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Terrestrial limitation of Amazon River productivity: why the Amazon River is not green

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ABSTRACT

Questions: What factors control the continental scale distribution of phytoplankton biomass in the Amazon River? How do its tributaries influence the overall Amazon River system?

Data: Continuous along-track measurements of chlorophyll, pH, temperature, and beam transmittance along the length of the Amazon River during the high-water season of 1982. Additional vertical stations downstream, upstream, and in the mouth of every major tributary measured the same parameters and collected discrete samples for nitrate/nitrite and phosphate analysis.

Results: Along-track chlorophyll values were low ($0.6–2.5\ \mu g \cdot l^{-1}$), while light attenuation and nutrients were high along the entire mainstem. Erosion in the Andean headwaters generates heavy sediment loadings that block light. Strong mixing offers no chance for stratification or settling that might increase light levels. When the river leaves the highlands, suspended sediment decreases. However, light attenuation remains very high due to the input of polyphenolic plant products (humic acids) from black water tributaries. These biologically produced compounds absorb light very strongly across the visible spectrum. When the river meets the Atlantic Ocean, chlorophyll values soar to 10–20 times those of the mainstem.

Conclusions: Amazon River plankton are light- not nutrient-limited along the entire course of the mainstem due to physical and evolutionary forcing functions. The high concentrations of humic acids in the mainstem illustrate the continental scale influence that a terrestrial system can exert on aquatic systems as a consequence of the evolutionary responses to an entirely different set of challenges on land. Thus the very biogenic compounds that have evolved to ‘keep the terrestrial Earth green’ reverse ecological roles when they enter the aquatic realm.

Keywords: Amazon, black water, chlorophyll, continental scale ecology, HSS, humic acids, limiting factors, productivity, tannins.

INTRODUCTION

The Amazon River watershed drains $6.2 \times 106\ km^2$, an area approximately the size of the continental United States. The river begins as a series of small eastward flowing meltwater tributaries high in the Andes Mountains, which conjoin to form the mainstem Amazon

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River in Peru at the confluence of the Maranon and Ucayali Rivers. Additional tributaries along its nearly 4000-km path, from both the north and south, provide input to the mainstem and generate a river of enormous additive composition, discharging 6300 km^3 annually to the Atlantic Ocean, and comprising 18% of the total freshwater input to the seas.

Rainfall in the mountainous headwater regions of the Andes and precipitation within the lowlands of the Amazon Basin comprise two distinctly different sources. Andean waters, often referred to as white water, have very high sediment loadings and are rich in nutrients (N and P). The water is principally alkaline as it takes on the character of the ancient marine sediment rich in calcium, magnesium and alkali-earth metals (Junk and Furch, 1985). Precipitation within the lowland basin results in the formation of black waters owing to the high tannin and humic acid contents that absorb light so strongly they give it the appearance of water without colour, or black. These waters are characterized by low nutrient, sediment, and oxygen contents, and by acidic pH (Sioli, 1975).

Amazonian River flow and discharge volume vary with seasonal rainfall caused by the migration of the Intertropical Convergence Zone (ITCZ). Discharge rates lag briefly behind the rainy season so that peak flows occur from February to March with a gradual decrease through August. Tributaries occur both to the north and south of the equator so that seasonal inputs extend over a significant portion of the calendar year (Marengo, 2006).

The basin contains the oldest, most productive, and diverse vegetated area on Earth. The vast majority of species are insects and flowering plants with extensive co-evolutionary histories. Herbivory is so intense that virtually no plant is left untouched. The top-down hypothesis of Hairston, Smith, and Slobodkin (HSS) argued that top-down predator control generates a cascading influence in which predators keep herbivore populations at densities that prevent defoliation, and thus the Earth is green (Hairston *et al.*, 1960; Slobodkin *et al.*, 1967). However, there are many insects that have evolved a myriad of mechanisms at molecular to mandible scales to forage successfully on their photosynthetic prey. An evolutionary countermeasure to this has been that well-defended plants generate large amounts of polyphenolic compounds (humic and tannic acids) in their leaves, rendering themselves unpalatable and indigestible (Allison, 2006). These water-soluble compounds ultimately find their way into receiving water bodies forming black water rivers (Janzen, 1974).

