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Regional-scale linkages of terrestrial and Lotic ecosystems in the Amazon basin: a conceptual model for organic matter

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With 4 figures and 1 table in the text

Abstract

Terrigenous organic matter originating at the margins of streams in headwater regions of the Amazon basin accounts for a large part of the organic matter carried by the major tributaries of the basin. The purpose of this paper is to articulate our present understanding of terrestrial to lotic transfers in these headwater regions in the form of a conceptual model. On a regional scale, the headwaters of the Amazon basin may be subdivided into four dominant terrain types: (1) terra firme forests developed on oxisols and ultisols, (2) campina forest developed on spodosols, (3) savanna developed on oxisols, ultisols, and alfisols and (4) montane forest developed on ultisols and inceptisols. Within these terrains terrigenous organic matter is transferred to streams via direct litterfall and blow-in, groundwater baseflow, stormflow, and seepage from fringing wetlands.

Based on the limited available data and data from other systems, our current conceptual model is as follows. Direct litterfall contributions from overhanging canopies are similar across the basin and on the order of 0.7 kg/m2/year. Blow-in contributions are probably on the order of 20% of direct litterfall fluxes. Groundwater baseflow contributions of organic matter (OM) are strongly correlated with soil type and fall into two distinct classes, one draining the campina terrain which is characterized by high dissolved organic carbon (DOC) concentrations (> 20 mg/l) and another draining terra firme, savanna, and montane terrains which is characterized by lower DOC concentrations (< 5 mg/l). Groundwater OM contributions are also compositionally distinct, with elevated proportions of hydrophobic organic molecules in groundwater draining campina. Stormflow contributions across the basin are dominated by saturation overland flow originating in riparian areas, and transferred OM consists primarily of litter washed in from the surrounding forest floor and material flushed from fringing wetlands. In montane terrains, however, there may also be a significant erosive input of soil OM. Contributions of OM from fringing wetlands are most prevalent in lowland terrains where broad, flat riparian zones provide ample sites for wetland development. Both stormflow and seepage from fringing wetlands transfer a wide spectrum of OM composition, ranging from freshly fallen leaves to heavily decomposed and refractory dissolved molecular forms.

Introduction

The Amazon River and its major tributaries transport vast quantities of organic matter from the interior of the South American continent to the western margin of the Atlantic Ocean (Richey et al. **1990).** Detailed analyses of the isotopic, elemental, and molecular compositions of this material suggest a predominantly terrestrial source, as well as a substantial degree of processing prior to entering the lotic system (Ertel

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et al. 1986, HEDGES et al. 1994, 1986). Thus processes operating near and at the margins of streams in headwater regions of the basin appear to be instrumental in producing the compositional signals carried by organic matter in the major tributaries of the basin. Furthermore, differences in the nature of organic matter between the major tributaries should originate in large part from differences in the sequence of processes operating in their respective headwater regions.

Terrigenous organic matter (OM) enters lotic environments largely via direct litterfall and blow-in, groundwater baseflow, stormflow, and seepage from fringing wetlands. Due to differences in transport time and path-specific processes, these pathways transfer OM of distinct composition and concentration. The majority of this material is derived from riparian forests and soils along stream margins, but some portion may also derive from surrounding upland forests or other terrains. Litterfall and groundwater baseflow inputs are ubiquitous and continuous in the tropical landscapes of the Amazon basin, while stormflow and seepage from fringing wetlands are more spatially and temporally variable. In addition to differences between pathways, compositions and concentrations of OM may also vary geographically in response to regional changes in large-scale catchment properties such as soil type, vegetation type, geomorphology and climatic regime. These larger-scale changes in catchment characteristics, coupled with changes in the proportions of different pathway contributions (e.g. more or less wetland seepage input), are believed to give rise to the major biogeochemical differences between the large tributaries of the basin.

As part of a larger effort to develop a regional to continental-scale model of controls on the processing and river export of bioactive elements in the Amazon basin, we present here a conceptual mode1 addressing the large-scale controls on the concentration and composition of organic matter crossing the terrestrial-lotic interface. Emphasis is placed on smaller streams and rivers feeding the larger reaches of the river system. We do not consider processes operating within the expansive floodplains bordering the mainstem of the river or in the tundra regions of the Andes.

