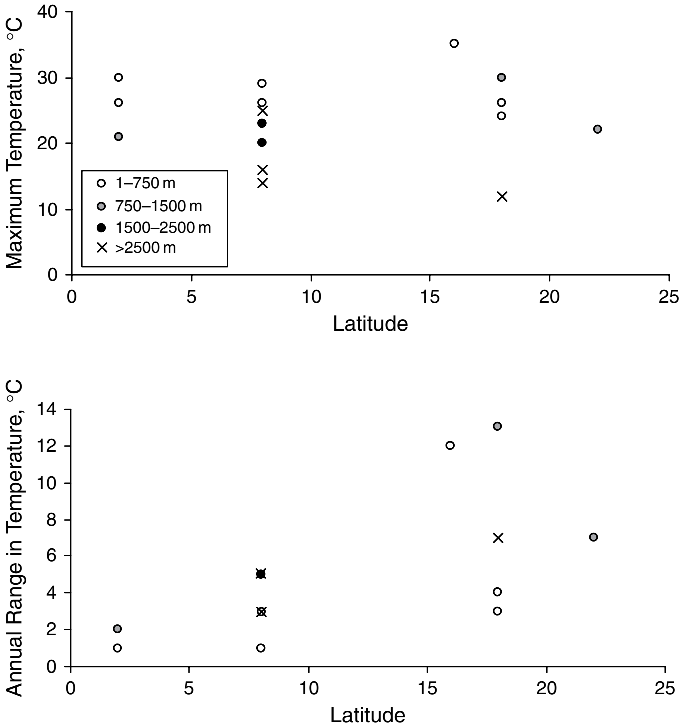

*FIGURE 6* Examples of maximum temperature and annual range of temperatures for tropical running waters over a range of elevations and latitudes. All data except for the Mameyes are derived from a series of individual daytime measurements at a specific site, rather than true daily averages. Data for sites 1 through 8 are from a review by Ward (1985), who gives the original sources. Locations 9 through 14 are from Petr (1983), and locations 15 and 16 are from Ortiz-Zayas (1998). 1 = Black Alice River, Queensland, Australia; 2 = Amazon River main stem; 3 = Orinoco River main stem; 4 = forest streams of the central Amazon; 5 = the Luhoho River, equatorial Africa; 6 = Zambezi River, southern Africa; 7 = Mogi Guassu River, headwaters, Brazil; 8 = Matadoro headwaters, Ecuadorian Amazon; 9–13 = Curare, New Guinea; 15–16 = Mameyes, Puerto Rico (coastal).

(above 3000 m) are not so low, however, as would be expected from the application of the mean normal lapse rate to a base temperature of 30°C or more for sea level. Streams at high elevation are small, and thus are subject to a large diel fluctuation in temperature (see also Chapter 8 of this volume). Because Fig. 6 gives random daytime temperatures rather than 24-hour average temperatures, except for the Rio Mameyes, the observations exceed the daily mean temperature. There may be other reasons as well for the discrepancy between expected and observed temperatures, but they could only be elucidated if the bias associated with daytime sampling were first eliminated.

### C. Overview of Range in Water Temperature

Annual range of water temperature follows patterns related to latitude, humidity, size of water body, and proximity to coastal waters. Annual range of temperature is lowest for the largest water bodies within 10° of the equator (approximate annual range of daily means: 1°C, as in the Orinoco and Amazon main stems). The highest ranges (above 7°C) are for waters located above 15° latitude, but the range is substantially suppressed for waters that are coastal (e.g. Rio Mameyes, Puerto Rico).

Because reliable, continuous temperature-recording instruments now are inexpensive, more detailed data on temperature should become available in the future. The influence of 24-hour

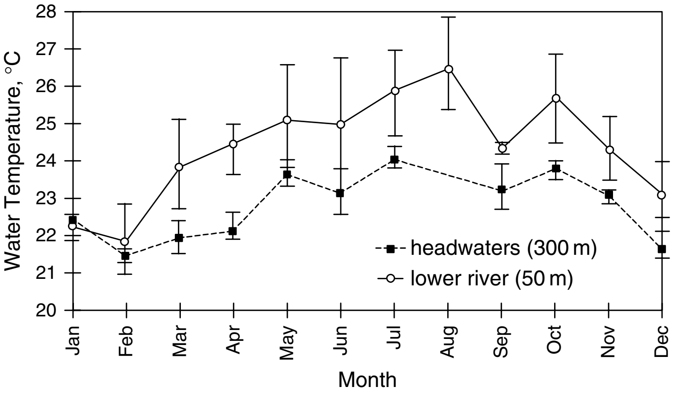

*FIGURE 7* Seasonal variation in water temperature in the headwaters and in the lower part of Rio Mameyes. Bars indicate the range of diel temperatures.

records on the interpretation of temperature can be inferred from data on the Rio Mameyes, Puerto Rico, as reported by Ortiz-Zayas (1998: Fig. 7): a daytime maximum could easily be 2°C higher than a daily average.

## D. Effects of Temperature on Metabolism and Oxygen Saturation

The main significance of temperature for flowing waters is through its effect on metabolism and the capacity of water to hold dissolved oxygen. Drastic suppression of metabolism by temperatures approaching 0°C is very rare in the tropics (it can occur in very small flowing waters at the highest elevations). At sea level, for equatorial waters in humid portions of the tropics, the annual and daily fluctuations are so minor that they hardly need to be considered. Over the full range of latitudes, elevations, and humidities within the tropics, however, there is sufficient thermal variation to affect metabolism substantially (Table II). The range in mean temperatures with latitude, elevation, and humidity correspond to an approximate twofold range in metabolic rate that must be taken into account.

Much of the tropics is characterized by water temperatures that correspond to low oxygen content at saturation. This is an important practical consideration, especially when coupled with high metabolic rates. Tropical flowing waters as a whole have a lower oxygen reserve and a higher potential oxygen demand for a given amount of organic loading than temperate waters,

*TABLE II* Approximate Effects of Temperature on Aquatic Metabolism and Oxygen Availability (Shown as Concentration Equal to 100% Saturation) for a Representative Range of Conditions within the Tropics

| | *Temperature,* °C | | *Metabolic rate** | | $O_2$ *concentration,* mg $L^{-1}$ | |
|---|---|---|---|---|---|---|
| *Location* | *Mean* | *Range* | *Mean* | *Range* | *Mean* | *Range* |
| Low elevation | | | | | | |
| 0–10° latitude, humid, 0 m | 27 | 25–29 | 81 | 70–93 | 7.9 | 7.6–8.1 |
| 15–25° latitude, dry, 0 m | 29 | 23–35 | 93 | 61–142 | 7.6 | 7.0–8.4 |
| Montane | | | | | | |
| 0–20° latitude, 1000 m | 21 | 18–24 | 52 | 43–65 | 7.7 | 7.3–8.1 |
| 0–20° latitude, 2000 m | 14 | 10–18 | 33 | 25–43 | 7.8 | 7.2–8.5 |

* Given as a percent of the rate at 30°C, assuming $Q_{10} = 2.0$

except when temperate waters briefly reach the height of summer warmth. Thus, tropical waters are more vulnerable to organic loading (Lewis, 1998).