The Cousteau Society Amazon Expedition 1982–1983

The Cousteau Amazon Expedition explored and documented the beauty, richness, and fragility of the Amazon River Basin through the production of seven hours of documentary films. *Calypso*'s crew and invited scientists also carried out a wide range of inquiries that have been compiled and documented in a cruise report (Constans *et al.*, 1988; Dustan, 1988a, 1988b, 1988c, 1988d). My goal was to try to understand the mesoscale ecology of the river in terms of its biology at the beginning of the food chain: How are the phytoplankton distributed and what are their limiting factors? I proposed to construct a mesoscale model of chlorophyll distribution that examined the influence of major tributaries to the overall Amazon River system and to the Atlantic Ocean.

During the high-water period of June and July 1982, R/V *Calypso* traversed the course of the Amazon River from Belem to the Rio Tigre on the Maranon River, approximately 200 km to the west of the confluence of the Ucayali and Maranon Rivers, the 'official'

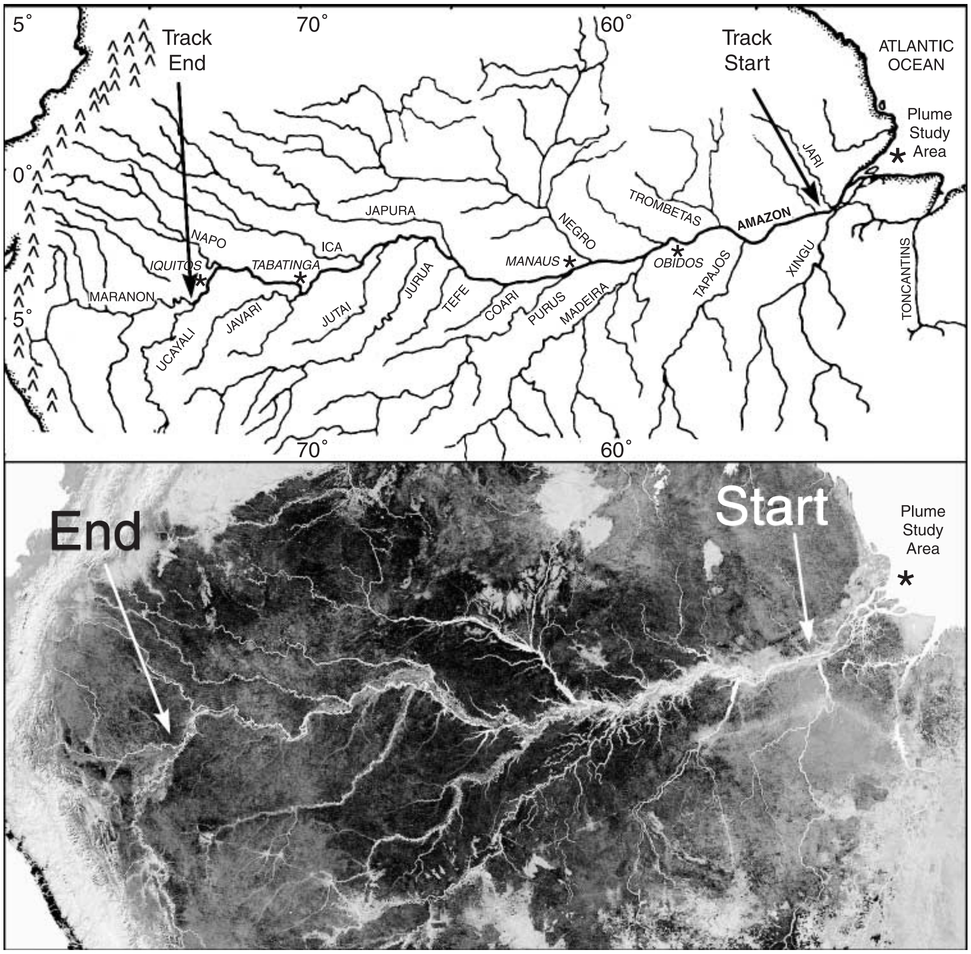

Fig. 1. Map and radar image of the Amazon River basin showing river names and major cities (*italics*). Arrows mark Cousteau Society Amazon Expedition cruise track end points. Note the width and reticulate nature of the mainstem river path. Dark areas of radar image denote dense rainforest vegetation in the Amazon Basin. The star at the river mouth is placed at the entrance to Canal Norte and marks the 0 km point of the Amazon River transect of Figure 4. (Radar image PIA03388 credit NASA/JPL/NIMA.)

starting point of the mainstem Amazon River. In May 1983, again during the high-water period, we explored the interaction of the plume of the river with the Atlantic Ocean (Fig. 1).

METHODS

Horizontal sampling

The horizontal (along-track) distributions of chlorophyll, pH, percent light transmittance at 670 nm, and temperature were measured continuously while *Calypso* was underway using a flow-thru sampling system. Recording on paper strip charts began slightly upstream of the Rio Xingu (53° W longitude, Km 385 in figures) and continued to the confluence of the Rio Ucayali and Rio Maranon (73°30′ W longitude), a total distance of 3685 km (Fig. 1).

Phytoplankton biomass was estimated with continuous underway measurements of chlorophyll fluorescence (Turner 111 w/high volume flow-thru door) using standard oceanographic techniques (Smith *et al.*, 1981). Chlorophyll content estimates the standing stock of phytoplankton and is strongly correlated with potential primary production (Smith and Baker, 1978). Replicate discrete water samples (50 ml, GFF filters) were taken frequently for calibration, especially in regions of rapidly changing fluorescence. Filtered samples were immediately placed in a deep freezer and within 2 weeks were extracted in 90 acetone w/$MgCO_3$ for 48 h and measured in the same instrument (discrete door) that had been calibrated with dilutions of a chlorophyll a standard (Sigma chl a, whose optical density had been determined by spectroscopy before dilution).