As with all modelling efforts such as this, we are immediately faced with the problem of scale and the inescapable condition that, while our objectives lie in predicting the characteristics of a region, we must draw much of our data from isolated studies which are often limited in space and time. In some instances no data may be available from the region. Our strategy during this conceptual stage of the modelling has been to strive for simplicity so that we might avoid over-interpreting the data. We look for more general characteristics and clear inter-regional patterns. As a consequence, our discussions are only semi-quantitative, but this is necessary to maintain the intergrity of the approach.

Dominant terrains of the Amazon basin

The Amazon basin encompasses approximately 7 million km2 of northern South America (Fig. 1), extending from the Andean Cordillera east to the Atlantic Ocean. The basin is bounded in the north and south by uplands of the Guyana and Brazilian shields, respectively. The interior of the basin is a broad low-lying region of undulating topography and incised depositional plains. From its source on the slopes of Nevado Mismi in southern Peru, the river travels 6500 km and drops more than 5000 m.

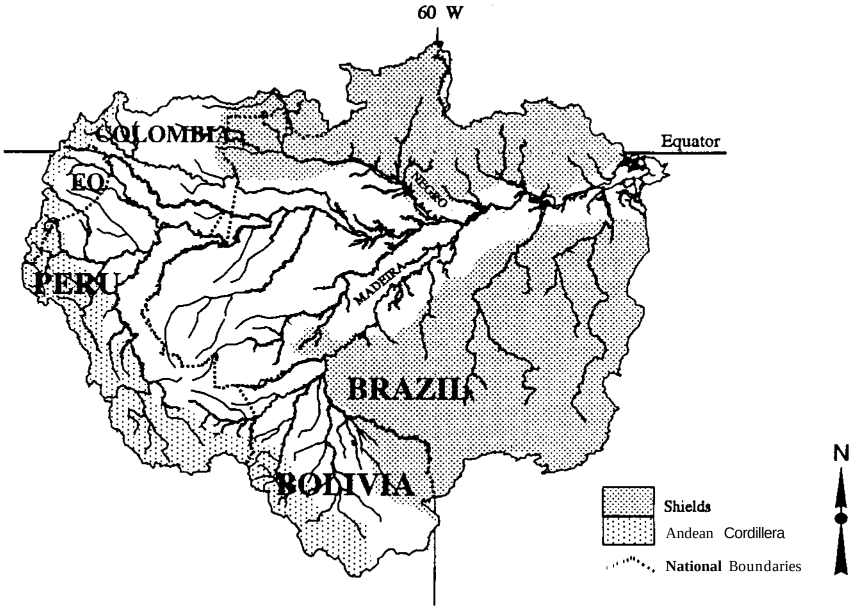

Fig. 1. Map of the Amazon basin showing the river network, major structural features, and political boundaries. Figs. 1 and 2 were produced using Arc/Info GIS software and data from the Digital Chart of the World and the Centro Intemacional de Agricultura Tropical (CIAT).

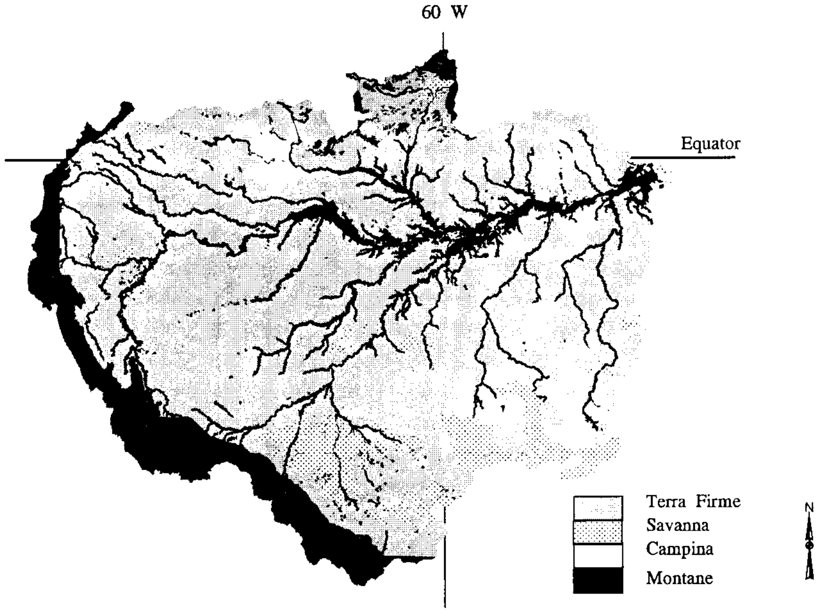

Fig. 2. Map of the Amazon basin showing the distribution of dominant terrain types. Terrains are described in the text.

