134 Rylands, A. B., The behaviour and ecology of three species of marmosets and tamarins (Callitrichidae, Primates) in Brazil. Doctoral Dissertation, University of Cambridge, Cambridge 1982.

135 Rylands, A. B., The distributions of amazonian primates, in: Ecology and Behavior of Neotropical Primates, III. Eds R. A. Mittermeier and A.F. Coimbra-Filho. In preparation.

136 Rylands, A. B., Tree-gouging and exudate-feeding in marmosets (Callitrichidae, Primates), in: Tropical Rain forest: The Leeds Symposium, pp. 155–168. Eds S. L. Sutton and A. C. Chadwick. Leeds Philosophical and Literary Society, Leeds (1984).

137 Rylands, A. B., Personal observations of *Saimiri sciureus, Callicebus moloch, Cebus albifrons, Cebus apella, Chiropotes albinasus, Ateles paniscus* and *Lagothrix lagotricha* at Dardanelos, Rio Aripuanã, Mato Grosso (10° 10' S., 59° 27'W.), 1977–1979.

138 Rylands, A. B., Personal observations of *Callithrix argentata* occupying forest patches in amazonian type savanna at Alter do Chão, near Santarém, Pará (2° 32'S., 55°3'W.), 1983.

139 Rylands, A. B., and Clutton-Brock, T. H., Personal observation of *Pithecia albicans* on the Rio Bauana, Lago de Tefé, Amazonas (3° 22'S., 64° 45'W.), 1980.

140 Rylands, A. B., and Mittermeier, R. A., Conservation of primates in brazilian amazonia. Int. Zoo Yearbook *22* (1982) 17–37.

141 Sabatier, D., Fructification e dissémination en forêt guyanaise: l'exemple de quelques especies ligneuse. Academie de Montpellier, USTL. These de 3ème cycle (1983) pp. 258, dessins en annexe.

142 Salati, E., Marques, J., and Molion, L. C. B., Origem e distribuição das chuvas na Amazônia. Interciência *3* (1978) 200–205.

143 Smythe, N., The seasonal abundance of night-flying insects in a neotropical forest, in: The Ecology of a Tropical Forest, pp. 309–318. Eds E. G. Leigh Jr, S. Rand and D. M. Windsor. Smithsonian Institution Press, Washington, D. C. 1982.

144 Smythe, N., Glanz, E., and Leigh, E. G. Jr, Population regulation in some terrestrial frugivores, in: The Ecology of a Tropical Forest, pp. 227–238. Eds E. G. Leigh Jr, S. Rand and D. M. Windsor. Smithsonian Institution Press, Washington, D. C. 1982.

145 Soini, P., Ecology and population dynamics of the pygmy marmoset, *Cebuella pygmaea.* Folia primat. *39* (1982) 1–21.

146 Soini, P., The pygmy marmoset, genus *Cebuella,* in: Ecology and Behavior of Neotropical Primates, II. Eds R. A. Mittermeier, A. B. Rylands, G. A. B. da Fonseca, and A. F. Coimbra-Filho. Editora Littera, Belo Horizonte, in press (1987).

147 Stevenson, M. F., and Rylands, A. B., The marmosets, genus *Callithrix,* in: Ecology and Behavior of Neotropical Primates, II. Eds R. A. Mittermeier, A. B. Rylands, G. A. B. da Fonseca, and A. F. Coimbra-Filho. Editora Littera, Belo Horizonte, in press (1987).

148 Struhsaker, T. T., and Leland, L., Palm nut smashing by *Cebus a. apella* in Colombia. Biotrop. *9* (1977) 124–126.

149 Terborgh, J., Five New World Primates. A Study in Comparative Ecology. Princeton University Press, Princeton 1983.

150 Thorington, R. W. Jr, Feeding and activity of *Cebus* and *Saimiri* in a colombian forest, in: Progress in Primatology, pp. 180–184. Eds D. Starck, R. Schneider and H. J. Kuhn. Gustav Fischer Verlag, Stuttgart 1967.

151 Thorington, R. W. Jr, The relevance of vegetational diversity for primate conservation in South America. Symp. 5th Congr. Int. Primat. Soc., pp. 547–553. Japan Science Press, Tokyo 1974.

152 Torres de Assumpcão, C., *Cebus apella* and *Brachyteles arachnoides* (Cebidae) as potential pollinators of *Mabea fistulifera* (Euphorb.). J. Mammal. *62* (1981) 386–388.

153 van Roosmalen, M. G. M., Habitat preferences, diet, feeding strategy and social organization of the black spider monkey (*Ateles paniscus paniscus,* Linnaeus, 1758) in Surinam. Doctoral Dissertation, Wageningen University, Wageningen 1981.

154 van Roosmalen, M. G. M., Mittermeier, R. A., and Milton, K., The bearded sakis, genus *Chiropotes,* in : Ecology and Behavior of Neotropical Primates, I, pp. 419–441. Eds A. F. Coimbra-Filho and R. A. Mittermeier. Academia Brasileira de Ciências, Rio de Janeiro 1981.

155 Waterman, P. G., Distribution of secondary metabolites in rainforest plants: toward an understanding of cause and effect, in: Tropical Rain forest: Ecology and Management, pp. 167–179. Eds S. L. Sutton, T. C. Whitmore and A. C. Chadwick. Blackwell Scientific Publications, Oxford 1983.

156 Waterman, P. G., Food acquisition and processing by primates as a function of plant chemistry, in: Food Acquisition and Processing by Primates. Ed. D. J. Chivers. Plenum Press, New York 1984.

157 Whitmore, T. C., Gaps in the forest canopy, in: Tropical Trees as Living Systems, pp. 639–655. Eds P. B. Tomlinson and M. H. Zimmerman. Cambridge University Press, Cambridge 1978.

158 Wolda, H., Fluctuations in abundance of tropical insects. Am. Nat. *112* (1978) 1017–1045.

159 Wolda, H., Seasonality of Homoptera on Barro Colorado Island, in: The Ecology of a Tropical Forest, pp. 319–330. Eds E. G. Leigh Jr, S. Rand and D. M. Windsor. Smithsonian Institution Press, Washington, D. C. 1982.

160 Worbes, M., Vegetationskundliche Untersuchungen zweier Überschwemmungswälder in Zentralamazonien – vorläufige Ergebnisse. Amazoniana *8* (1983) 47–65.

161 Wright, P. C., The night monkeys, genus *Aotus,* in: Ecology and Behavior of Neotropical Primates, pp. 211–240. Eds A. F. Coimbra-Filho and R. A. Mittermeier. Academia Brasileira de Ciências, Rio de Janeiro 1981.

162 Wright, P. C., Adaptive advantages of nocturnality in *Aotus.* Am. J. phys. Anthrop. *57* (1982) 242 (abstract).

163 Yoneda, M., Ecological studies of *Saguinus fuscicollis* and *Saguinus labiatus.* Kyoto Univ. Overseas Res. Rep. New World Monkeys (1981) 43–50.