Temperature was measured with a thermister (YSI 43D) calibrated to discrete measurements to the nearest 0.1°C with a 0–50°C mercury thermometer with 0.1°C gradations traceable to NBS calibration standards. The pH was measured with a Corning digital pH meter #135 and transmittance at 670 nm with a fibre-optic colorimeter (Syborn/Brinkman, PC801).

Strip chart recordings were hand digitized, calibrated to discrete measurements, and then re-sampled to 30 s of underway recording time. Data were re-examined, recalibrated where necessary and re-sampled to represent the mean of approximately 10 km of river transect. Point-to-point calibration interpolation was used to convert the recorded fluorescence signal to chlorophyll content. We did so because fluorescence to chlorophyll ratios was variable, which would invalidate regression calibration techniques. As a check on calibration, the along-track data were compared with samples from station bottle casts that were not used to calibrate the along-track data. There were no significant differences between the two data sets. Data recorded whenever *Calypso* was at anchor, or at a reoccupied station, did not vary significantly, suggesting that conditions at each point on the river do not vary much over short time periods. Thus, the along-track data represent the distribution of parameters along the course of the river and not simply random fluctuations.

Vertical sampling

Hydrocast stations were placed upstream, downstream, and in the mouth of each major tributary. Hydrocasts, utilizing 1.5-litre Niskin bottles and with protected and unprotected reversing thermometers sampled at 1, 3, and 5 m, with additional bottles spaced between 5 m and just off the river bottom. Temperature was corrected for pressure, ambient temperature, and calibration standards. Tributaries were sampled from a small boat driven a few kilometres upstream of the mainstem confluence. Submarine spherical irradiance was measured using a quantum scalar irradiance profiling system (QSI 100, Biospherical Instruments).

Water samples were processed for all the along-track variables (chl, temperature, pH, and transmittance). Replicate 45-ml water samples for nutrient analysis were filtered through GFF filters, preserved with 5 ml chloroform, and transported to the USA where they were analysed for phosphate and combined nitrate/nitrite in the laboratory of Steven Wofsy at Harvard University.