Along its course it accumulates the flow of thousands of tributaries, culminating in more than 200,000 m^3/s of flow at its mouth. Due to its continental scale and extremes of altitude and tectonic regimes, the Amazon basin contains a bewildering number of geologic and climatic zones, resulting in an even more complex mosaic of inter-related vegetation and soil types. When viewed at a basin-wide scale, however, certain predominant landscape patterns emerge.

The most widespread terrain is one where terra firme forest develops on oxisols and ultisols. This forest/soil combination occurs throughout the interior portions of the basin and on the margins of the shields (Fig. 2). Its geomorphology is variable but generally consists of relatively low-relief, rolling topography dissected by flat-bottomed valleys. Terra firme is a somewhat generic term for upland forests with tall, multi-storied, and closed canopies. These forests are the classically envisioned Amazon jungle, and although they may vary locally in species composition, they share a common physiognomy (PIRES & PRANCE 1985). The soils on which these forests develop vary somewhat as a function of position in the landscape. Clay content generally increases with lower position on hillslopes, but hydromorphic soils of the valley bottoms are often sandy (LUCAS et al. 1984, 1988).

Interspersed throughout the interior portions of the basin, but concentrated north of Manaus and in the headwater regions of the Negro river, are smaller terrains of campina forest developed on spodosols (Fig. 2). This forest/soil type sometimes occurs at the base of long (> 1 km) hillslopes and is believed to represent the endpoint of podsolization reactions operating over the entire region (LUCAS et al. 1984, 1988). Campina is a low and open forest, with vegetation concentrated in islands separated by areas of partially exposed white sands. The floral community is one specially adapted to the extremely low nutrient levels and low water-holding capacity of the underlying spodosols. As a consequence of these harsh conditions, the species diversity of campina forest is less than that of terra firme forest (PRANCE 1975). At the margins of streams where water is available year-round, vegetation is more dense and the canopy above low-order streams is closed.

Savannas also occur as isolated terrains throughout the interior portions of the basin, but the largest conterminous savannas occur in the southern portions of the basin (Fig. 2). They are generally flat and may be well or poorly drained. Beneath poorly drained savannas alfisols develop, while oxisols and ultisols develop under well-drained conditions. Although they may vary widely in moisture regime and structure of vegetation, one feature shared by all savannas is an intrinsic seasonality linked to water availability (SARMIENTO 1984). Another important feature is the occurrence of riparian forests along stream channels. Under natural conditions, these forests develop irrespective of the surrounding vegetation, be it grassland or woody scrub. The effect is that streams draining savannas receive direct litterfall inputs just like streams draining regions of unbroken forest. Additionally, in these riparian forests, water tables are generally shallow and prolonged anaerobic conditions may develop, leading to accumulations of organic matter which may be transferred to adjoining streams. This is an excellent example of the equalizing role played by riparian zones. While the landscape may be dominated by forest or grassland, from the stream's perspective both are forest.

Montane forest dominates Andean landscapes as well as certain raised plateau regions at the northern margin of the basin (Fig. 2). Montane forests develop on relatively shallow and often organic-rich soils. They share many structural features in common with lowland forests but are somewhat less dense and have a shorter canopy height (Grubb et al. 1963). Due to the cold and intermittent dryness of Andean montane systems, organic matter decomposition rates are reduced and soils are characterized by dark, organic-rich epipedons (Alexander & Pichott 1979, Storie 1953). Montane soils are also characterized by poorly developed vertical profiles, again brought by climatic factors and high rates of erosion and sedimentation (Beek & Bramao 1968). Soil creep on the steep hillslopes contributes to this erosion by transferring hillslope soil to the valley floor where it may be easily eroded by storm waters. The Andean montane terrain is characterized by deeply incised stream-cut valleys at low and mid elevations and glacier-cut valleys at high altitudes. Andean systems also include areas of alpine tundra, but these are not considered.

Conceptual model of organic matter transfers

In view of the described major transport pathways and dominant terrains of the basin, we may now construct our conceptual model ‘of the relative magnitudes of organic matter transfers across the terrestrial-lotic interfaces of the different terrains.