The geographic and seasonal mean oxygen saturation concentrations corresponding to expected water temperature, discounting unusual extremes, spans a relatively narrow range (7.5–8.5 mg $L^{-1}$). The narrowness of this range, which represents about 90% of tropical flowing waters, is explained by the inverse effects of elevation and temperature on oxygen saturation. While much higher saturation concentrations would be expected at the lower temperatures of tropical waters at high elevation, the temperature effect is largely offset by reduced barometric pressure at higher elevations (see also Chapter 8 of this volume).

In contrast with conditions in the tropics, saturation concentrations for oxygen over a range of geographic and elevation conditions representing the bulk of flowing waters in the temperate zone would span the range 7.5–14 mg $L^{-1}$. Thus, the range for temperate latitudes is not only much broader, but also centers around a considerably higher oxygen concentration, which provides a much larger oxygen reserve to offset other respiratory losses at night or under other conditions when respiration exceeds photosynthesis.

## IV. PRECIPITATION

Precipitation is more abundant within the tropics than at higher latitudes as a whole. Factors contributing to high annual precipitation in the tropics include the high moisture-holding capacity of warm air and the constant uplift of moist air in conjunction with the ITCZ. The amount and seasonality of precipitation at a given latitude can be predicted to some degree simply from the position of the ITCZ. In the winter of the northern hemisphere, the precipitation maximum lies below the equator, but in July it is north of the Equator (Fig. 8). Mean annual precipitation is highest near the equator, but especially so in the northern hemisphere, reflecting a bias in the position of the ITCZ toward a northern-hemisphere position. Aggregate precipitation (Fig. 8) fails to indicate orographic effects of precipitation or variations in precipitation with distance from the coast. These two factors and other regional phenomena cause significant basin-scale variability in precipitation at any particular latitude within the tropics.

The degree and pattern of seasonality are dictated to some extent by movement of the ITCZ. Within the equatorial zone, each year there are two wet seasons and two dry seasons corresponding to the twice-annual passage of the ITCZ over this area. At the margins of the tropics, the two wet seasons and the two dry seasons are merged because the ITCZ pivots around these latitudes during its reversal of direction rather than passing over them twice. In general, the degree of seasonality increases with latitude, reflecting the greater annual range in distance of the ITCZ for higher latitudes within the tropics. There are numerous deviations from these patterns. Jackson (1989) and Talling and Lemoalle (1998) provide maps that give more details on the geographic distribution of rainfall in the tropics.

## V. RUNOFF

Runoff is about 60% of precipitation in the moist portions of the tropics (Lewis *et al.*, 1995); under semi-arid conditions, this percentage may be as low as 20%. Runoff generally reflects the seasonality of precipitation, but the spatial heterogeneity of precipitation in large basins smooths the extremes that might be observed in small basins. Much of the precipitation within the tropics is accounted for by convective mechanisms producing thunderstorms (McGregor and Nieuwolt, 1998), which are local rather than regional. Therefore, the

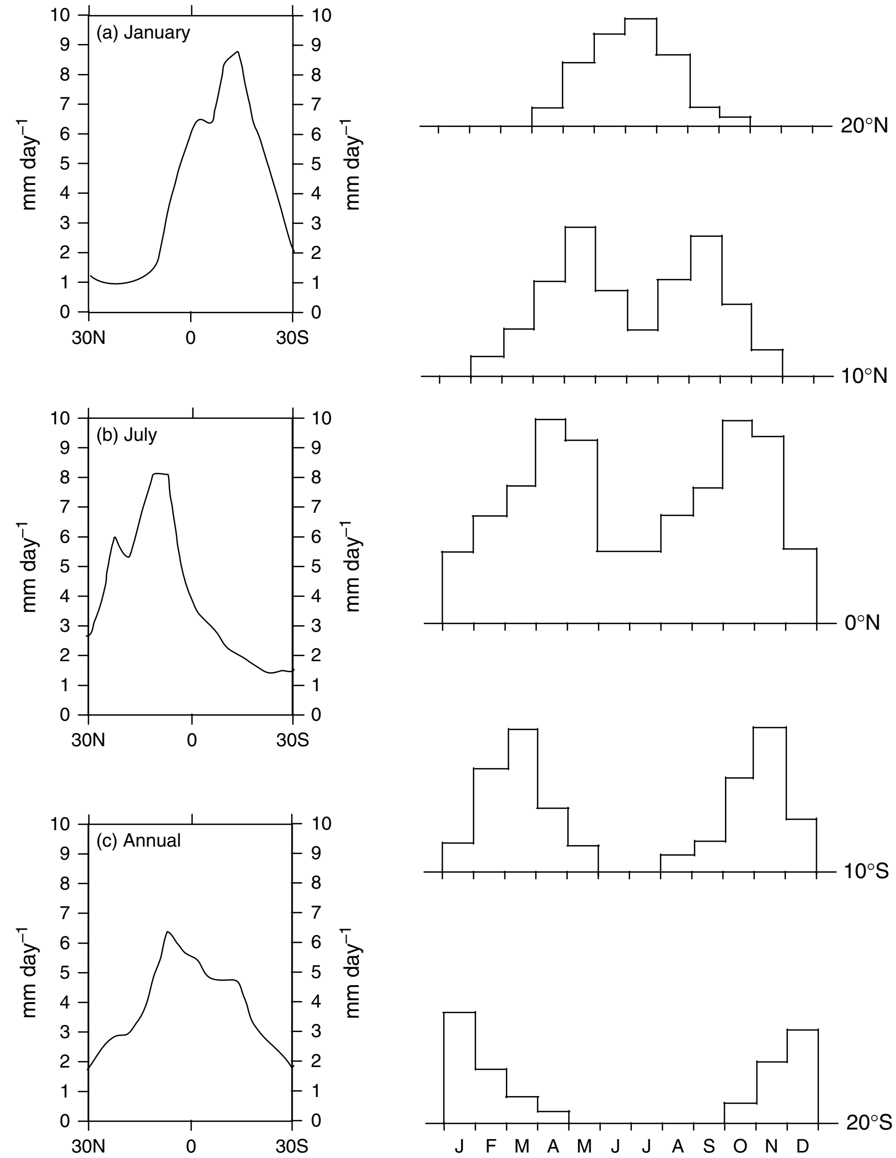

*FIGURE 8* Latitudinal distribution of rainfall in the tropics (left panels) and expected seasonal patterns (right panels). There are numerous deviations from these patterns at specific locations, as explained in the text. Redrawn and slightly modified from McGregor and Nieuwolt (1998).

hydrograph of a small stream in the moist tropics may show numerous spikes in discharge that are temporally uncorrelated with similar spikes in discharge at other locations in the drainage network (Fig. 9). Through combination of discharges showing different temporal patterns, there is a progressive suppression of short-term extremes in discharge extending from streams of lower order to streams of high order. In streams of the highest order, the smoothing effect on discharge is extended further by latitudinal breadth of coverage for the drainage basin. Even though hydrographs of large rivers tend to be smooth, the seasonal contrasts may be quite extreme, including seasonal alternation between drought and massive flooding (Fig. 10). Because the ITCZ at a given longitude is centered over specific latitude bands at specific times, movement

