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STUDY OF BENTHIC MICRO-FAUNAL COLONIZATION OF SUBMERGED LITTER LEAVES IN THE CENTRAL AMAZONIAN BLACKWATER STREAM TARUMÃ-MIRIM (TARUMANZINHO)

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RESUMO - ESTUDO SOBRE A COLONIZAÇÃO DA LITEIRA SUBMERSA PELA MICRO-FAUNA BÊNTICA NO RIO TARUMÃ-MIRIM (AMAZÔNIA CENTRAL)

Estudou-se a colonização de folhas individuais da serrapilheira do igapó pelos pequenos invertebrados bênticos. Séries de 12 folhas cada foram expostas no fundo do rio durante diversos períodos experimentais (de 1 dia até 4 meses) nos períodos de enchente (Janeiro-Maio) dos anos 1984-1986. Após um tempo inicial de ocupação (1-2 semanas), a composição faunística (% morfoespécies em dados grupos taxonômicos por série) e o número de morfoespécies por folha, permaneceram estáveis. No entanto, o número de morfoespecies por série, e por isso a diversidade entre as folhas individuais, aumentaram com o tempo de submersão. Características de sucessão foram identificadas, tais como: 1. aumento de diversidade faunística; 2. aumento relativo e absoluto de oligoquetos por folha; 3. a partir do segundo mês, mineração da mesófila das folhas por quironomídeos e oligoquetas (não diminuindo, porém, a superfície foliar), causando a destruição de 10-40% da mesófila por série no 3º e 4º mês.

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Estimou-se o estoque da biomassa fresca da microfauna bentica em 250 mg/m^2, e a densidade de organismos (com exceção dos protozoários) em 11.000-40.000/m^2. A densidade média de quironomídeos foi de 21/folha e de 8316/m^2. Nota-se o tamanho excessivamente pequeno dos quironomídeos (Tab. 8).

ABSTRACT - STUDY OF BENTHIC MICRO-FAUNAL COLONIZATION OF SUBMERGED LITTER LEAVES IN THE CENTRAL AMAZONIAN BLACKWATER STREAM TARUMÃ-MIRIM

Colonization by the small benthic invertebrates of individual leaves of leaf litter submerged in an igapo was studied. Series of 12 leaves each were exposed at the bottom of the river for different experimental periods (1 day to 4 months) during flood season (January-May) in 1984-1986. After an initial occupation time (1-2 weeks), the faunistic composition (% morphotypes in certain taxonomic groups per series) and the number of morphotypes per leaf appeared stable. However, the number of morphotypes per series, and therefore the diversity between individual leaves, increased with submersion time. Such criteria of succession were identified as: 1. increased faunistic diversity; 2. relative and absolute increase of oligochetes per leaf; 3. after the second month, mineralization of leaf mesophyll by chironomids and oligochetes (however without reduction of leaf suface), causing destruction of 10-40% of the mesophyll per series in the 3rd and 4th months.

Fresh biomass stock of benthic microfauna was estimated at 250 mg/m^2, and density of organisms (excluding protozoans) at 11.000-40.000/m^2. Mean density of chironomids was 21/leaf and 8316/m^2. The extremely small size of chironomids was noted (Tab. 8).

INTRODUCTION

In recent years it has become increasingly clear that the fauna in acid forest streams and rivers is largely dependent on underwater decomposition of tree litter, mainly of dead leaves. The consumers on the lowest trophic level feed on the decomposing tissues with their fungal and bacterial flora (CUMMINS et al., 1973; SAUNDERS, 1975). FITTKAU (1967) and SIOLI (1975) observe similar conditions in amazonian water bodies. Thereby fungi seem to be the principle decomposers in acid waters (BÄRLOCHER and KENDRICK, 1981; ROSSET et al., 1982; ROSSET and BÄRLOCHER, 1985), and WALKER (1986) presents some evidence that fungal decomposition of litter leaves from the amazonian blackwater inundation forest causes, and stabilizes, acid pH- values in experimental containers. Certain is that decomposing litter leaves from acid water of amazonian streams and inundation forests are invariable overgrown by fungal hyphae; fungi also spread through the mesophyll (personal observations). The importance of the litter-fungi input for the foodweb of the microfauna and of the macrofauna of central amazonian forest streams wasshown by WALKER (1985) and by HENDERSON and WALKER (1986).

It thus became imperative to know more about the colonization of submerged litter by the riverine fauna. Systematic sampling began in 1983 and is continuing to the present, and some earlier results were communicated in the previous volume of this journal (WALKER, 1986).

As from 1984 some special sample series were designed to detect possible patterns of succession. In this place I report the data on the microfauna colonizing single leaves in these succession series.