Direct litterfall and litter blow-in

Direct litterfall and blow-in transfer leaves and wood to streams directly from the over-hanging tree canopy and from the near-stream forest floor. Direct litterfall rates to the stream surface may be considered approximately equal to litterfall rates over the surrounding forest floor. For a given region the time-integrated total flux of litter (L_T) to streams may be expressed as,

$$L_T(t) = \int^t \left[D(t) \cdot \Sigma W_c\right] + \left[B(t) \cdot \Sigma\Lambda\right] dt \qquad (1)$$

where D and B are average direct litterfall (kg/m*) and blow-in (kg/m), respectively, ΣW_c is the total area of canopy-covered stream surface, and $\Sigma\Lambda$ is the total length of streams in the region.

The available data for litterfall in Amazonian forests are presented in Table 1. No data are available for savanna terrains. Inundation forests listed in Table 1 are seasonally flooded by adjoining blackwater rivers and are included to illustrate the relative consistency of litterfall values across very different systems.

In general litterfall values fall into a relatively narrow range of 0.24 to 1.02 kg/m^2/year, with an average of 0.68 kg/m^2/year. The forests which depart most from the average are the campina bana forest and the high altitude (3370 m) montane forest. The campina bana is a low and open forest which develops as a result of water stress. Thus it occurs away from stream channels and is not relevant to our direct litterfall discussion. Decreased litterfall in montane forests at high altitudes is a typical occurrence (Veneklaas 1991). At 2550 m, however, no decrease is observed in litterfall relative to lowland forests, suggesting that only at the highest altitudes are litterfall rates significantly diminished. Given that tree-line in Andean environments lies near

Table 1 Litterfall data for Amazonian forests overlying different soil types. Terra firme forest is separated into upland and riparian categories. NA indicates not applicable.

Forest Type	Soil Type	Total Litterfall (kg/m²/yr)	Leaf Litterfall (kg/m²/yr)	% N	% P	Source
Montane (2.550 m)	Inceptisol	0.70	0.46	1.2	0.09	Veneklaas (1991)
(3370 m)		0.43	0.28	0.7	0.04	Veneklaas (1991)
Upland	Oxisol	0.80		1.3	0.04	Dantas & **Phillipson** (1989)
Terra Firme		0.74	0.56	1.4	0.03	Klinge & Rodrigues (1968)
		0.79	0.64	–	–	Franken et al. (1979)
		0.83	0.54	1.8*	0.02*	Luizao (1989)
		1.02	0.76	1.6*	0.03*	Cuevas & **Medina** (1986)
Riparian	Oxisol	0.64	0.43	1.2	0.02	Franken et al. (1979)
Terra Firme		0.74	0.47	1.4*	0.03*	**Luizao** (1989)
Campina	Spodosol	–	–	1.0	0.05	**Klinge** (1985)
(Tall Caatinga)		0.56	0.40	0.7	0.05	Cuevas & Medina (1986)
(Bana)		0.24	0.21	0.6	0.02	Cuevas & Medina (1986)
Inundation	NA	0.68	0.53	–	–	Adis et al. (1979)
	NA	0.67	–	1.4	–	**Irmler** (1982)
Average		0.68	0.48	1.2	0.04	
SD		0.19	0.15	0.4	0.02	

* – Calculated as percent of leaf litter

3000 m (Grubb et al. 1963, Montes de Oca 1989), montane forests with decreased litterfall occupy only a small area at the upper extreme of the forested portions of the basin. Disregarding the litterfall of the high montane forest and campina bana, the overall average of litterfall in forests of the Amazon basin rises to 0.74 kg/m²/year with a standard deviation of 0.12. There is seasonality in litterfall related to water stress, but such seasonality should be reduced at the margins of perennial streams where water is always available. Table 1 also indicates that the N and P contents of litter across the basin are similar, with an average N content of 1.2% (SD = 0.4) and an average P content of 0.04% (SD = 0.02).

Blow-in contributions of litter to Amazonian streams have not been examined. Studies in temperate systems suggest that blow-in contributions may be as much as

50% of direct litterfall in very small streams (CONNERS & NAIMAN 1984), but in general blow-in contributions are probably closer to 20% of direct litterfall (COMISKY 1978, FISHER & LIKENS 1973). There are no data to suggest how litter blow-in may differ between regions of the basin.