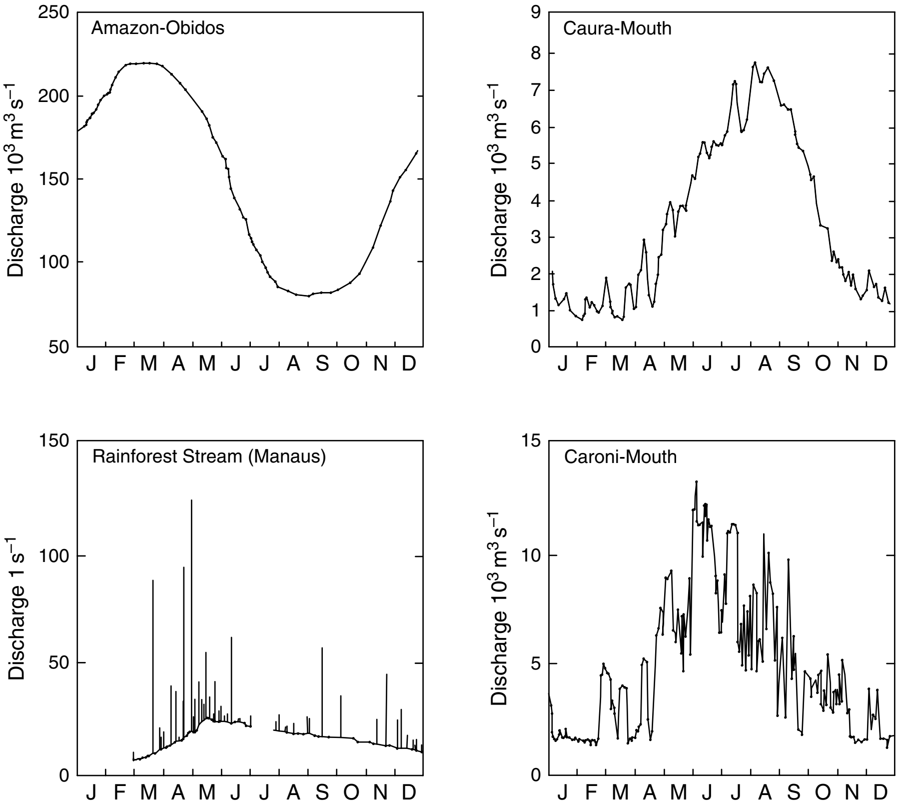

*FIGURE 9* Tropical hydrographs illustrating seasonal and short-term variations in discharge. The Amazon shows the smoothing effects of area-based and latitudinal averaging because of its great size. The Caura, a tributary of the Orinoco, shows an intermediate degree of smoothing, and the Caroni, adjacent to the Caura, shows the effects of hydroelectric regulation superimposed on a regime essentially identical to that of the Caura. Extreme short-term variation is illustrated by an Amazonian rainforest stream. Modified from Lewis *et al.* (1995), with permission from Elsevier; rainforest stream data from Lesack (1988).

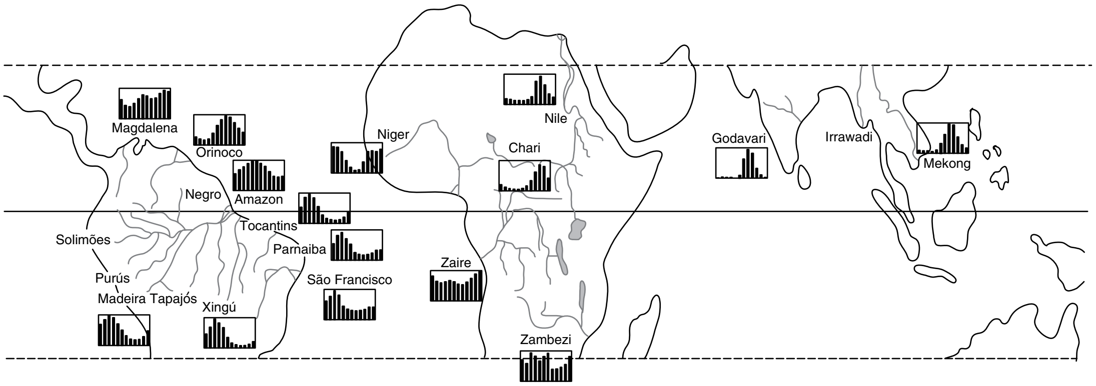

*FIGURE 10* Multi-year average hydrographs for large rivers at tropical latitudes showing latitudinal tendencies in seasonal discharge. Redrawn from Vorosmarty *et al.* (1998).

*TABLE III* Characteristics of 20 of the Largest Tropical Rivers (Amazon Tributaries are Indented)

| *Location* | *Latitudinal span* | *Orientation* | *Area*, $10^3$ km$^2$ | *Discharge (Q)*, m$^3$ s$^{-1}$ | *Q/Area*, mm y$^{-1}$ | *TSS*, mg L$^{-1}$ | *TDS*, mg L$^{-1}$ |
|---|---|---|---|---|---|---|---|
| Magdalena | 2 N–11 N | N–S | 270 | 7000 | 830 | 780 | 120 |
| Orinoco | 2 N–10 N | E–W | 950 | 38000 | 1300 | 80 | 25 |
| Amazon | 15 S–2 N | E–W | 6100 | 220000 | 1200 | 220 | 41 |
|   Solimões | 12 S–0 | E–W | 1200 | 43000 | 1200 | 380 | 82 |
|   Purús | 12 S–6 N | N–S | 370 | 11000 | 1000 | 74 | – |
|   Negro | 4 S–3 N | E–W | 620 | 30000 | 1600 | 7 | 6.5 |
|   Madeira | 20 S–4 S | N–S | 1300 | 30000 | 740 | 540 | 60 |
|   Tapajós | 13 S–3 S | N–S | 500 | 14000 | 910 | – | 18 |
|   Xingú | 15 S–2 S | N–S | 510 | 17000 | 1200 | – | 28 |
| Tocantins | 16 S–2 S | N–S | 820 | 18000 | 680 | – | – |
| São Francisco | 20 S–8 S | N–S | 640 | 2800 | 140 | 60 | – |
| Parnaiba | 10 S–3 S | N–S | 320 | 2300 | 220 | – | – |
| Nile[2,3] | 0–31 N | N–S | 2960 | 950 | 10 | 0 | 208 |
| Niger[2,3] | 5–15 N | E–W | 1210 | 6090 | 159 | 208 | 53 |
| Zaire[2,3] | 10 S–10 N | E–W | 3820 | 39600 | 327 | 34 | 38 |
| Zambezi[2,3] | 20 S–10 S | E–W | 1200 | 7070 | 186 | 148 | 70 |
| Chari[3] | 5 N–15 N | E–W | 600 | 1320 | 69 | – | 64 |
| Godavari[2] | 17 N–20 N | E–W | 310 | 2660 | 271 | 1143 | – |
| Mekong[1,2,3] | 10 N–33 N | N–S | 790 | 14900 | 595 | 340 | 105 |
| Irrawaddy[1,2] | 15 N–29 N | N–S | 430 | 13600 | 995 | 619 | – |

Source for South America is Lewis *et al.* (1995); source for discharge and area outside South America is Vorosmarty *et al.* (1998) except as noted. Hyphens show missing data. See Fig. 10 for hydrographs. TSS = total suspended solids, TDS = total dissolved solids.