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The biology of streams as part of Amazonian forest ecology

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Summary. Data on long-term research on the ecology of Central Amazonian forest streams are presented and they reveal the following basic features: Firstly, the essential input of nutrients into these waters consists of forest litter and of the fungi that decompose this litter; consequently, the bulk of the fauna is concentrated in accumulations of submerged litter. Secondly, the nutrients released by the decomposition of this litter do not appear in solution in the stream water, but are tied up throughout in the food web of the aquatic fauna. Thirdly, this food web is relatively robust. This is due to the absence of food specialists in the major channels of energy transfer. One of the staple foods for invertebrate predators consists of chironomid larvae. Fourthly, the degree of acidity and/or the content of dissolved humic substances (more or less black water) has a marked effect on the density and to a lesser extent on the species diversity of the invertebrate fauna, black waters being richer in both. Fifthly, the annual inundations of the forest in the middle and lower courses of the smaller rivers lead to drastic periodic changes of animal densities, and in some cases to annual periodicity of breeding, as exemplified by a three-year study of shrimp populations in the river 'Tarumazinho'.

Key words. Stream ecology; benthos; Amazonas.

I. Introduction

Streams conduct the water and nutrients not utilized by the forest to the large rivers and ultimately to the sea. That the large scale topography of the Amazon Basin does not permit this process to run smoothly and therefore is responsible for massive annual inundations, which virtually play the role of seasonality, is an Amazonian fact of life that has been widely publicized from many different points of view; sociological[3], economic[3,21], hydrological[25,12], and ecological[25,7]. It is also known from a series of investigations that the forest utilizes practically all the nutrients available and releases almost nothing into its streams[23,25,26,29]. Mineral poverty is reflected by low electric conductivity, which ranges between 6 and 12 μS_{20} in Central Amazonian streams[23]. Even the Rio Negro contains less minerals than rainwater[26,27]. Our own measurements in the streams and sampling sites shown in figure 1 range from 8.4 to 17.2 μS_{20}. The patchy distribution of different soils[4,24] leads to a mosaic of stream chemistry: water draining sandy podzols is reddish-brown, transparent (called 'black') owing to dissolved humic and fulvic acids[17]; water draining clay-rich, heavy latosols is colorless and crystal-clear (called 'crystalline' in the following). Larger rivers are more or less black depending on the nature of their smallest affluents. The Tarumãzinho, for example, carried 5.4 mg/l dissolved organic matter in 1971[23]; the 'Igarape (= stream, small river) da Cachoeira' is darker than the Tarumãzinho despite a number of crystalline affluents (table 4); the very small streams Barro Branco and Ig. do Beija-Flor are pure crystalline, whereas the Ig. da Campina is of non-mixed black water with a high humic acid content[17] (see VI. Conclusions).

The low mineral content means that primary production is negligible[22,25]. Whatever the animal life in these streams, it must ultimately depend on allochthonous organic matter; on fruits, leaves and dead wood fallen into the water. If this is true, then the food chains should have their origin in the decomposition of submerged litter. The results presented and discussed in the following center therefore on the ecology of animal life associated with

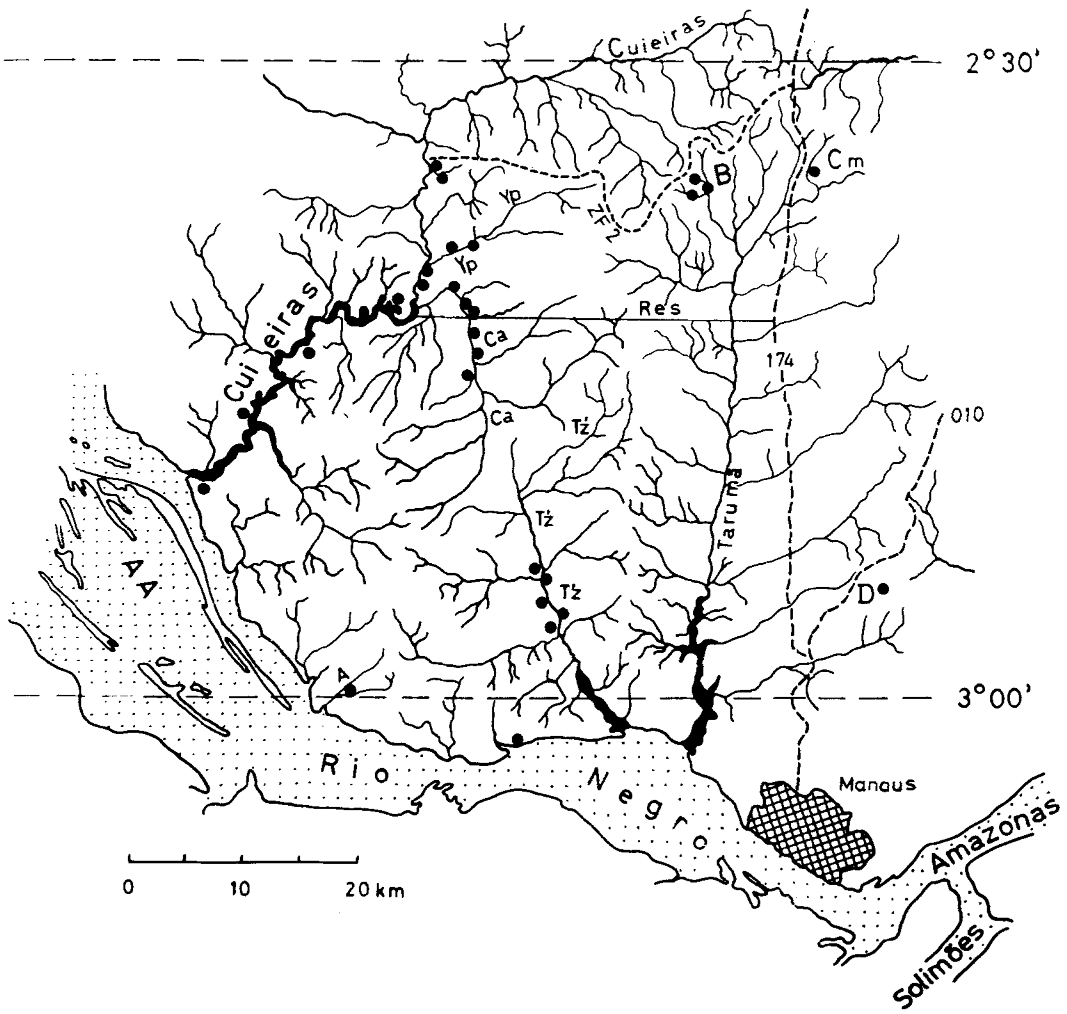

Figure 1. The basins of the rivers Cuieiras, Tarumã and Tarumãzinho (or Tarumã Mirim = small Tarumã, T'Z) adapted from the 'Projeto RANDAMBRASIL', 1:250.000. Black circles: approximate collection sites. AA = Arquipélago das Anavilhanas (National Nature Reserve). A = Igarapé (= small river, stream) Arara. B = experimental hydrographic basin (3 streams sampled). Ca = Ig. da Cachoeira. Cm = Ig. da Campina (black). D = INPA forest reserve 'Ducke' with the crystalline stream 'Barro Branco'. Res = southern boundary of the INPA forest reserve 'km 60'. Yp = crystalline river Ypiranga. ZF 2 = local road and northern boundary of the forest reserve. 174 and 010 = national highways to 'Boa Vista and Itacoatiara respectively.

submerged litter, which is always present in small forest streams and which, depending on the force and direction of water flow, forms moderate to massive accumulations in larger streams and rivers, notably on the insides of certain meanders.