RESULTS

Vertical profiles

Vertical profiles of both chlorophyll and calibrated temperature from reversing thermometers did not vary significantly with depth (Fig. 2). The confluence of the Rio Negro was the most vertically heterogeneous station occupied, but still varied less than 1°C or 1 $\mu g \cdot l^{-1}$ chl over the depth range of the cast (90 m). Chlorophyll profiles showed little change in the ratio of chlorophyll a to phaeophytin with depth, which suggests that there is little degradation in phytoplankton pigments with depth. The Ra/Rb chlorophyll ratios were consistent with the range of values expected for healthy growing phytoplankton (Smith *et al.*, 1981).

Along-track mainstem transect

Chlorophyll

The phytoplankton chlorophyll content of the Amazon River ranged from 0.4 to 2.5 $\mu g \cdot l^{-1}$ (Fig. 3). Beginning at the confluence of the Rios Ucayali and Maranon, chlorophyll content declined from 1.5 to approximately 0.6 $\mu g \cdot l^{-1}$ near the Jurua River. Along this course, each tributary affected the chlorophyll content of the mainstream Amazon River

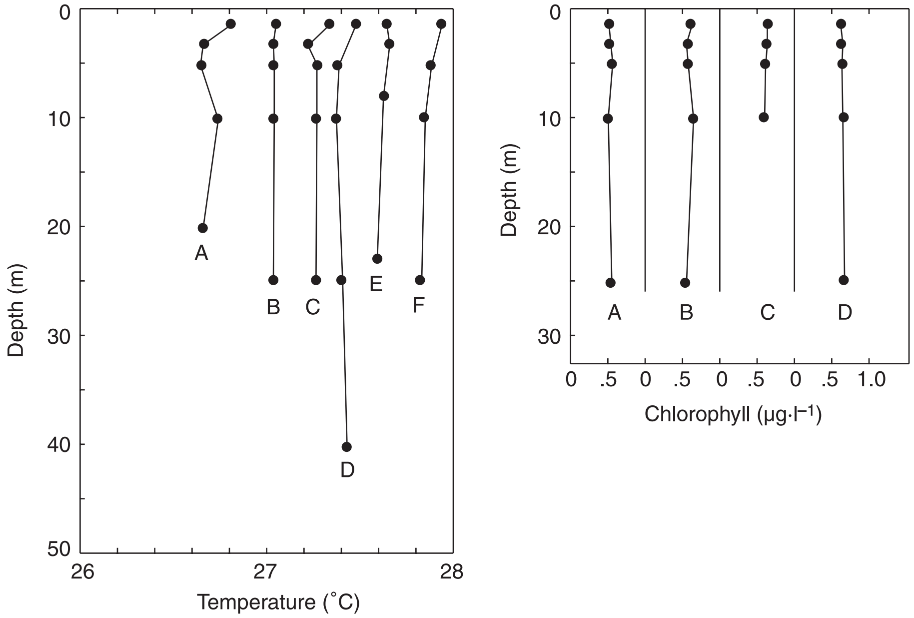

Fig. 2. Vertical temperature and chlorophyll profiles at selected stations on the Amazon River that demonstrate the well-mixed properties of the river water column. Temperature profiles were taken downstream: A, Napo; B, Tefe; C, Jurua; D, Coari; E, Ucaylai; F, Purus. Vertical chlorophyll profiles are from stations between the Jurua and Jutai Rivers: A, downstream Jurua; B, upstream Jurua; C, downstream Jutai; D, upstream Jutai.