[1] Watershed narrow above tropic of Cancer.

[2] Sediment from Milliman and Meade (1983).

[3] Meybeck (1976).

of the ITCZ across a basin of great latitudinal breadth smooths the seasonal precipitation signal for the basin as a whole.

Table III shows total runoff and specific runoff for 20 of the largest tropical rivers. In aggregate, these drainage basins account for 45% of the total land area of the tropics. All are large enough to reflect the regional averaging of thunderstorms as well as the latitudinal averaging of seasonal effects mentioned earlier. Hydrographs for these rivers generally reflect, however, the expected pattern of precipitation in relation to latitude in the tropics (Fig. 10), with a few exceptions that reflect well-known irregularities in the latitudinal distribution of precipitation.

## VI. SUSPENDED AND DISSOLVED SOLIDS

Sediment load has been studied extensively in connection with erosion and continental denudation (Milliman and Meade, 1983). Although the emphasis of such studies is on transport, which is only indirectly related to ecological processes in streams and rivers, sediment concentration, which can be calculated from load and discharge if bedload is ignored (which it usually is), affects transparency, and thus photosynthesis, in flowing waters.

Transport and concentration of total dissolved solids is loosely related to that of suspended solids, but the overall ratio of suspended to dissolved solids is about 5 : 1 (Meybeck, 1976). Inorganic dissolved solids (mostly salts) are much less significant ecologically than suspended solids except at high concentrations (>2000 mg $L^{-1}$) (Wetzel, 2001), but can be generally equated with the availability of specific nutrients, such as phosphorus and silicon.

Factors affecting both suspended and dissolved load and concentration include slope (topography), annual precipitation, lithology, disturbance, and natural or anthropogenic impoundment. A useful frame of reference proposed by Carson and Kirkby (1972) and used by Stallard and Edmond (1983) in explaining variations in denudation rates for tropical Latin America is based on the contrast between weathering and transport in controlling denudation rates. Watersheds with limited weathering produce rock-weathering byproducts (dissolved and suspended solids) at rates that are below the potential for transport. As a result, such watersheds have thin soils, reflecting weak or temporary accumulation of weathering byproducts, are wet, and have steep slopes, thus showing efficient removal of weathering byproducts. In contrast, transport-limited landscapes receive or produce weathering byproducts at a rate that exceeds the removal rate. Such landscapes have thick soils containing a large inventory of weathering byproducts. Watersheds may be mainly transport-limited or weathering-limited, but may also present a mosaic of types, as in the case of a steep terrain draining to a flat valley floor.

Topography is of overriding importance at the continental scale in determining the rate of transport for suspended and dissolved solids. In the Amazon drainage, for example, over 80% of both dissolved and suspended solids for the entire drainage derive from the Andes, which account for only 12% of the total drainage area (Drever, 1997, as obtained from Gibbs, 1967); Callède *et al.* (1997) put the percentage Andean contribution of suspended solids as high as 97% for the Amazon. Stallard (1985) makes a similar point in a different way, through a combination of topography and rock type in relation to load of dissolved solids (Fig. 11). The main factor differentiating physiographic regions with respect to dissolved solids content of water is topographic, but erodibility of rock plays an important secondary role within a given physiographic region, as is evident particularly for the Andes. Worldwide precipitation would account for substantial variation as well (Meybeck, 1976), but in the tropics the diversity of moisture regimes is lower than it is worldwide.

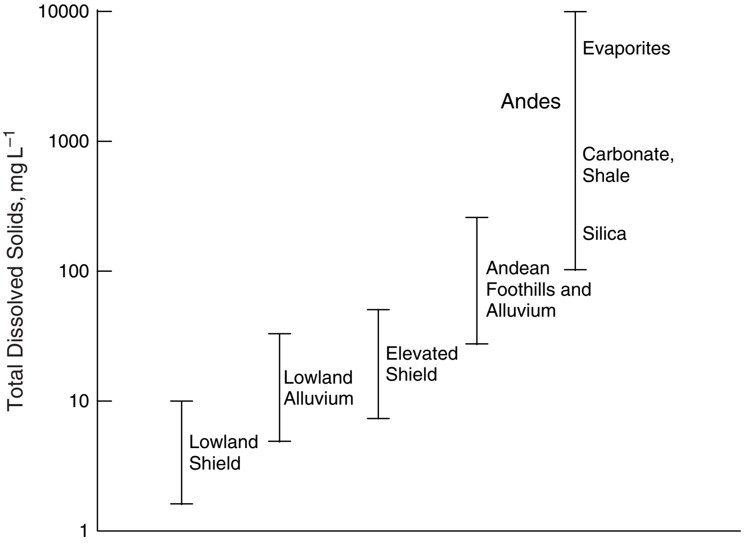

*FIGURE 11* Amounts of total dissolved solids characteristic of physiographic regions of tropical South America showing the dominance of topography and secondary role of lithology in controlling export of total dissolved solids. Modified from Stallard (1985), with permission from Kluwer Academic Publishers.

The 20 major rivers listed in Table III illustrate the degree of variation in concentrations of suspended and dissolved solids, some of which can be explained by the main variables that control sediment transport. For perspective, Meybeck and Helmer (1989) give the most typical natural concentrations as 150 mg $L^{-1}$ (suspended) and 65 mg $L^{-1}$ (dissolved); weighted averages are much higher for suspended solids and slightly higher for dissolved solids because of some very potent sources (e.g. large Asian rivers, such as the Yangtze and Ganges). Among the 20 rivers of Table III, the Rio Negro is extreme in its low concentration of dissolved and suspended solids, as explained by absence of high relief in the watershed, with the exception of some elevated shield that does not weather as efficiently as montane topography because of its rectangular cross-section (Stallard and Edmond, 1983). In addition, shield lithology is extremely resistant to weathering, thus producing only small amounts of chemical weathering byproducts. For similar reasons, tributaries coming to the Orinoco main stem from the south are poor in suspended solids. The Orinoco main stem, which is very strongly influenced by the large contribution of runoff from the Guyana Shield, carries a low concentration of suspended solids among the rivers listed in Table III, even though it receives enough suspended solids from the Andes and the Andean alluvial plain to bring its suspended solids above the baseline reflected by the Rio Negro and other adjacent shield rivers lacking major montane influences. Similarly, the Amazon main stem shows the mixed influences of extensive shield drainage in the center of the watershed and mountainous headwaters to the west.