Most collections referred to were carried out in the interphase between the 'terra-firme' and the 'igapo' (= blackwater inundation forest) under the high canopy of undisturbed forest, where annual inundations following the period of 'enchente' (= rising waters, Dec.–June) alternate with a dry forest floor during the period of 'vazante' (= falling waters, July–Nov.). Furthermore, it seems reasonable to assume that variation in stream chemistry may have its impact on the aquatic animal community. Hence, some aspects related to periodic inundation on the one hand and to black and crystalline water conditions on the other will be considered as far as is permitted by the results obtained so far.

II. Material and methods

The fauna discussed in this paper is associated with either submerged leaf litter or with fine detritus produced by biological activity from submerged litter, mostly feces of oligochetes and chironomids. The fauna itself can conveniently be divided into two parts: 'Macrofauna' including animals which can be seen by the naked eye and collected by hand in the field, and 'Microfauna' which necessitates special methods of collection. The microfauna includes the very young stages of part of the macrofauna, such as the smallest larvae of aquatic insects. In this review we concentrate on some basic aspects of Amazonian stream ecology, the extensive data have been, are being, and will be published in special papers which will be cited in due course. For this reason the explanation of the methodology is reduced to the minimum that is necessary to understand the pertinent results and discussion.

The microfauna. 1) Fine stream detritus which settles in places of low current is remarkable for its Thecamoebae. An extensive study on Thecamoebae densities and diversity in the streams shown in figure 1, together with a description of 129 morphotypes, was published in 1982[29]. Relative densities can be estimated reliably by a constant-effort method: one sample consists of the number of Thecamoebae that can be found within 10 min under a low power microscope with standardized magnification[31]. By a sequence of such counts from the same material the approximate absolute density per ml of settled detritus can be extrapolated.

2) The microfauna that swims or drifts in the free water above the stream bottom and between dead wood, and forest vegetation during inundation periods, was collected in 70-ml sample bottles with a small piece of fish bait, which were suspended for 2–3 days from an isopor swimmer fixed on overhanging vegetation. The bottles were closed with 1-mm^2 mesh nylon tissue; this allowed small organisms to enter and leave the bottle but prevented larger organisms from doing so and removing the bait. After retrieval, these quasi-natural microecosystems were observed daily for up to one month under the stereo-microscope. For closer observation and identification parts of the material were examined under high power. A detailed food web of stream microorganisms was constructed largely on the basis of such observations[30].

3) Colonization of submerged leaves by microfauna: pairs of recently fallen, undamaged leaves collected from the dry forest floor were placed in small baskets (wire frame 15 × 5 × 3 cm covered with 1 cm^2 nylon net) and exposed for various periods on the bottom of the stream in places of moderate current. After retrieval one leaf was washed in water and the other in alcohol. The water sample was set up as a small, experimental ecosystem[28] with a few pellets of dried yeast, in order to observe and list the developing microorganisms (Protozoa, Nematoda, Rhabdocoela, Rotifera, Gastrotricha, smallest Oligochaeta, Acari and microcrustacea). The alcohol sample was examined for larger oligochaetes, microcrustacea and insect larvae. Assuming that the leaf was colonized by a single representative only of each fast-breeding morphotype found in the water sample, and adding the number of morphotypes distinguished to the number of individuals counted in the alcohol sample, we arrive at a minimal estimate of the microfauna that occupied a single leaf at the time of the retrieval. This is certainly an underestimate because firstly, we lose some organisms when the basket is lifted out of the water; secondly, some organisms are probably killed when the leaf is washed with the paint brush and thirdly, because it is not possible, for the time being, to distinguish between closely similar species in the lower groups. The data presented in the following are the preliminary results of a long-term project on the decomposition of submerged litter, which started in September 1983.

The macrofauna. 1) A four-year study on the population dynamics of freshwater shrimps in the Rio Tarumãzinho has been completed and will be published shortly[32]. The evaluation is based on monthly collections with hand nets in submerged litter accumulations. A single net sample includes on average roughly 70 g dry weight of litter and fauna that is visible to the naked eye under field conditions; the volume of natural leaf habitat sampled is approximately 8 l/net.

2) The dynamics of litter colonization is studied by exposing collected forest litter (see paragraph 3 above) in 20 × 15 × 6 cm baskets (1 cm^2 nylon mesh) for determined periods in the same places as the small baskets for the collection of the microfauna. The mean dry weight of litter per basket is 20–25 g. After retrieval the leaves are washed in a basin and the visible animals collected by hand and stored in alcohol.

The food web. The food web was constructed on the basis of 529 predator/prey interactions in microorganisms which include 76 distinguishable morphotypes, and on the stomach contents of 670 dissected macroorganisms which include 10 species of litter-dwelling fish[9] and 54 distinguishable morphotypes of macroinvertebrates. Details on shrimp diet are published in Kensley and Walker[13].

Statistical evaluation: If not explicitly mentioned otherwise, differences between comparative results which are discussed in the text are significant ($p < 0.05$ in exceptional cases, generally < 0.01). Tests applied: F-test; t-test and adjusted t-test where variances are different; X^2-test; mean-square-successive-difference-test for nonrandom variation in time[6].

Table 1. Colonization of single, submerged leaves by aquatic invertebrates after diverse periods of exposure. Morphotypes: number of species that can be distinguished with confidence in routine examinations (biased heavily towards underestimation). *Includes Rhabdocoela, Nematoda, Rotifera and Gastrotricha. Ind/leaf: mean total number of individuals per leaf.! The low number of morphotypes is due to the low number of leaves examined so far.