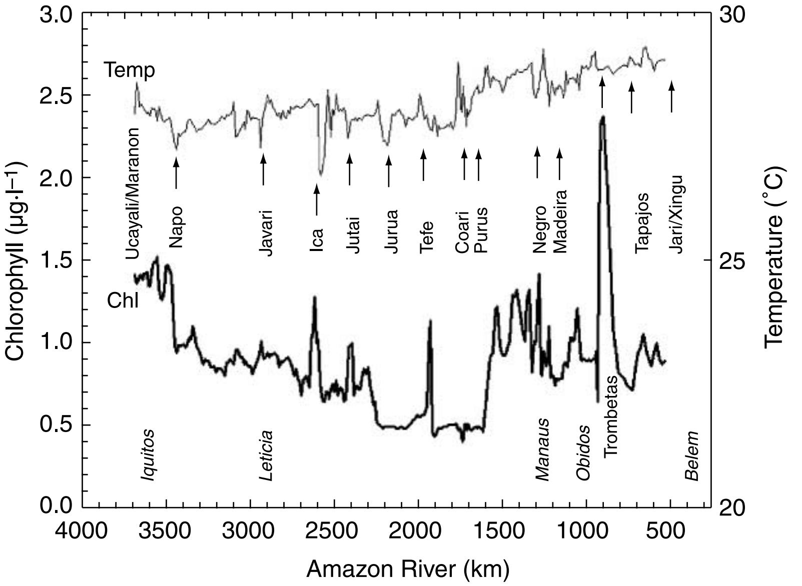

Fig. 3. Distribution of chlorophyll and temperature along the Amazon River mainstem from a few miles upstream of the Rios Jari and Xingu to the confluence of Rios Ucayali and Maranon in Peru. Arrows denote tributary entrance points and major city names are in *italics*.

differently. Some tributaries, like the Napo, dilute the Amazon chlorophyll levels, while chlorophyll spiked at the Ica and Jutai. Values decreased downstream of the Jutai. Chlorophyll remained low and relatively invariant between the Jurua and Purus Rivers except for a sharp pulse at Tefe. Chlorophyll increased sharply after the Purus River in a series of peaks that continued past Manaus to just downstream of the Madeira River.

Continuing towards the sea, the river is compressed through its narrowest point, Obidos. Downstream of Obidos we encountered a section of extremely high turbidity, but no real change in chlorophyll levels. However, chlorophyll spiked again a few kilometres downstream, at the confluence of the Rio Trombetas. Chlorophyll levels subsequently decreased as the water then became much more turbid just upstream of the Rio Tapajos. We encountered a phytoplankton bloom in the mouth of the Tapajos River (one of the few clear water tributaries) at the confluence of 'white' and black waters, first described by Bates in 1848 (Bates, 1915). Between the Tapajos and the sea are two more major tributaries, Jari and Xingu, from which we obtained surface samples but not along-track data.

Temperature

The Amazon River increased in temperature from approximately 27 to 29°C from the confluence of the Ucayali and Maranon Rivers to the sea (Fig. 3). Tributaries entering the Amazon cause short-term perturbations in temperature that are quickly absorbed by the mainstem volume of the Amazon. This increase in temperature represents considerable thermal conduction when one considers the volume of water that is being conducted away from the continent.

Nutrients

Both nitrate/nitrite and phosphate were highest in the Andean source waters and declined towards the sea. Nitrate/nitrite ranged from 16 to 4 µm and phosphate from 1.4 to 0.4 µm. Both declined significantly in the plume at the edge of the Atlantic Ocean (Fig. 4).

pH: The pH of the mainstem ranged from 7.99 to 6.55. The waters of the Amazon River became more acidic as they flowed towards the sea. Many of the tributaries are low in pH. Their confluences with the Amazon are seen as pulses in the pH trace, with corresponding peaks in transmittance, and changes in water temperature (Fig. 4, Table 1).

Light transmittance

The Amazon is most turbid in its upper parts and gradually becomes less turbid as it flows toward Obidos. There is a sharp increase at the Trombetas and then a sharp dip in transmittance slightly downstream of Obidos near the Tapajos, and then the river clears slightly (Fig. 4, Table 1).

Attenuation: Vertical light profiles allowed the calculation of attenuation coefficients (K_d), which indicated the same pattern as the transmittance data. While attenuation decreases in the middle of the track, the photic zone of the Amazon River is still extremely shallow, typically less than 0.5 to 1.5 m. Attenuation increases sharply near the mouth of the river, forming a turbidity maximum zone downstream of Obidos.