Of the rivers listed for the American tropics, the Magdalena carries the highest concentrations of dissolved and suspended solids because of the high proportion of steep terrain within its watershed and probably some effects of land cover disturbance. The São Francisco shows relatively low suspended solids because of impoundment.

The African rivers show surprisingly low concentrations of suspended solids, as explained mainly by low population densities, but also by impoundments (the Zambezi) or natural lakes (the Zaire). The Nile once carried $110 \times 10^6$ t $yr^{-1}$ of sediment, corresponding to a concentration of over 3000 mg $L^{-1}$ (Milliman and Meade, 1983), but virtually all of its sediment now is captured behind the Aswan Dam. In Asia, the Godavari, Mekong, and Irrawaddy all derive sediment from Himalayan sources, but also are influenced by substantial augmentation from intensive land use, particularly for the Godavari and Irrawaddy.

Although suspended and dissolved load are presented most often as discharge-weighted annual averages, seasonal variability is ecologically important. For example, concentration of total suspended solids in the Orinoco main stem varies by a factor of almost 10 (Fig. 12). The minimum coincides with lowest discharge and the maximum appears on the rising limb of the hydrograph, but prior to the hydrographic peak (the same is true of the Amazon: Seyler and Boaventura, 2001).

Because much of the ecological significance of suspended solids is related to the interception of light, it is useful to relate concentrations of suspended solids to the penetration depth for 1% photosynthetically available radiation (PAR), which is the approximate threshold for positive net photosynthesis. This relationship is shown in Fig. 13 on the basis of an equation provided by Owen Lind (Baylor University: personal communication) and derived from measurements in Lake Chapala, Mexico, which has a wide seasonal and interannual range of suspended solids ($\eta = 2.018 + 0.0605 \times \text{TSS}$ where $\eta$ is given as units/$m^2$ and TSS is given as mg $L^{-1}$: $n = 76$; $r^2 = 0.80$). While the relationship may differ slightly from one source of suspended solids to the next, the general indication of Fig. 13 is that photosynthesis over most of a stream or river channel is virtually impossible at concentrations of suspended solids exceeding 100 mg $L^{-1}$. Penetration of PAR can be matched to rivers of varied size by use the of detached axis to the right, which shows river size (as discharge) matching the penetration depths on the Y axis as derived from the equation of Church (1996). Where substantial dissolved color (mainly humic and fulvic acids derived from degradation of plant biomass in soils: Wetzel, 2001) is present,

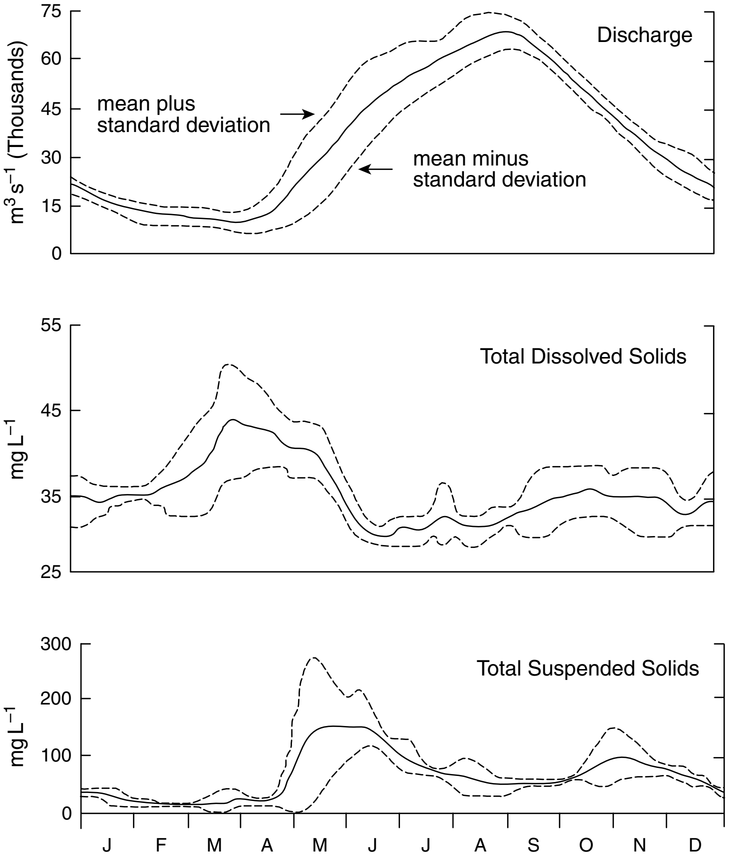

*FIGURE 12* Illustration of seasonal changes in concentrations of dissolved and suspended solids in a large tropical river (the Orinoco). Standard deviations indicate interannual variation for a given time of the year. Redrawn from Lewis and Saunders (1989), with permission from Springer-Verlag.

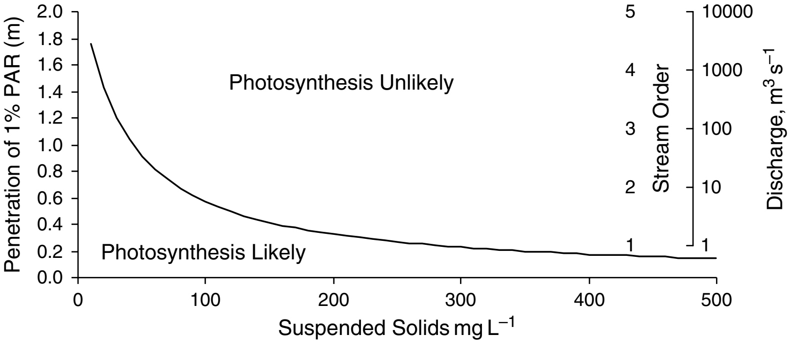

*FIGURE 13* Relationship between suspended solids and depth of penetration for 1% of photosynthetically available radiation (PAR assumed here to be the threshold for positive net photosynthesis). Approximate mean depth for streams of various order indicate the approximate range of suspended solids consistent with net photosynthesis for streams of a given order. The detached axis to the right shows river size (expressed as discharge) corresponding to light penetration on the Y-axis on the left.

even the smaller amounts of suspended solids may not be consistent with photosynthesis in deep water columns because of the additional removal of PAR by dissolved color. Comparison of Fig. 13 with Table III shows that benthic photosynthesis would not be expected in large rivers of the tropics.

## VII. PHOSPHORUS, NITROGEN, AND CARBON

The amounts of phosphorus, nitrogen, and carbon in tropical streams and rivers are of special interest because of the regulatory role that these elements play in aquatic ecosystems. Extremes in concentrations of phosphorus, nitrogen, and dissolved organic carbon would follow from unregulated water pollution, which has already occurred in the most populous regions of the tropics. Of greater fundamental interest is the range of concentrations of these key elements to be expected under natural conditions, and a general view of the factors that control natural concentrations. For present purposes, the natural range of concentrations will be presented for various tributary drainages in the Amazon and Orinoco basins, as reported from the literature (Lewis *et al.*, 1995). Not only do these basins reflect natural conditions, they also offer a wide range of geologic and physiographic conditions for comparison, and are represented by a reasonable amount of field data spanning periods of more than one year.