From the litterfall data available and inferences regarding blow-in, it appears that direct litterfall contributions to the canopy-covered portions of streams across the Amazon basin are similar and ca. 0.7 kg/m2/year. Blow-in contributions are unknown but are probably ca. 20% of direct litterfall. The N and P content of this litter is also likely to be very similar across the basin. The large-scale controls on contributions from this pathway are forest type, degree of seasonality, and stream size. Given that at the resolution of this conceptual model total litter input rates do not vary significantly on an area1 or temporal basis, the primary controls on total litter input fluxes to streams become the area of overhanging canopy (W_c) and length of streams (A).

Groundwater baseflow

Groundwater contributions to baseflow in perennial streams are continuous and arise via groundwater discharge from streamside soils and soils beneath the stream bed. For a given region where subsurface losses are negligible, the time-integrated groundwater baseflow flux (Q_{gb}) may be approximated as,

$$Q_{gb}(t) = \int^{t} k_g S_g(t)\, dt \tag{2}$$

where S_g is storage of groundwater and k_g is a transfer constant. S_g is a function of groundwater recharge (R), transpiration (T) and stream discharge from the region (D), where $dS_g/dt = R-T-D$.

We may consider the chemistry of these groundwater baseflow contributions to reflect that of surrounding groundwater, recognizing that groundwater OM is dominantly in the dissolved form (DOM) and groundwater chemistry may be altered somewhat upon passing through the hyporheic zone and stream-bed sediments (FRIEBIG & LOCK 1991, FORD & NAIMAN 1989). There are no published data concerning groundwater DOM concentrations or compositions in the Amazon basin. Presently we have only unpublished data and inferences drawn from seep and stream chemistry. MCCLAIN (unpubl.) measured dissolved organic carbon in 289 Amazonian groundwater samples collected from 14 nearstream piezometers in two contrasting watersheds north of Manaus, Brazil. One watershed lies within the campina terrain while the other lies within the terra firme terrain. Groundwater DOC concentrations averaged 36.1 mg/l (SD = 10.0) in spodosols underlying campina forests. In contrast, groundwater in the watershed containing oxisols underlying terra firme forest averaged just 2.6 mg/l (SD = 1.9) of DOC. The elevated DOC concentrations in the campina watershed are consistent with high concentrations of DOC measured in small streams draining campina forests (LEENHEER 1980, MCCLAIN unpubl.). Piezometers were monitored for roughly one year, during which time DOC concentrations showed no seasonal variability.

A relationship between DOM concentrations of Amazon streams and associated soil types was first put forth by SIOLI (1954, 1955) and has since been supported by other investigators (Klinge 1967, Leenheer 1980). This relationship is founded in the widely observed mechanism whereby DOM leached from the litter layer is immobilized in the soil column via sorption to clay surfaces and Al and Fe hydroxides (Cronan & Aiken 1985, Easthouse et al. 1992, Nelson et al. 1990). In oxisols and ultisols the immobilization of DOM is highly effective, producing groundwater of low DOC concentrations (< 5 mg/l). Conversely, in the upper horizons of largely clay-free spodosols, DOM is not effectively immobilized and groundwater DOC concentrations are high (> 20 mg/l). This mechanism of DOM removal leads to compositional differences as well as concentration differences. Water from seeps in spodosols and streams draining spodosol regions each carry elevated proportions of acidic molecular forms, which include humic and fulvic acids (Leenheer 1980). Hydrophobic molecular forms accounted for ca. 55% of DOC in rivers draining spodosol regions while accounting for only 20-40% of DOC in rivers draining areas of oxisols and ultisols (Leenheer 1980).

Based on the available groundwater data and strong linkages between soil type and groundwater DOM concentrations and compositions, we can initially identify two distinct classes of groundwater basetlow input; one, occurring in regions of spodosols (campina terrain), which is characterized by high DOC concentrations (> 20 mg/l) and increased proportions of hydrophobic molecular forms, and another, occurring in regions of oxisols and ultisols (terra firme and savanna terrains), which is characterized by low DOC concentrations (< 5 mg/l) and lower proportions of hydrophobic molecular forms. In montane terrains where inceptisols are the dominant soil type, groundwater baseflow probably corresponds to that of oxisol and ultisol regions. This supposition is supported by the very low DOC concentrations of Andean rivers and streams (Guyot & Wasson 1994). Within this context the primary control on DOM concentration and composition in groundwater baseflow is soil type and storage of groundwater in the region (S_g in equation 2). Total subsurface baseflow OM contributions (SB_T) to streams in a region via groundwater baseflow may be stated simply as,

$$SB_T(t) = OM_g \times \mathrm{Q\&t)} \qquad (3)$$

where OM_g is the average concentration of OM in groundwater baseflow as a function of soil type, and Qgb is baseflow flux from equation (2).