Time of exposure	24–48 h		Two weeks		One month		Two months	
Organisms	Ind. leaf	Morphotypes	Ind. leaf	Morphotypes	Ind. leaf	Morphotypes	Ind. leaf	Morphotypes
Protozoa	1.75	13	1.64	27	2.18	26	1.75	10
Lower Metazoa*	0.95	9	1.41	12	2.81	15	4.58	5
Oligochaeta	0.09	2	1.11	4	1.50	5	4.92	7
Acari	0.06	2	0.60	4	0.19	2	1.05	3
Microcrustacea	0.55	6	5.83	11	6.06	8	7.22	7
Chironomidae	1.47	3	12.57	(6)	6.38	(5)	7.84	(5)
Other insects	0.28	9	2.53	11	1.73	7	0.82	4
Total	5.15	44	25.69	75	20.85	(69)	28.18	41!
% leaves colonized by Chironomidae	75.0		93.3		72.7		84.2	
No leaves/No series	130/4		68/4		55/3		35/2	

III. The litter community and its foodweb

1. Colonization of submerged litter. Already a very superficial examination of the various stream habitats shows that the bulk of the fauna is associated with submerged leaf litter, and this fauna is not necessarily scarce. For instance, four casual samples taken with the hand net below the waterfall of the Ig. da Cachoeira yielded 104 small fishes, 58 shrimps and 7 Odonata larvae[30]; the two highest numbers of shrimps ever collected in a single net sample were 141 and 80[32].

Upon submersion, dead leaves are colonized almost immediately (table 1), and the number of individuals and morphotypes per leaf increases substantially during the following two weeks. From then on the density of individuals remains roughly 20–30 per leaf, but the distribution between the different categories of organisms becomes more equitable; oligochetes increase and chironomids decrease. On the whole, chironomids are the most substantial colonizers; a minimum of 72% of leaves immersed from 1–60 days carries several chironomid larvae. If chironomids were to sting man, the myth of the toxicity of black waters would never have arisen[11]! The values in table 1 do not include the 10–15 macroinvertebrates per 100 leaves, two thirds of which are attributable to a single species of Ephemeroptera. This value is, however, likely to vary considerably with the seasons of enchente and vazante, and this information is still lacking (see also fig. 3).

The microfauna recovered by the sample bottles in the free water is essentially similar to the litter fauna (table 2). It could be shown that the number of morphotypes found

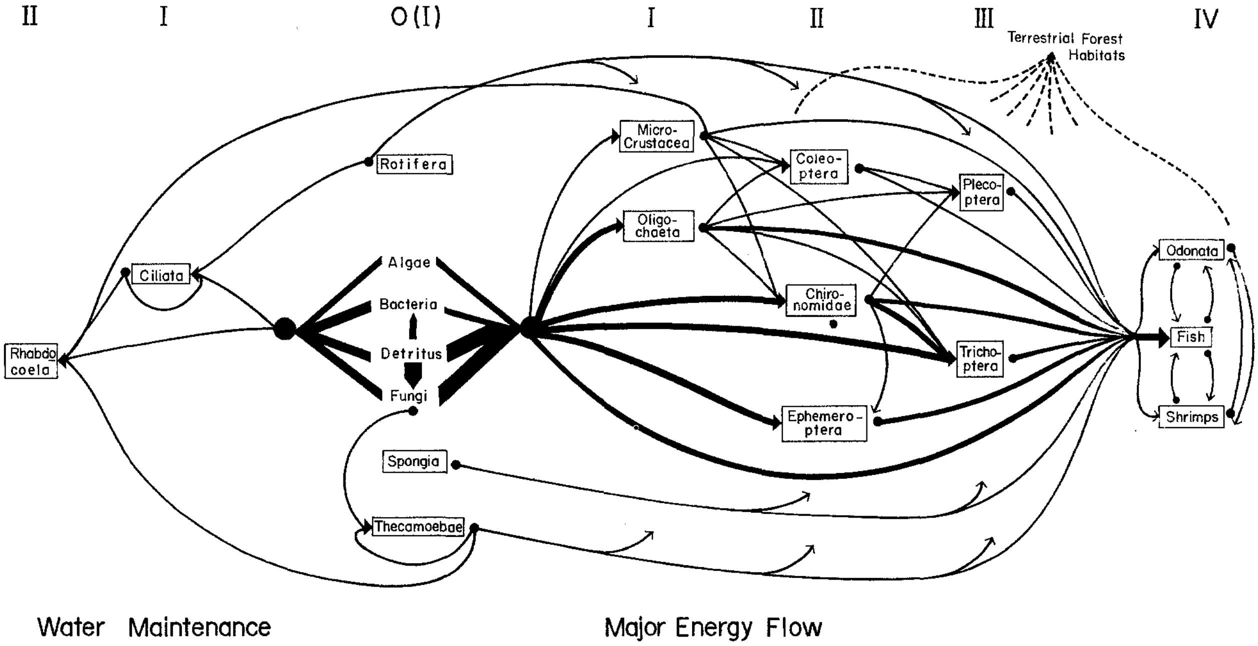

Figure 2. The food web in submerged litter of Central Amazonian forest streams. Arrows lead from prey (round end) to predators and span a single trophic step in the respective food chains. Thick arrows for major biomass flow. 0–IV: trophic stations as determined by longest, common food chains. Further explanation see 'The food web' in Material and methods.

Table 2. Composition of the microfauna recovered from the Ig. da Cachoeira in 4 seasonal collections (June, Oct. 1978 and 1979); number of morphotypes distinguished in a total of 181 sample bottles. Range of frequency in % of samples per collection that contained representatives of the animal group. Numbers in brackets are certain to be underestimates.

Organisms	Number of morphotypes	Range of frequency (%)
Thecamoebae	51	0–77.1
Ciliata	31	6.7–86.2
Other Protozoa (incl. micro-protozoa)	(8)	52.0–94.3
Spongia	2	0–3.4
Rhabdocoela (incl. 1 Planaria)	15	26.5–76.3
Nematoda	(2)	0–22.4
Gastrotricha	3	0–10.3
Rotifera	(10)	10.0–82.9
Naididae	3	0–24.2
Acari	7	3.4–46.7
Microcrustacea	17	48.4–70.7
Chironomidae	(5)	35.0–70.7
Other insects	7	13.8–54.3

per sample varies directly with water flow; intensive flow stirs up the detritus and tears part of the fauna off leaf surfaces[30]. This fact is reflected by the enormous range of frequency in table 2. Note, however, that even in virtually standing water during enchente (June 78 and 79; as shown by the lower limit of the range in table 2) half of the samples contain microcrustaceae and one third chironomids. The richest collection was during vazante in Oct. 79 after heavy rains; a total of 142 morphotypes were recovered in 58 samples exposed for 70 h, with a mean of 14 ± 7 morphotypes per sample. Thus, heavy rains in the region of the headwaters replenish the lower courses of larger streams and rivers with litter, detritus and its fauna and quite generally, distribute the micro-fauna through the igapó during the period of rising waters.