### A. Phosphorus

Particulate and total dissolved phosphorus, which together make up total phosphorus, are subject to very different kinds of control mechanisms in the watersheds from which they originate. In world rivers, particulate phosphorus accounts for over 90% of total phosphorus (Meybeck, 1982). The dissolved fraction, although present in much smaller amounts, cannot be discounted because it is more readily available to autotrophs.

Within the minimally disturbed watersheds of South America represented in Fig. 14, concentrations of particulate phosphorus range over two orders of magnitude and are in all cases lower than the world average for rivers as reported by Meybeck (1982). The relatively lower concentrations of particulate phosphorus are explained by the absence of water pollution and by the lower extremes of suspended solids in the Amazon and Orinoco basins as compared with the basins of Asiatic rivers, particularly where land disturbance plays a major factor in liberating suspended solids to surface waters (Downing *et al.*, 1999).

The wide variation in particulate phosphorus reflects variation in total suspended solids (Meybeck, 1982); the relationship between these two variables is quite close for undisturbed watersheds. Therefore, particulate phosphorus can be categorized by a scheme similar to the one that is used for suspended solids, i.e. according to weathering rate as determined by slope and rock type. In general, Andean streams and rivers carry a few hundred $\mu g\ L^{-1}$ of particulate phosphorus; Andean alluvium carries less than $100\,\mu g\ L^{-1}$; and streams running on flat terrain over shield or continental alluvium carry $10\,\mu g\ L^{-1}$ or less.

Total dissolved phosphorus falls within a much narrower range of concentrations than particulate phosphorus (Fig. 14). The shield drainages and continental alluvium, which share slow weathering rates, tend to have low concentrations, although the Rio Negro shows as much as $19\,\mu g\ L^{-1}$. Montane and Andean alluvial watersheds have concentrations that range mostly between 10 and $50\,\mu g\ L^{-1}$. There is little understanding at present of the reasons for differences in TDP concentrations within these groups of rivers. Given the importance of phosphorous to autotrophs in flowing water (Wetzel, 2001), studies of the mechanisms controlling TDP in tropical rivers and streams are needed.

One counterintuitive conclusion from phosphorus concentrations in undisturbed tropical rivers and streams is that they contain sufficient TDP to support a substantial amount of

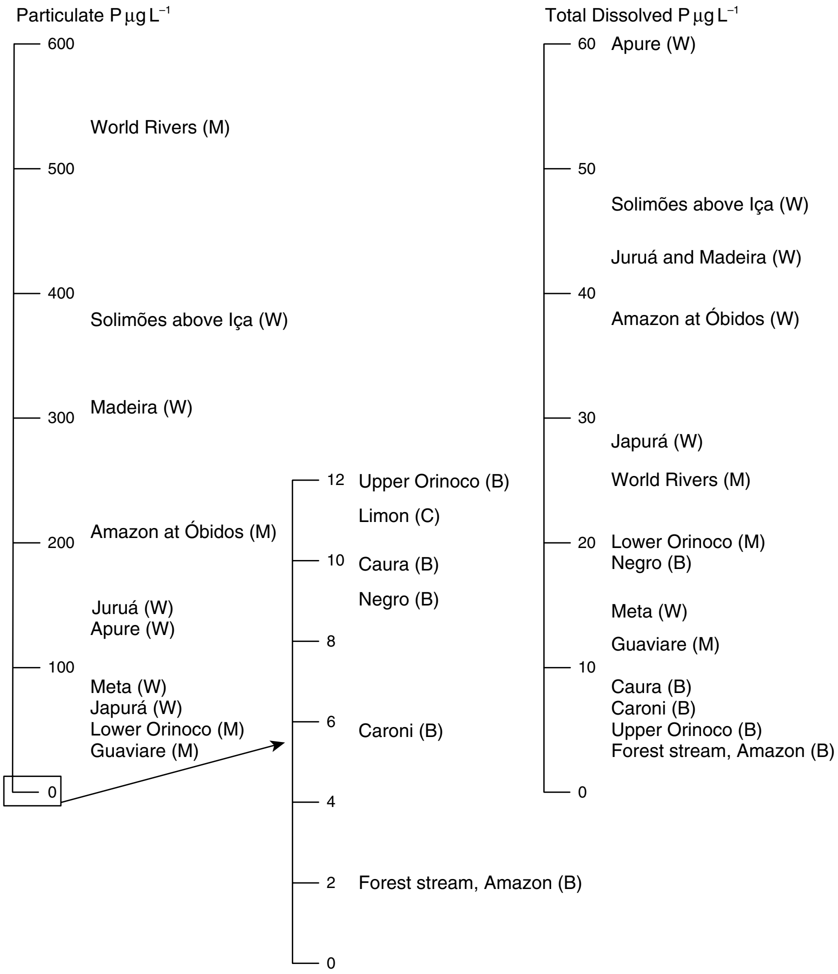

*FIGURE 14* Concentrations of particulate phosphorus and total dissolved phosphorus in undisturbed or minimally disturbed rivers of South America (central and northern South America). Apure, Meta, Guaviare, Caura, and Caroni are the main tributaries of the Orinoco main stem. Juruá, Negro, and Japurá are tributaries of the Amazon/Solimóes. Limon is a second order montane drainage near the Caribbean coast of Venezuela. Letters indicate general classification (W = white water, B = black water, C = clear water, M = mixed). All data are from Lewis *et al.* (1995). Data on world rivers are from Meybeck (1979).

autotrophic growth, as judged by nutrient responses in temperate streams and rivers (Dodds *et al.*, 2002). Even on continental alluvium and shield, there is sufficient TDP to support moderate growth of periphyton although canopy conditions in these areas may minimize photosynthesis. The presence of TDP in the amounts as shown in Fig. 14 is contradictory to the notion that nutrient cycling in tropical forests is especially tight (literature summarized by Schlesinger, 1997). It appears that there is sufficient leakage of TDP from tropical forest nutrient cycles to sustain substantial growth of autotrophs (Lewis, 1986; Lewis *et al.*, 1990; Ortiz-Zayas *et al.*, 2005).