We found significant differences in nutrients, chlorophyll, and submarine light attenuation coefficients between the Amazon River and its tributaries. The river possessed higher levels of nutrients, but lower chlorophyll and light than most of the tributaries (Table 2). Tributaries have unique characteristics that are related to their specific drainage basins, with associated geochemical and biological processes (Gibbs, 1967; Sioli, 1975), but their individual effect is quickly consumed by the mainstem.

Table 1. Statistical analysis of along-track parameters

Parameter	Correlation (*r*)
Transmittance increases towards the river mouth	0.71***
pH decreases towards the river mouth	0.41**
Nitrates/nitrites increase upstream	0.32
Phosphates increase upstream	0.46*
Chlorophyll increases downstream	0.19***

***$P < 0.001$, **$P < 0.01$, *$P < 0.05$.

Table 2. Summary of limiting factors

Source	PO_4 ***	NO_2/NO_3 ***	Attenuation coefficient, K_d ***	Chlorophyll *
Amazon	+	+	–	Lower
Tributaries	–	–	+	Higher

***$P < 0.001$, *$P < 0.05$.

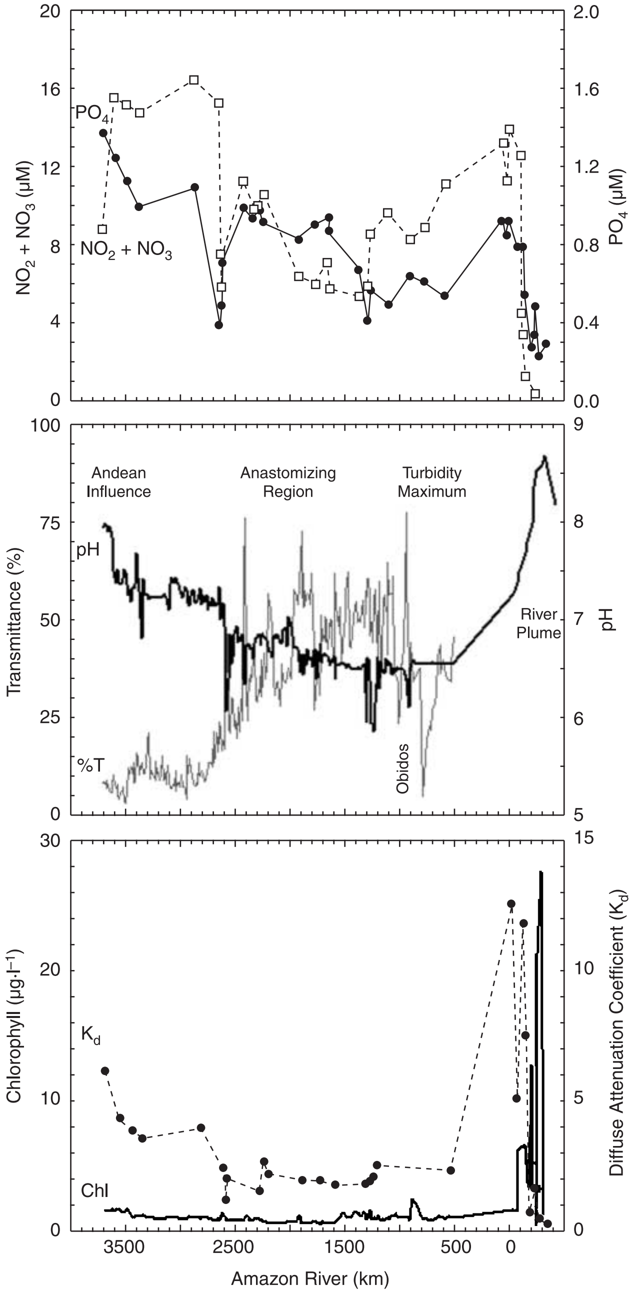

Fig. 4. The distribution of nutrients, pH, transmittance, light attenuation, and chlorophyll along the Amazon River from the confluence of the Maranon and Ucayali Rivers to the Atlantic Ocean (see Fig. 1 and text for details).