2. *The food web.* It has been amply demonstrated during recent years that forest litter in the streams of the temperate zone is decomposed primarily by fungi[2], and that so-called detritus-feeders ingest these fungi along with dead plant material. The same ecological pattern appears to apply to tropical forest streams, although information is still scarce[10,20]. The fungi concentrate the utilizable nutrients and are therefore far better food than the actual litter. Randomly collected underwater leaves from the Rio Tarumãzinho were cut into 5 mm × 5 mm squares, and it was shown that 80% of these squares were grown over by fungal hyphae[9]. The figures given in table 3, together with the consideration that Chironomidae, Ephemeroptera and Decapoda are prevalent – if not dominating – faunal groups, suggest that fungus feeding might be an ecological key factor in Amazonian black and clear waters[30] and that the entire food web of these systems might depend heavily on it. The observation that leaf area diminishes slowly in underwater decomposition (ref. 24 and our own observations) and yet is colonized intensely, indicates that much of the colonizing fauna subsists on what it scrapes and catches on the surface. This does not mean to say that litter material is not ingested. During the second month of immersion the mesophyll of 45% of the leaves was mined by chironomids and/or oligochaetes and in a further 24.8% the mesophyll was partly removed by unidentified organisms (150 leaves examined). In some leaves the mesophyll was completely gone. However, only 28.9% showed a visible loss of surface area. Thus, the surface, which remains largely intact for long periods, deceives the observer[24]. The nymphs of at least one Ephemeroptera species, and the larvae of several chironomids and Trichoptera, are usually stuffed like sausages with litter tissue and its fungi. According to Cummins[5], one such shredder produces 2–7 mg (wet weight) of feces per day; this is where the substantial quantity of fine stream detritus comes from.

Table 3. Fungus feeding by stream invertebrates. * in some, but certainly not all, cases, fungi may have entered the gut via fungus-feeding prey.

Major Taxa	Number of morphotypes distinguished		Number of individuals observed feeding or with identifiable stomach contents	
	Number observed	Accepted fungi	Number observed	Number with fungi
Ciliata	14	7	∞	28
Thecamoebae	20	18	75	67
Other *Rhizopoda*	?	2	?	4
Rhabdocoela	13	2	∞	10
Rotifera and Gastrotricha	4	2	∞	2
Chironomidae	6	5	36	27
Ephemeroptera	3	2	34	24
Trichoptera	5	4	24	11
Plecoptera	1	1	12	2*
Odonata	14	2	90	2
Hemiptera	5	3	31	3
Coleoptera	7	2	17	3
Decapoda (Shrimps)	6	6	135	72*
Mysidae	1	1	1	1

On the basis of the material listed in Section II a simplified food web was constructed in order to show what appear, so far, to be the major channels of energy transfer (fig.2). A detailed analysis of the food web of the microfauna[30] strongly suggests that the lower invertebrate groups constitute an insignificant input for the higher trophic levels. Bacterial densities are normally very low in acid stream water; the microfauna, therefore, subsists on larger, particulate food, such as fungus spores, diatoms, thecamoebae etc. Still, these organisms can resort to filterfeeding on bacteria, and may thus play a potentially important role in water maintenance in that they clear the water of bacteria in areas of high density, where the occasional cadaver or larger fruits decay.

The major energy input is indubitably the detritus (including litter) with its fungi. All higher organisms resort either directly to this food source or, in the case of obligatory predators, to prey which relies on it; logically so, because animals with longer generations and relatively low fertility, which are not in command of 'Dauerkörper' (cysts, spores, gemmulae, etc.), must have guaranteed resources. In this ecosystem, litter with fungi is the food source that is available at all times and in all places. Another aspect of robustness in this food web is the multiplicity of channels that lead to the higher tropic stations (as determined by the longest, 'normal' food chain, as for instance: Fungi – Oligochaeta – Chironomidae – Trichoptera – Decapoda). All six shrimp species inhabiting the middle courses of the Tarumãzinho and

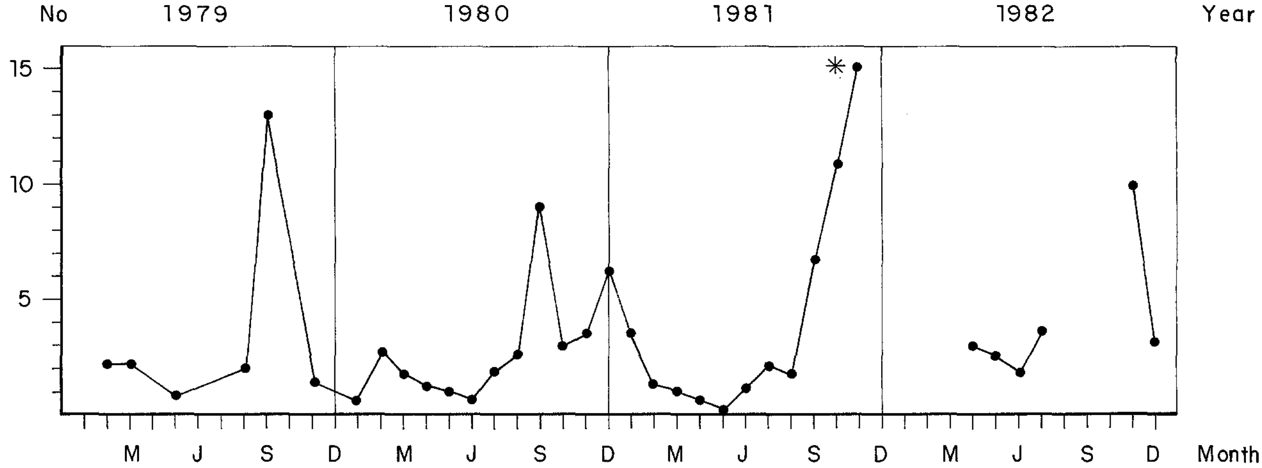

Figure 3. Mean number of shrimps per net sample in monthly collections in a minimum of 5 different litter sites in the river Tarumãzinho. The data refer to a total of 2136 samples and include all species occurring in the river[13,32]. Highest water levels: Mai–June; lowest levels: Sept.–Nov. Asterisk: Nov. 81 refers to a single, large litter bank in a meander.

the Ig. da Cachoeira, for instance, feed on fungi, algae, fruits and flowers, sponges, cladoceres, mites (Acari), midges (Chironomidae), mayflies (Ephemeroptera) and water beetles[13]; litter-dwelling fishes present much the same picture[9]. The theory of 'niches' is in serious trouble here. Diverse food chains with any number of trophic levels are chosen opportunistically by almost all consumer species that have been analyzed so far[16,33].