Stormflow

Stormflow is prevalent in regions of high rainfall coupled with large areas of poorly-drained or low-permeability soils. Where nearly saturated riparian soils border streams, rainstorms commonly produce saturation overland flow which routes rainwater directly to stream channels. Large amounts of rainfall on well-drained but low-permeability soils may produce shallow throughflow and infiltration-excess overland flow (Bruijnzeel 1990). In the Amazon basin, stormflow contributions to streamflow have been investigated at two sites in the central lowlands (Lesack 1993, Nortcliff & Thornes 1984) and one site in the foothills of the Andes (Elsenbeer & Cassel 1990). These three sites lie within the terrain of terra firme forest underlain by oxisols and ultisols, and no data are available for savanna, campina, or montane terrains. In the central basin, both Nortcliff & Thornes (1984) and Lesack (1993) found stormflow to originate exclusively via saturation of riparian soils adjacent to the stream channels; neither study reported infiltration excess overland flow on surrounding hillslopes. In contrast, in the Andean foothills of Peru, Elsenbeer & Cassel (1990) reported frequent occurrences of overland flow on hillslopes owing to a low permeability horizon at shallow soil depths. These authors did not report on the occurrence of saturation overland flow in riparian soils, so it is unknown how hillslope and riparian overland flow pathways compare. None of the three studies examined shallow throughflow, although Elsenbeer & Cassel (1990) attributed the overland flow that they observed to return flow from subsurface flowpaths.

In all of these catchments, stormflow probably accounts for only a small proportion of the total annual stream discharge. In the only study to have calculated this, Lesack (1993) found that 5% of annual discharge occurred as stormflow.

Inter-regional differences in the magnitude and nature of stormflow are impossible to specify at this time as data are available for only one of the basin's four dominant terrain types. Streamside soils are probably near saturation in all of the dominant terrains, however, and saturation overland flow near the stream margin is most probably ubiquitous. The area over which saturation overland flow occurs, and therefore the flux of overland flow should be proportional to the area of saturated or nearly saturated riparian soils. In contrast, infiltration excess overland flow on surrounding hillslopes is less prevalent and perhaps exceedingly rare (Dunne et al. 1975). Assuming saturation overland flow to be the dominant source of stormflow, the time integrated stormtlow flux, Q_S for a particular region may be approximated as follows,

$$Q_s(t) = \int^t \left[P(t) \times A_s(t)\right] dt \tag{4}$$

where P is average precipitation and A_S is the area of saturated or nearly saturated soils in the region. Total stormflow contributions of OM (SF,) for a region may then be expressed as,

$$SF_T\,(t) = Q_s(t) \int^t OM_s(t)\, dt \tag{5}$$

where OM, is the average OM concentration of stormflow and Qs is from equation (4). Unlike groundwater, the OM concentration stormflow is variable as a function of time.

There are no data concerning organic matter concentrations in Amazon stormflow. Thus our current conceptual model of stormflow OM input to streams is necessarily vague. Increases in stream OM concentrations and fluxes during storms are well documented in temperate as well as in other tropical stream systems (Easthouse et al. 1992, Frangi & Lugo 1985, Grieve 1990, McDowell & Asbury 1994, Newbold et al. 1995), indicating that the OM contribution of stormflow is greater than the combined fair-weather contributions of direct litterfall and groundwater baseflow, at least in non-spodosol regions. In the central Amazon, unpublished data show a doubling of stream DOC concentrations during storms, perhaps due to the flushing of fringing wetlands (MCCLAIN, unpubl.). In Andean streams, rains lead to significantly increased loads of suspended sediments (Bourges et al. 1990, GUYOT 1992): which are probably accompanied by higher loads of soil-dervied POM. This is a unique feature of streams in montane terrains, as lowland streams draining intact forests and savannas receive little input of eroded soil material.

Compositionally, stormflow OM should be diverse. In the case of saturation overland flow, much of the transported OM will be litter material washed into the stream channel from the surrounding forest floor. Saturation overland flow in riparian areas also flushes fringing wetlands, thereby transferring, in a somewhat diluted form, the compositional spectrum of these waters.