DISCUSSION

Vertical sampling demonstrated that the Amazon River is a well-mixed system. Furthermore, station chlorophyll concentrations and the chlorophyll Rb/Ra acid ratios (Smith *et al.*, 1981) indicate that the phytoplankton from below the photic zone are not degraded. Phytoplankton at all depths have similar chlorophyll values and thus the rate of vertical mixing is faster than the rate of phytoplankton degradation. Turbulence frequently mixes the phytoplankton into the surface waters, supporting the contention that near-surface measurements are realistic proxies for the entire water column. Along-track measures are therefore valid indicators of the Amazon River as a whole, and not just its surface features.

The along-track data tracings make it very clear that the Amazon River system is a very complex and heterogeneous aquatic ecosystem. The river itself is generally thought to be a heterotrophic system with phytoplankton supplying an almost negligibly small fraction of the total carbon loading (Wissmar *et al.*, 1981). Although respiration does dominate photosynthesis, along-track phytoplankton populations are about as abundant as in the near shore nutrient-limited temperate seas (0.4–3.0 $\mu g \cdot l^{-1}$ chlorophyll). On this scale, the tributaries are variable and any one particular tributary may generate local spikes. This would argue for light limitation in the mainstem Amazon and nutrient limitation in the tributaries as controlling factors for phytoplankton production. This is a somewhat general and broad conclusion, but it seems valid, especially for black water tributaries.

The mainstem, however, is much larger than any particular river and the effect or impact of a single tributary is quickly absorbed, or diluted, by the sheer size of the mainstem volume as the river quickly returns to its equilibrium state. On a larger geographic scale, the river changes slowly as it flows through the geographic provinces of Amazonia and chemical composition takes on the additive effects of the entire continental-scale floodplain upstream of the point of measurement. Future sampling programmes in the Amazon River system should take great care to ensure that any single point sampling occurs in regions where the river is well mixed and not undergoing relatively rapid small-scale changes. Otherwise, such data may reflect the magnitude of small-scale perturbations and not be relevant to the river system as a whole.

While the mainstem contained relatively high levels of phosphate and nitrate/nitrite, the unexpected low, along-track phytoplankton chlorophyll levels and strong light attenuation strongly suggest that, on a continental scale, phytoplankton are light- and not nutrient-limited. In the upper reaches, erosional sediment from the Andean highlands of the watershed dominates the light field far into the lowlands. The soils in this region are former marine sediments that are rich in calcium, magnesium, and alkali-earth metals (Junk and Furch, 1985). Their chemical composition imparts an alkaline signature to the mainstem. Sediment concentration, as estimated by transmittance (%T), begins to decrease in the vicinity of the Peru/Brazil Columbian border (67–68° W longitude). The mainstem widens and numerous tributaries flow into the Amazonas (Rio Ica from the west, Jutai and Rio Jurua from the south, Rio Japura from the north). Mainstem pH changes from alkaline to acidic about 10 miles downstream from the confluence of the Rio Ica. From this point to the confluence of the Rio Negro, the mainstem becomes a maze of anastomizing rivers during the high-water seasonal flood, making the flooded forest an enormous web of water.

The lowland tributaries originate in the archaic shields of Guiana and central Brazil, old geological formations with low relief and very poor, sandy soils. Rates of erosion are much lower than the Andes watershed and the soils yield little in the way of sediments and dissolved minerals. It is in this stretch that the pH changes from alkaline to acidic as black water tributaries increase their contributions to mainstem flow (*sensu* Janzen, 1974). The Andean headwaters become more dilute and even though beam transmittance increases, the diffuse attenuation coefficient remains high due to the increasing concentration of humic acids. Their polyphenolic compounds absorb light very strongly and remain in the water column because they are relatively resistant to microbial decomposition (Allison, 2006). Strong mixing prevents any stratification, nutrients are plentiful, but phytoplankton simply do not spend enough time exposed to sunlight to flourish.