Figure 2 points to yet another general aspect of this ecosystem; that is, the massive return of nutrients to the land. With the exception of water beetles and some water bugs almost all adult insects return to the land and serve as input for terrestrial food chains, mostly via frogs, birds and bats. Innumerable bird species are fishing, as are some mammals, including river-dwelling man. This continuous output to the land, and the likelihood that nutrients which are degraded to the mineral level, are utilized immediately by the fungi and other microorganisms (small algae, bacteria), and probably also by the root system of the igapó, may explain the somewhat surprising fact that the larger black water rivers have as low a mineral content, or in some cases an even lower one, than their smallest affluents at their sources, despite the substantial input of litter provided by the forest (6–10 t/ha · y dry weight[1,14,15,19], and despite the intensive biological activity that is involved in its decomposition all along the water courses. Thus, the Tarumãzinho in its middle and lower courses showed conductivity values of 5.6 to 9.0 μS_{20}[23,10] whereas the small creeks in the proximity of their sources show values of 8.4 to 17.2[29]; (for exceptional values see ref. 17, and VI. Conclusions). The Rio Negro that collects all these waters, ranges from 7.2–10.4 μS_{20}[26]. In any event the combined data on the food web and on water properties support Sioli's[25] suggestions that the biological overall structure of Amazonian acid streams is relatively stable and that the dangerous factors of instability arise from leakage of nutrients from the system rather than from minor changes in species composition; and further, that the circulation of nutrients is 'to be maintained as closed as possible'.

IV. *Possible effects of the natural water quality on the animal community (table 4)*

1. Shrimps (Decapoda). The first hint that water in Amazonian forests is not just water as far as its fauna is

Table 4. Possible influence of black and crystalline water qualities on the invertebrate stream fauna.

Black water		Mixed water (± black)		Crystalline water	
A) Diversity of microfauna (n = No. morphotypes per sample bottle)					
Ig. da Cachoeira Oct. 1979		Tarumãzinho Sept. 1983			
Samples	$\bar{n} \pm s$	Samples	$\bar{n} \pm s$		
58	13.98 ± 6.92	60	8.75 ± 3.92		
B) Density of shrimps (x = no individuals per litter sample)					
Ig. da Cachoeira, June 1979		Tarumãzinho June 1980–81		Ypiranga, June 1979	
Samples	$\bar{x} \pm s$	Samples	$\bar{x} \pm s$	Samples	$\bar{x} \pm s$
97	3.17 ± 3.15	266	1.27 ± 1.32	45	0.57 ± 0.77
C) Density of Thecamoebae (x = no individuals per 10 min-sample)					
Ig. da Cachoeira, black affluent streams, June 79				Ig. da Cachoeira, crystalline affluent streams, June 79	
Samples	$\bar{x} \pm s$			Samples	$\bar{x} \pm s$
7	38.9 ± 5.3			6	11.6 ± 3.2
				Ypiranga, June 1979	
				5	18.4 ± 7.2
Ig. da Campina 1978–80				Barro Branco 1978–80	
52	52.3 ± 22.0			37	16.8 ± 6.7

concerned, came in June 1979 from the local forest guide who showed our party through the inundation forest to the entrance of the crystalline stream Ypiranga. Upon hearing that I wanted to collect shrimps he replied tartly: 'não tem' (there aren't any), and he suggested I had better go collecting in the Ig. da Cachoeira. He was right (see table 4; the data include all seven species found in the streams mentioned).

2. Thecamoebae. With the explicit idea in mind that differences in the extremely rich and diverse Thecamoebae fauna associated with fine stream detritus might be indicative for natural water quality, and perhaps for evolutionary patterns as well, a systematic study comparing various streams was undertaken between 1977 and 1980[29]. Segregation of the data according to black and crystalline water shows unmistakably higher densities in the former and, incidentally, revealed some qualitative differences as well: the Euglyphidae, for example, are much richer in species in black water. Overall species richness, however, was remarkably similar for similar volumes of collections, namely 64 to 76 morphotypes/stream for the five streams belonging to the basin of the Tarumã. All streams sampled together contribute to a total of 129 distinguishable morphotypes. This figure is indicative of considerable variation between streams.

3. The microfauna. A recent (Sept 1983) collection of the microfauna in the free water of the Tarumãzinho with baited 70-ml bottles, under what appeared to be very similar conditions to those for the October collection four years previously in the Ig. da Cachoeira (interphase between igapó and terra-firme, period of vazante, steep banks, fast flow due to temporarily risen waters as a consequence of heavy rains during the 70-h exposure), arouses the suspicion that the whole litter-dwelling micro-fauna might be affected. The low number of morphotypes in the Tarumãzinho might not be the expression of low densities only (as rarer types are not found in a series of only 60 samples), the collections from individual submerged leaves also give the impression that the Tarumãzinho might be rather poorer in species than the Ig. da Cachoeira. However, this impression needs confirmation by more, strictly comparable data; we have, so far, no collections from single leaves from the Ig. da Cachoeira.

4. The general pattern. Summarizing the general pattern appearing in table 4 we may say that all data point in the same direction, that is that black water is richer in its fauna than crystalline water. This is true at least for mere densities, and possibly also for number of species. At all events the data disprove the suggestion that black water is generally inhibitory to animal development because of toxic substances released by the litter[11]; the very fact that the bulk of the fauna is associated with submerged litter would already be sufficient evidence to the contrary.

V. Enchente and vazante

That annual differences in water levels of 6–12 m affect not only ecosystems alternately laid dry (during vazante) and inundated (igapó during enchente), but the entire aquatic community structure, has been recognized for a long time, and numerous studies have been[10,25], and are being published on diverse biological aspects, notably of the richer, and therefore economically more interesting white-water regions[7]. The most obvious factor is the expansion and contraction of living space. With the rising water level the aquatic fauna disperses into the inundation forest (= igapó). Hence, predators of relatively slow-breeding prey suffer deprivation[21] (this includes man; fish prices rise steeply on the Manaus market during 'enchente'), whereas organisms depending directly on decomposition and on fast-breeding microorganisms have their days of plenty. Irmler[10] in his study of the soil fauna of the igapó in the lower Tarumãzinho found that Ostracoda, Tubificidae and several *Chironomus* species flourished during the months of highest water level (March to June), whereas the ephemeropteran *Brasilocaenis irmleri* was substantially present during the period of rising waters only (Jan. to April), and certain Naididae (Oligochaeta) had their population peaks during the months of fastest reduction of water levels (July to Sept.). Apart from expansion and contraction of the inundated area, the O_2-content of the water and/or depth affected density and distribution of a number of species.

The effect of mere contraction of the area during vazante was brought into evidence by a long-term study on the population dynamics of shrimps in the middle course of the Tarumãzinho[37] (fig. 3). In September the water retreats into the river bed, hence obligatory aquatic organisms are forced to follow suit. For those shrimp species that are abundant in the area, it could be ascertained that they breed predominantly, or even exclusively, during the period of rising waters. This results in relatively small variation of population densities from January to June, despite the continuous expansion of the habitat. The sharp decline during later vazante must be attributed to high death rates, although emigration may also play a role. This suggestion is inferred from a marked seasonal change in species composition. *Euryrhynchus amazoniensis* dominates the scene from March to May; the two *Macrobrachium* species *M. inpa* and *nattereri* from June to July, and *Pseudopalaemon chryseus* from Nov. to Dec.[32] (for species description see ref. 13). All four species, however, are present all year round.