Fringing wetland seepage

Wetlands are a prominent feature of Amazonian landscapes, especially in flat, low-lying regions where drainage waters accumulate. JUNK & FURCH (1993) estimated that more than 20% of the entire Amazon basin is subject to periodic flooding, including river and stream floodplains and flooded savannas. The majority of these wetlands occur seasonally and interact with streams only during the rainy season. In low-order catchments from the dominant terrains addressed in this article, flooding is event-based and corresponds more to the saturation overland flow discussed in the preceding section. Between events, however, there are isolated saturated areas which accumulate organic matter and drain into stream channels. These fringing wetlands contribute to baseflow and may be significant contributors of terrestrial OM to stream systems. For a given region, the total time-integrated seepage from fringing wetlands (Q_w) may be approximated by the following,

$$Q_w(t) = \int^t k_w S_w(t)\,dt \qquad (6)$$

where S_w is the storage of water in fringing wetlands and k_w is a transfer constant. S_w is a function of groundwater exfiltration into depressions beneath the level of the surrounding water table (EX_{gw}) and wetland seepage losses (Q_w), where $dS_w/dt = EX_{gw} - Q_w$.

There are no available data for the Amazon basin concerning the contributions of fringing wetlands to stream flows nor the concentration and composition of OM derived from them. Fringing wetland OM contributions should be enhanced in lowland environments and diminished in cordillera environments where gradients are steeper and wetlands are less abundant. **GUYOT & WASSON (1994)** reported increases in DOC concentrations as rivers exited the cordillera and moved across the lowlands. They attributed this increase in DOC to contributions from wetlands. Similar increases in DOC as a function of percent wetland were reported for 42 separate catchments in southern Quebec, Canada (ECKHARDT & MOORE 1990) and HEMOND (1990) went so far as to hypothesize that, in glaciated catchments, fringing wetlands are the dominant source of humic substances to streams. Clearly, a common feature of wetland contributions is elevated OM concentrations due to the accumulation of litter decomposition products.

Compositionally, fringing wetlands should be sources of a wide spectrum of OM, ranging from freshly fallen leaves to heavily decomposed and refractory material. Within the dissolved fraction there should be increased concentrations of hydrophobic organic acids, as organic matter decomposing in these surface waters has minimal contact with mineral surfaces and thus adsorption losses are reduced. However, as with stormflow, an absence of data requires that our conceptual model for fringing wetland contributions of OM to Amazonian streams must remain vague until new data are available.

Summary and conclusions

On a regional scale, the Amazon basin may be subdivided into four dominant terrain types: (1) terra firme forests developed on oxisols and ultisols, (2) campina forest developed on spodosols, (3) savanna developed on oxisols, ultisols, and alfisols, and (4) montane forest developed on ultisols and inceptisols. The first three terrains cover the lowland portions of the basin while the fourth occurs at higher altitudes in the Andean cordillera. Within these terrains terrigenous organic matter is transferred to streams via direct litterfall and blow-in, groundwater baseflow, stormflow, and seepage from fringing wetlands. Our present conceptual model describing the concentration and composition of organic matter transferred to low-order streams along these pathways is illustrated schematically in Figs. 3 and 4 and may be summarized as follows.

(1) Direct litterfall contributions from overhanging canopies are similar between all terrains and on the order of 0.7 kg/m^{2}/year. Blow-in contributions are probably on the order of 20% of direct litterfall fluxes. In low-order streams with closed canopies the flux of direct litterfall is proportional to stream width, while in larger streams and rivers with open canopies, this flux is proportional to the width of overhanging vegetation at the streamsides. The elemental composition of litterfall and blow-in is also similar across the basin, with N and P contents averaging 1.2% and 0.04%, respectively. Compositionally, litterfall is dominated by relatively fresh and labile organic material.

(2) Groundwater baseflow contributions of DOM are strongly correlated with soil type and fall into two distinct classes, *one* draining campina terrains which is characterized by high DOC concentrations (> 20 mg/l) and elevated proportions of hydrophobic organic acids, and another draining terra firme, savanna, and montane terrains which is characterized by lower DOC concentrations (< 5 mg/l) and diminished proportions of hydrophobic organic acids due to adsorption to mineral surfaces. Groundwater-derived OM falls within a relatively narrow compositional spectrum consisting of old and refractory molecules (Fig. 4).