The Rio Negro, at about 60°W longitude, increases mainstem flow by approximately 30% (Gibbs, 1967). Its black waters meander downstream side-by-side for approximately 60 km before merging completely into the mainstem. The Madeira enters shortly thereafter, again greatly increasing flow, and continues the acidification of the mainstem. This trend continues to the choke point provided by the narrows at Obidos.

At Obidos, due to the almost horizontal nature of the landscape, the Amazon begins to interact with tides generated by the Atlantic Ocean, still hundreds of kilometres to the east. Obidos, the site of the principal gauging station because it is the narrowest point in the lower Amazon, is only about 2 km wide. Its water is very turbulent with 4–6 kt currents. Large logs, vegetation patties, and debris are common. Vertical profiles demonstrated that the water column is well-mixed. There are 1- to 2-m standing surface waves and low transmittance. Transmittance continues to decrease downstream, reaching a minimum (turbidity maximum) a few kilometres upstream of the confluence of the Rio Tapajos at Santarem. Continuing towards the east, the Amazon receives the last 10% contribution towards the total water discharge from four acidic tributaries: Tapajos, Xingu, Jari, and Toncantins.

Both physical and biological factors contribute to light limitation in the mainstem Amazon River. The attenuation coefficients (*K*par) of both the white, sediment-laden Andean waters and lowland black water tributaries are two to three orders of magnitude higher than oceanic waters. Andean sediments initially contribute strongly to light attenuation. However, as they become diluted light attenuation remains high due to the increasing concentration of biologically produced tannins. These compounds persist in the water column until they reach the sea. There, in the plume, sediments settle out of the surface waters as they continue to plate out across the surface of the more dense sea water. Under high irradiance the dissolved, long-chain organic acids undergo photochemical oxidation, which releases CO_2 into the atmosphere and leaves behind smaller carbon compounds that are more easily metabolized by the microbial loop (Amor and Benner, 1996). Phytoplankton chlorophyll values soar to 10 and 20 times those of the river mainstem and the waters change from turbid brown to bright pea soup green as light limitation is finally released (Fig. 4) (Smith and Demaster, 1996).

Lotka (1925) described the world as a ‘singularly futile engine, which, with seriousness strangely out of keeping with the absurdity of the performance, carefully and thoroughly churns up all the energy gathered from the source. It spends all its work feeding itself and keeping itself in repair, so that no balance is left over . . . ’. Hairston, Smith, and Slobodkin (HSS) elaborated on this theme and posed the question of top-down versus bottom-up regulation of the performance integrated with the theme that populations are the pathways of energy and nutrient flow. Their major premise was that ultimately, energy, and not nutrients, limit biomass. Alternatively, plants mount significant defences to combat herbivory. In the case of the Amazon River, the interplay of geological inputs (sediments) and biological inputs (dissolved organic carbon) as phytoplankton light-limiting factors illustrates the influence that terrestrial systems can exert on aquatic systems at continental scales. A physical forcing function dominates production in the headwaters where precipitation-driven erosion generates high sediment loads. As elevations decrease and the river flows through the vast Amazon Basin, the cause of light limitation shifts to the biologically produced high levels of dissolved organic carbon, compounds produced to reduce herbivory in terrestrial plants. In a way, it is ironic that the very biogenic compounds that have evolved to 'keep the terrestrial Earth green' may reverse roles when they enter the aquatic realm as a superfluous consequence of the evolutionary responses of forest plants to high levels of herbivory in nutrient-poor soils (Janzen, 1974).

The work of Gibbs (1967) and Sioli (1975) illustrated how the Amazon River is an expression of its watersheds. Gibbs' classic geochemical study revealed that each tributary has an almost unique mineralogical signature, while Sioli described the origins of the principal water types, white, black, and clear. The Cousteau Amazon Expedition elaborated on this theme, providing insight into the light-limiting role of physical and biological forcing functions on watershed properties. Tagged onto the observations that the earth is green (HSS) and soils are brown, I offer the observation that connectivity between ecosystems sometimes leads to mesoscale control of ecological processes that are beyond the scope of feedback loops, or at least as yet undiscovered.

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