VI. Conclusions

The substantial input of nutrients into Central Amazonian forest streams occurs in the form of litter. The aquatic, biological system, therefore, must be regarded as a decomposition community, and in this, it is akin to the soil fauna of the forest itself. For this reason, several aspects of these biotopes are directly comparable, such as the composition of the decomposing fungal flora and the rate of its growth; rates of disappearance of nutrients from the litter; structure and complexity of the food web and its quantitative, energetic properties. Both biotopes start out with the same input of litter: 6–10 t/ha/y dry weight[1,14,15,19]. According to an estimate from the map in figure 1 the area of water surface is at the very least 600 m^2/km^2. It is the aim of the INPA projects involved in these studies of decomposition to arrive at comparable data in the long run, and by doing this to contribute to the elucidation of nutrient cycling in the overall ecosystem. One striking similarity has already been brought out by this study; just as the nutrients in the terrestrial system remain tied up in organismic, living biomass throughout their recurrent cycles, and therefore do not appear in solution in the water 'excreted' by the forest into its streams, nutrients leaving the decomposing submerged litter never appear in solution in the stream water. They are handed directly from one trophic level to the next and return in considerable quantities to the very forest that provided the litter in the first place. The streams are thus part and parcel of the massive recycling apparatus rather than simply the excretory system of the forest.

Not everything returns, though. The forests of the terra firme and of the lower and higher situated igapó are functionally related. During the period of low water levels, vazante, the forest streams of the higher situated igapó, and of the terra-firme in its vicinity, are the refuge of the aquatic fauna of the inundation forest. This refers also particularly to places of litter accumulations in the larger streams which are no longer covered by the canopy. This litter, and its fauna of microorganisms and insect larvae (above all, chironomids!), are to a substantial degree provided by the terra-firme from where they are swept downstream with each heavy rain. In this way, the terra-firme contributes to the maintenance of the fauna of the igapó. Deforestation of the headwaters of larger streams and rivers deprives the fauna of the igapó of this input.

Further down-river, in the 'river-lakes'[25], before the waters reach the Rio Negro, the fine detritus, produced by the shredders all along the streams and rivers, is compacted into the muddy bottom substratum with its peculiar fauna which supports a variety of water birds during vazante, and allows for some algal growth, and for occasionally dense planktonic populations[8].

That the different forest soils described by Chauvel and Ranzani[4] are responsible for either black or crystalline creeks was proposed by Sioli[24] as early as 1954, and has been fully confirmed by Leenheer's[12] detailed study, which follows the process from the forest floor through the soils into the streams. A superficial consideration offers no explanation for the fauna being richer in black waters. Both types of waters are strongly acid and poor in minerals. And yet, the few data given in table 4 merely confirm what is already common knowledge among the local inhabitants; the Ypiranga is known as poor, the Ig. da Cachoeira as relatively rich, and the Tarumãzinho as rather poor; all this, of course, with regard to fishing.

A closer look at Leenheer's[17] data might nevertheless suggest a possible answer. He found that the black water of the Ig. da Campina contained 34.6 mg/l dissolved organic carbon (DOC), its conductivity was 28 μS_{20} and its pH = 3.75, whereas the respective measurements for the crystal clear stream Barro Branco were 4.7 mg/l, 9.0 μS_{20} and pH = 4.5. Furthermore, the fine detritus from the black stream contained roughly twice as much humic acids as the detritus from the crystalline stream[18]; the two types of detritus also differ visibly in color. For the several streams and rivers analyzed, Leenheer found that, quite generally, ~ 53% of the acidity of black waters was attributable to humic solutes ~ 85% to humic solutes plus colorless organic acids, and only ~ 15% to dissolved CO_2. If we add the data for the Tarumãzinho, namely 5.4 mg/l dissolved humic substances (not DOC), pH = 4.7 and a conductivity of 5.6 μS_{20}[23] to 9 μS_{20}[10], the pattern that suggests itself is that a substantial content of humic solutes is associated with specially low pH, with higher conductivity and with richer animal biomass. It is conceivable that these water qualities intensify the growth of fungi and thus increase the primary input into the respective food webs. Obviously, the information at hand so far raises more questions than it answers, but then, arriving at clear questions is more than just a beginning. This is certainly true for the complex Amazonian forest ecosystems.

Acknowledgment. The projects reported on in this study were supported jointly by the CNPq (Brasilian Research Council), the OAS (Organization of the American States) and by the SUFRAMA (the local governmental financing body).

1 Adis, J., Furch, K., and Irmler, U., Litter production of a Central Amazonian black water inundation forest. Trop. Ecol. *20* (1979) 236–245.

2 Baerlocher, F., and Kendrick, B., Role of aquatic Hyphomycetes in the trophic structure of streams, in: The Fungal Community. Eds D.T. Wicklow and G.C. Carroll. Marcel Dekker, New York 1981.

3 Benchimol, S., Amazônia, um pouco-antes e além-depois. Editora Umberto Calderaro, Manaus 1977.

4 Chauvel, A., Lucas, Y., and Boulet, R., On the genesis of the soil mantle of the region of Manaus, Central Amazonia, Brazil. Experientia *43* (1987) 234–241.

5 Cummins, K.W., Structure and function of stream ecosystems. Bioscience *24* (1974) 631–641.

6 Documenta Geigy, Wissenschaftliche Tabellen. Basel 1963.

7 Fittkau, E.J., Irmler, U., Junk, W.J., Reiss, F., and Schmidt, G.W., Productivity, biomass and population dynamics in Amazonian water bodies, in: Tropical Ecologial Systems. Eds F.B. Golley and E. Medina. Springer, Heidelberg/New York 1975.

8 Hardy, E.R., Composição do Zooplacton em cinco lagos da Amazônia Central. Acta amazon. *10* (1980) 577–610.

9 Henderson, P.A., and Walker, I., On the leaf litter community of the amazonian black water stream Tarumãzinho. J. trop. Ecol. *2* (1986) 1–17.

10 Irmler, U., Ecological studies of the aquatic soil invertebrates in three inundation forests of Central Amazônia. Amazoniana *5* (1975) 339–406.

11 Janzen, D.H., Tropical black water rivers; animals and mast fruiting by the Dipterocarpaceae. Biotropica *6* (1974) 69–103.

12 Junk, W.J., As águas da região Amazônica, in: Amazonia, Desenvolvimento, Integração, Ecologia, Eds E. Salati, H.O.R. Schubart and W. Junk. CNPq editora brasiliense 1983.

13 Kensley, B., and Walker, I., Palaemonid shrimps from the Amazon Basin, Brasil (Crustacea: Decapoda: Natantia). Smithsonian Contributions to Zoology *362* (1982) 1–28.