## B. Nitrogen

Transport of total nitrogen and all nitrogen fractions increases steeply as a function of runoff from tropical watersheds (Lewis *et al.*, 1999). The rate of increase in transport is somewhat

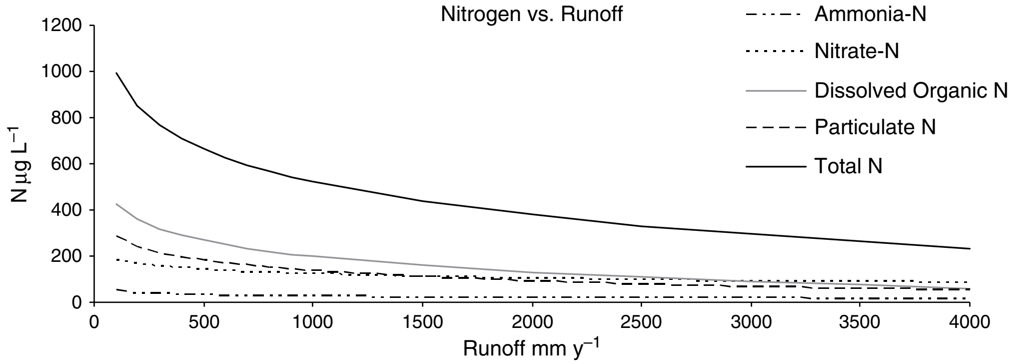

*FIGURE 15* Concentrations of total nitrogen and nitrogen fractions (discharge-weighted) over a range of annual runoff as determined by Lewis *et al.* (1999).

lower, however, than the rate of increase in discharge. Thus, there is certain amount of dilution of total nitrogen and nitrogen fractions between the lowest and the highest rates of runoff (Fig. 15). At runoff between 400 and 2000 mm $yr^{-1}$, which would encompass most tropical watersheds, the amounts of all nitrogen fractions, except for ammonia, are substantial and could support autotrophic growth under appropriate light conditions, as judged by response of temperate streams and rivers to nitrogen (Dodds *et al.*, 2002). Here, as in the case of phosphorus, the ability of tropical forests to retain and recycle nitrogen has probably been overstated, as shown by the consistent presence of substantial amounts of nitrogen (all fractions), where anthropogenic disturbance has been minimal or non-existent (Lewis *et al.*, 1999).

There appears to be little difference across latitudes in the concentrations of total nitrogen and nitrogen fractions for a given amount of runoff (Lewis, 2002). The underlying mechanisms are not well understood. In the tropics, moisture stimulates nitrogen fixation, which allows constant export of nitrogen. At temperate latitudes, nitrogen fixation is partially suppressed by cool weather, but the demand for nitrogen also is suppressed by the same mechanism, thus resulting in nitrogen export.

Nitrogen delivery to streams and rivers is controlled hydrographically. The time course of nitrogen concentrations has not been extensively studied, but the existing information suggests peaks of nitrate and dissolved organic nitrogen concentrations occur on the rising limb of the hydrograph (Lewis and Saunders, 1989), as would be typical also of undisturbed temperate watersheds.

### C. Organic Carbon

Dissolved organic carbon (DOC) is one basis for distinguishing different basic water types of the tropics (Sioli, 1984). In the Amazon and elsewhere, waters that are darkly colored with humic and fulvic acids (limnohumic acids) are designated as ‘black waters.’ Waters of high turbidity are ‘white waters,’ and waters with neither characteristic are ‘clear waters’ (Sioli, 1984). In general, black waters emanate from sandy soils or shield, and white waters emanate from mountains or montane alluvium. Clear waters are much scarcer than the other two types, and their deficiency of dissolved color remains poorly explained.

The visual contrast between black waters and white waters has led to the widespread notion that black waters contain large amounts of DOC in the form of humic acids, whereas white waters do not. This notion is misleading, as the amount of DOC in most tropical waters falls between 3 and 10 mg $L^{-1}$, regardless of the visual classification (Lewis *et al.*, 1995). While it is possible to find specific examples of black waters with unusually high DOC, this is not typical.

Most black waters owe their striking appearance to the absence of inorganic turbidity, which would offset some of the absorbance of light through backscatter, combined with impressive absorption of short wavelengths of light by DOC within an otherwise clear water column.

In undisturbed tropical watersheds, rivers and streams carry modest amounts of particulate carbon. In the lower range, which is typical for shield waters, the concentrations of particulate organic carbon (POC) may be less than $1\,\mathrm{mg\,L^{-1}}$. Concentrations often approach $10\,\mathrm{mg\,L^{-1}}$ where slopes are higher. The ratio of POC to DOC is highly variable (Meybeck, 1982; Lewis *et al.*, 1995).

As is typical of temperate watersheds, DOC often shows peak concentrations on the rising limb of the hydrograph, rather than at peak discharge or at minimum discharge (Lewis and Saunders, 1989; Saunders and Lewis, 1989), but some rivers show nearly static DOC concentrations (Lewis *et al.*, 1986). The same is true of POC, but probably for different reasons (flushing of soils for DOC, resuspension of particles for POC). Most POC is accounted for as byproducts of vascular plants rather than suspended organisms (Devol and Hedges, 2001).

## VIII. CONCLUSIONS

Tropical flowing waters in some ways differ as a group from their counterparts at higher latitudes, but in other respects latitudinal differences are weak or nil (for further discussion of such differences see Chapter 9 of this volume). Tropical streams and rivers are stable thermally but should show seasonality driven by hydrology. Their metabolic potential is higher and more stable than that of their temperate counterparts, but supplies of suspended and dissolved solids, as well as nutrients, span the same ranges and show the same responses to hydrology as would be expected at higher latitudes. The rivers and streams of the tropics still offer opportunities to observe and analyze natural phenomena over a wide range of geologic and physiographic conditions, whereas those opportunities are all but lost in the highly modified flowing waters of temperate latitudes.

## REFERENCES

Barry, R.G., and Chorley, R.J. (2003). “Atmosphere, Weather, and Climate.” 8th Edition. Routledge, London.

Callède, J., Guyot, J.L., Ronchail, J., L’Hôte, Y., Niel, H., and De Oliviera, E. (1997). La variabilité des débits de l’Amazone à Obidos (Amazonas, Brèsil). *In:* “Sustainability of Water Resources under Increasing Uncertainty” (D. Rosbjerg, N.E. Boutayeb, Z.W. Kundzewicz, A. Gustard, and P.F. Rasmussen, Eds.), Vol. 240, pp. 163–172. IAHS, Wallingford.

Carson, M.A., and Kirkby, M.J. (1972). “Hillslope, Form and Process.” Cambridge, New York.

Church, M. (1996). Channel morphology and typology. *In:* “River Flows and Channel Forms: Selected Extracts from the Rivers Handbook” (G. Petts and P. Calow, Eds.), pp. 185–203. Blackwell Science, Oxford.

Devol, A.H., and Hedges, J.I. (2001). Organic matter and nutrients in the mainstem Amazon River. *In:* “The Biogeochemistry of the Amazon Basin” (M.E. McClain, R.L. Victoria, and J.E. Richey, Eds.), pp. 275–306. Oxford University Press, Oxford.

Dodds, W.K., Smith, V.H., and Lohman, K. (2002). Nitrogen and phosphorus relationships to benthic algal biomass in temperate streams. *Can. J. Fish. Aquat. Sci.* **59** (5), 865–874.

Downing, J.A., McClain, M., Twilley, R., Melack, J.M., Elser, J., Rabalais, N.N., Lewis, W.M. Jr, Turner, R.E., Corredor, J., Soto, D., Yanez-Arancibia, A., Kopaska, J.A., and Howarth, R.W. (1999). The impact of accelerating land-use change on the N-cycle of tropical aquatic ecosystems: current conditions and projected changes. *Biogeochemistry* **47**, 109–148.