(3) Stormflow contributions in all terrains are dominated by saturation overland flow originating in riparian areas; infiltration excess overland flow and shallow throughflow on surrounding hillslopes are not significant contribution pathways. Intra- and inter-terrain variability derives from differences in area of saturated streamside soils, precipitation patterns, and stream gradient. During storm events in terra firme, savanna, and montane terrains, stormflow organic matter contributions are greater than combined fair-weather contributions from litterfall and groundwater baseflow pathways. Erosive input of soil OM is greater in the montane terrain. Compositionally, stormflow transfers a wide spectrum of dissolved and particulate OM, ranging from freshly fallen leaves to heavily decomposed dissolved molecules flushed from fringing wetlands. The presence of litter leachate and particulate material washed

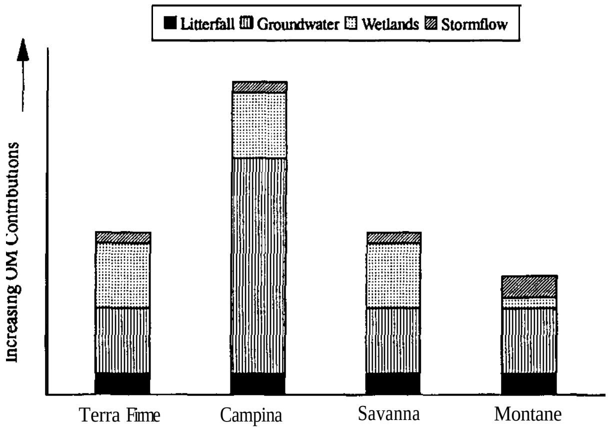

Fig. 3. Plot of the conceptualized relative magnitudes of OM contributions from the four dominant Amazonian terrains considered.

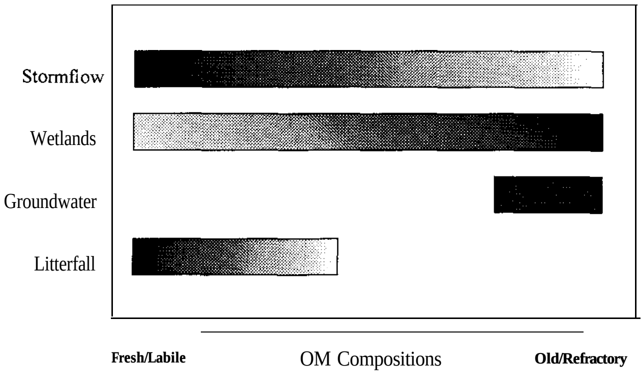

Fig. 4. Plot of the conceptualized compositional spectrums of OM transported via the major pathways linking terrestrial and lotic ecosystems. The darkness of shading is indicative of the proportion of OM falling in that portion of the spectrum.

in from the forest floor weights the stormflow compositional spectrum toward the fresh/labile side of Fig. 4.

(4) Contributions of OM from fringing wetlands are most prevalent in lowland terrains where broad, flat riparian zones provide ample sites for wetland development. Concentrations of OM in wetland seepage are high due to the accumulation of litter decomposition products. OM in wetland seepage is compositionally diverse but contains elevated proportions of refractory hydrophobic molecular forms in the dissolved fractions (Fig. 4).

Fig. 3 also illustrates the relative magnitudes of OM transferred from terrestrial to lotic systems in the terrains considered by our current conceptual model. The campina terrain exhibits the greatest total magnitude of OM transfers due to high groundwater OM concentrations. Total magnitudes of OM input to lotic systems in terra firme and savanna terrains are equal to one another and somewhat less than those in campina terrains. Finally, total magnitudes of OM transfers are lowest in montane terrains due to diminished magnitudes of wetland input. Magnitudes of stormflow OM transfers are somewhat elevated in montane terrains relative to the other terrains owing to inputs via soil erosion.

Clearly, much remains to be done before a more detailed model can be developed to simulate terrestrial to lotic transfers in the Amazon Basin. The most pressing need is for additional data concerning OM concentrations and compositions for different transfer pathways, especially stormflow and wetland seepage. Next, there must be some measure of inter-terrain versus intra-terrain variability in these concentrations and compositions. Finally, process-based relationships must be better elucidated and quantified between transfer pathways and organic matter pools in both terrestrial and lotic environments.

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