14 Klinge, H., Fine litter production and nutrient return to the soil in three natural forest stands of Eastern Amazônia. Geol. Trop. *1* (1977) 159–167.

15 Klinge, H., and Rodrigues, W., Litter production in an area of Amazonian terra firme forest. Part 1: litter fall, organic Carbon and total nitrogen contents of litter. Amazoniana *1* (1968) 287–302.

16 Knöppel, H.A., Food of Central Amazonian fishes. Contribution to the nutrient ecology of Amazonian rain forest streams. Amazoniana *2* (1970) 257–352.

17 Leenheer, J.A., Origin and nature of humic substances in the waters of the Amazon River Basin. Acta amazon. *10* (1980) 513–526.

18 Leenheer, J.A., Personal communication based on the analyses of the data cited above.

19 Luizão, F.J., Produção e decomposição da liteira em floresta de terra firme da Amazonia Central. Aspectos químicos e biológicos da lixiviação e remoção dos nutrientes da liteira. Tese de Mestrado. INPA/FUA, Manaus 1982.

20 Padgett, D.Ee., Leaf decomposition by fungi in a tropical rain forest stream. Biotropica *8* (1976) 166–178.

21 Petrere, M.Jr, Pesca e esforço de pesca no Estado do Amazonas, Tese de mestrado. INPA/FUA, Manaus 1977.

22 Rai, H., and Hill, G., Classification of Central Amazon lakes on the basis of their microbiological and physicochemical characteristics. Hydrobiologia *72* (1980) 85–99.

23 Schmidt, G.W., Chemical properties of some waters in the tropical rain forest region of Central Amazônia. Amazoniana *3* (1972) 199–207.

24 Sioli, H., Gewässerchemie und Vorgänge in den Böden im Amazonasgebiet. Naturwissenschaften *41* (1954) 456–457.

25 Sioli, H., Tropical rivers: the Amazon, in: River Ecology. Ed. B.A. Whitton. University of California Press, Berkeley and Los Angeles 1975.

26 Ungemach, H., Die Ionenfracht des Rio Negro, Staat Amazonas, Brasilien. Amazoniana *3* (1972) 175–185.

27 Ungemach, H., Regenwasseranalysen aus Zentralamazonien, ausgeführt in Manaus, Amazonas, Brasilien. Amazoniana *3* (1972) 186–198.

28 Walker, I., Rede de alimentação de invertebrados das águas pretas do sistema Rio Negro. 1. Observações sobre a predação de uma ameba do tipo *Amoeba discoides*. Acta amazon. *8* (1978) 423–438.

29 Walker, I., The Thecamoebae (Protozoa, Rhizopoda) of small Amazonian forest streams and their possible use as indicator organisms for water quality. Acta amazon. *12* (1982) 79–105.

30 Walker, I., On the structure and ecology of the micro-fauna in the Central Amazonian forest stream "Igarapé da Cachoeira". Hydrobiologia *122* (1985) 137–152.

31 Walker, I., and Lages, M.T., Adaptation of constant-effort sampling and of removal trapping for the estimation of microscopic organisms in dense substrates. Acta amazon. *10* (1980) 535–544.

32 Walker, I., and Ferreira, M.J.N., On the population dynamics and ecology of the shrimp species (Crustacea, Decapoda, Natantia) in the Central Amazonian river Tarumãzinho. Oecologia *66* (1985) 264–270.

33 Walker, I., and Franken, W., Ecossistemas frágeis: a floresta da terra firme da Amazônia Central. Ciênc. Interam. *23* (1983) 9–21.

0014-4754/87/0279-10$1.50 + 0.20/0

Conclusion. The forest as a functional entity

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The subjects of the seven articles are tightly interrelated by a straight sequence of causes and effects as well as by multiple cross-links.

Leopoldo et al. analyze the water cycle as a result of large scale geography on the one hand and of evapotranspiration on the other. Their table 7 leaves no doubt that 50–75% of precipitation is recycled more-or-less on the spot by the forest itself. This water balance, by the way, does not yet include the nightly dew formation which is a regular and marked feature of the Amazonian forest, notably also during the dry season (personal observations). In fact, dew produced by the swamp (stream valleys) and inundation forests may well balance, in part, the water deficit in the terra-firme forest of the plateau, established for the months of August to November by Ribeiro and Villa Nova[10]. The results of the water budget give strong support to the ever growing conviction that large areas of arid lands on this globe are man-made. The second, important aspect of this article is nutrient cycling. A considerable fraction of the scarce, but vital elements in exchangeable form, such as Ca, P, K, Mg (Klinge 1976 and Chauvel 1981 in Luizão and Schubart) are cycled via biological activity in the canopy and via leaf drip, for example by the activities of the monkey populations and their insect prey, dealt with in Rylands' article.

Chauvel et al. explain the transformation of the tertiary barreira sediments (sandstone interlaced with clay) into today's soils as a function of vertical and horizontal pedogenetic processes which are influenced by the infratopography and by the chemistry of decomposition under the forest canopy. Vertical dissolution of quartz and neoformation of kaolinite led to the heavy clay soils that dominate the plateau today and is responsible for the high silica content of Amazonian waters, whereas lateral disintegration and loss of clay particles over the shoulders of stream valleys leads to the transition to sandy podzols. The resulting mosaic of soil types gives rise to the mosaic of different streams mentioned in Walker's article: black water from podzols and crystal clear water from heavy latosols. The horizontal processes in particular imply that stream valley formation (sagging of the shoulders!) is largely the result of internal, quasi chemical erosion which leaves the soil surface and the vegetation cover intact. This interpretation agrees with data on soil hydrology[7,8] and on variation of stream discharge in relation to the magnitude of precipitation[3], which show that runoff is minimal and that streams swell essentially by percolation of the water through the soil; there is virtually no mechanical soil erosion despite the fact that approximately 70% of precipitation falls in the form of heavy rains (Leopoldo et al. article). The water of forest streams remains essentially clear and transparent during and after heavy rains, whereas streams in deforested, urbanized areas (for instance in Manaus) carry white water, i.e. water with a heavy load of suspended sediments. This observation makes one wonder how much of the Amazonian white water carried by the large white-water rivers (Amazonas, Rio Madeira, etc.), might be of man-made origin, perhaps in ancient times.

Guillaumet's comprehensive review shows evidence that local topography and soil types determine very different tree communities with surprisingly little species overlap: the high terra-firme (sensu stricto) forest on the latosols of the plateau, the open campina on the sandy podzols, the campinarana on the transition zone between the two and the swamp forest of the stream valley bottoms. The rich epiphyte flora with the tree orchids that Europeans know from their flower shops is characteristic of the sparse, open canopy of the campina, a forest formation which is of no immediate economic use. The campinas, therefore, need special protection. As it is not determined