Drever, J.I. (1997). “The Geochemistry of Natural Waters: Surface and Groundwater Environments.” 3rd Edition. Prentice-Hall, Upper Saddle River.

Gibbs, R.J. (1967). The geochemistry of the Amazon River System: I. The factors that control the salinity and the composition and concentration of the suspended solids. *Bull. Geol. Soc. Am.* **78**, 1203–1232.

Jackson, I.J. (1989). “Climate, Water and Agriculture in the Tropics.” Longman Group, England.

Kessler, W.S., McPhaden, M.J., and Weickmann, K.M. (1995). Forcing of intraseasonal Kelvin waves in the equatorial Pacific. *J. Geophys. Res.* **100**, 10613–10631.

Lesack, L.F.W. (1988). "Mass Balance of Nutrients, Major Solutes and Water in an Amazon Floodplain Lake and Biogeochemical Implications for the Amazon Basin". Ph.D. Thesis. University of California, Santa Barbara, CA, 484 pp.

Lewis, W.M. Jr (1986). Nitrogen and phosphorus runoff losses from a nutrient-poor tropical moist forest. *Ecology* **67**, 1275–1282.

Lewis, W.M. Jr (1987). Tropical limnology. *Annu. Rev. Ecol. Syst.* **18**, 159–184.

Lewis, W.M. Jr (1998). Aquatic environments of the Americas: basis for rational use and management. *Proc. 4th Int. Congr. Environ. Issues* **4**, 250–257.

Lewis, W.M. Jr (2002). Yield of nitrogen from minimally disturbed watersheds of the United States. *Biogeochemistry* **57/58**, 375–385.

Lewis, W.M. Jr, and Saunders, J.F. III. (1989). Concentration and transport of dissolved and suspended substances in the Orinoco River. *Biogeochemistry* **7**, 203–240.

Lewis, W.M. Jr, Saunders, J.F. III, Levine, S.N., and Weibezhan, F.H. (1986). Organic carbon in the Caura River, Venezuela. *Limnol. Oceanogr.* **31**, 653–656.

Lewis, W.M. Jr, Weibezahn, F.H., Saunders, J.F. III, and Hamilton, S.K. (1990). The Orinoco River as an ecological system. *Interciencia* **15**, 346–357.

Lewis, W.M. Jr, Hamilton, S.K., and Saunders, J.F. III. (1995). Rivers of Northern South America. *In:* "Ecosystems of the World: River and Stream Ecosystems" (C.E. Cushing, K.W. Cummins, and G.W. Minshall, Eds.), Vol. 22, pp. 219–256. Elsevier Science B.V., Amsterdam.

Lewis, W.M. Jr, Melack, J.M., McDowell, W.H., McClain, M., and Richey, J.E. (1999). Nitrogen yields from undisturbed watersheds in the Americas. *Biogeochemistry* **46**, 149–162.

List, R.J. (1951). Smithsonian meteorological tables. *Smith. Misc. Coll.* **114**, 411–447.

McGregor, G.R., and Nieuwolt, S. (1998). "Tropical Climatology: An Introduction to the Climates of the Low Latitudes." 2nd Edition. Wiley, Chichester, UK.

Meybeck, M. (1976). Total dissolved transport by world major rivers. *Hydrol. Sci. Bull.* **21**, 265–284.

Meybeck, M. (1979). Concentrations des eaux fluviales en elements majeurs et apports en solution aux oceans. *Rev. Geol. Dyn. Geogr. Phys.* **21**, 215–246.

Meybeck, M. (1982). Carbon nitrogen and phosphorus transport by world rivers. *Am. J. Sci.* **287**, 401–450.

Meybeck, M., and Helmer, R. (1989). The quality of rivers: from pristine state to global pollution. *Palaeogeogr. Palaeocl. Palaeoclim. (Global Planet. Change Sect.)* **75**, 283–309.

Milliman, J.D., and Meade, R.H. (1983). World-wide delivery of river sediment to the oceans. *J. Geol.* **91**, 1–21.

National Oceanic and Atmospheric Administration website: http://www.noaa.gov/ (2004).

Ortiz-Zayas, J.R. (1998). "The Metabolism of the Rio Mameyes, Puerto Rico: Carbon Fluxes in a Tropical Rain Forest River". Ph.D. Thesis. University of Colorado, Boulder, CO. 344 pp.

Ortiz-Zayas, J.R., Lewis, W.M. Jr, Saunders, J.F. III, McCutchan, J.H. Jr, and Scatena, F. (2005). Metabolism of a tropical rainforest stream. *J. N. Am. Benthol. Soc.* **24(4)**, 769–783.

Petr, T. (1983). Limnology of the Purari basin. *In:* "The Purari – Tropical Environment of a High Rainfall River Basin." (T. Petr, Ed.), pp. 141–178. Dr. W. Junk Publishers, The Hague.

Saunders, J.F. III, and Lewis, W.M. Jr (1989). Transport of major solutes and the relationship between solute concentrations and discharge in the Apure River, Venezuela. *Biogeochemistry* **8**, 101–113.

Schlesinger, W.H. (1997). "Biogeochemistry: An Analysis of Global Change." 2nd Edition. Academic Press, San Diego.

Seyler, P.T., and Boaventura, G. (2001). Trace elements in the mainstem Amazon River. *In:* "The Biogeochemistry of the Amazon Basin." (M.E. McClain, R.L. Victoria, and J.E. Richey, Eds.), pp. 307–327. Oxford University Press, New York.

Sioli, H. (1984). The Amazon and its main affluents: Hydrography, morphology of the river courses, and river types. *In:* "The Amazon Limnology and Landscape Ecology of a Mighty Tropical River and its Basin" (S. Sioli, Ed.), pp. 127–165. Dr. W. Junk Publishers, The Hague.

Stallard, R.F. (1985). River chemistry, geology, geomorphology, and soils in the Amazon and Orinoco Basins. *In:* "The Chemistry of Weathering." (J.I. Drever, Ed.), pp. 293–316. Reidel, Dordrecht.

Stallard, R.F., and Edmond, J.M. (1983). Geochemistry of the Amazon, 2. The influence of geology and weathering environment on the dissolved load. *J. Geophys. Res.* **88**, 9671–9688.

Talling, J.F., and Lemoalle, J. (1998). "Ecological Dynamics of Tropical Inland Waters." Cambridge University Press, Cambridge.

Vorosmarty, C.J., Fekete, B.M., and Tucker, B.A. (1998). Global River Discharge, 1807–1991, Version 1.1 (RivDis). Oak Ridge National Laboratory Distributed Archive Data Center, Oak Ridge, TN, USA (http://www.daac.ornl.gov).

Waliser, D.E., and Gautier, C. (1993). A satellite derived climatology of the ITCZ. *J. Clim.* **6**, 2162–2174.

Ward, J.V. (1985). Thermal characteristics of running waters. *Hydrobiologia* **125**, 31–46.

Wezel, R.G. (2001). "Limnology." 3rd Edition. Academic Press, New York.