MATERIAL AND METHODS

Locality: The river "Tarumã-Mirim" or "Tarumãnzinho"

is a small affluent of the Rio Negro ca 25 km up-river from Manaus. It drains heavy latossols and sandy podsols and carries more or less black, acid (pH: 3.5-4.7) and mineral-poor (electric conductivity: 10-14 μS_{20}/cm) water. All sampling (with the exception of a single series) was done in a meander ca 25 km upstream, with quiet flow as it is short- cut by a more recent canal with more rapid flow. There was no pollution as there are only two small subsistence farms further upstream. The meander is flanked by a wide and deep layer of forest litter, and the bottom of the canal, too, is covered by litter. The locality is described in detail as "site" in HENDERSON and WALKER (1986). The exceptional series was collected ca 500 m upstream (April, 1984, 1 month exposed) and substitutes a lost series in the meander site. The whole area lies in the region of the "igapó", that is, in the annually inundated forest with a well developed forest canopy. All sampling was done between January and May during rising waters, in the years 1984 to 1986.

Sampling method: Undamaged (less than 1% surface loss) litter leaves selected from the forest floor before inundation or, at high water level, in adjacent areas not inundated, were placed in wire baskets and exposed in the river for determined periods (Table 1). The baskets were set out in series of 12 along both sides of the meander at a distance of 2-5 m between baskets. They were placed on the bottom of the river and tied to tress flanking the canal. Water depth over the baskets ranged from 0.4-1.5 m in January, rising to ca 4.0-5.5 m in May, when the adjacent forest was covered by 3.5-4.0 m of water. The river bed and its smooth flank on the inside of the meander were covered by litter, and baskets exposed for longer periods than 2 weeks were often covered by newly deposited litter leaves when retrieved. The baskets (15 x 5 x 3.5 cm) were covered with nylon netting (1 cm^2 mesh) and contained 2 leaves each. Upon collection they were carefully lifted off the ground

and, supported by a hand net, lifted slowly out of the water, so as to loose the minimum of the adhering organisms. One leaf was then cut into 4 pieces and placed into a 250 ml bottle ca 1/2 filled with water from the collection site (henceforth called "water samples"). The other leaf was washed with a paint brush in 100% alcohol, and the lead wash of each leaf, separately, was stored for later examination (= "alcohol samples"). Later, in 1986, it was found to be more convenient to remove the two sample leaves from larger (20 x 45 x 6 cm) baskets with 20 leaves each, which served to sample the macrofauna and to determine the frequency of leaves mined by chironomids and oligochetes (Table 7). Estimates of surface loss and of mesophyll removed by miners in these 20 leaves were made in the field by naked eye, making use of the leaves' vascular system. One arrives thus at a precision of intervals of ca 10 ± 5%. This would still give the better results than prolonged and repeated handling of the brittle leaves for metrical assessment in the laboratory. Even after 4 months, the longest exposure time, the surface of most leaves was still intact. Collection of the microfauna of the two sample leaves presented thus no difficulty.

The water samples were kept in the laboratory at room temperature (23-26°C) for one month in order to breed the smaller organisms (Protozoa, Rhabdocoela, Rotifera, Gastrotricha, Oligochaeta, especially small Naididae, Acari and micro- Crustacea) up to appreciable numbers, so that their presence could be detected under a low power stereo-microscope (magnification: 30 x). Where necessary, types were ascertained under high power (160-400 x). Each morphotype listed counted for a single individual that had colonized that particular leaf. In the alcohol samples the larger organisms (Nematoda, larger Oligochaeta, insect larvae and adults) were typed and counted. Thus, from each such pair of leaves (water sample and alcohol sample of a single basket) we can estimate the number of morphotypes and a minimal

Table 1 - General pattern of colonisation. Mean values ($\bar{x} \pm s$) of n series. * single series with mean between 10 ± 2 leaves. ! extrapolated for 10 leaves per series.

Time exposed	n = 2 number series	Individuals per leaf $\bar{x}$ ± s		Types per leaf $\bar{x}$ ± s		Total types per series! $\bar{x}$ ± s
1 day	7	14.5	6.4	8.4	2.4	46.4
2 days	2	20.0	12.4	7.7	2.6	45.0
1 week	1*	55.8	-	11.1	4.9	67.0
2 weeks	2	61.9	35.8	15.4	0.6	66.0
1 month	4	38.4	18.4	13.0	1.8	63.5
2 months	2	28.4	1.1	12.1	1.7	62.0
3 months	1*	27.8	-	15.7	3.9	80.0
4 months	1*	49.7	-	13.6	5.9	78.0

number of individuals per single leaf.

Litter leaves: Naturally shed, undamaged leaves, which still exhibited a leathery, flexible consistency, were chosen. They were collected 2-20 h before exposure in the river. Care was taken to pick a series reasonably representative for the tree species in the area. The sample leaves include members of the following families: Leguminosae, Melastomataceae Lecithidaceae, Rubiaceae, Myrtaceae, Lauraceae, Malpighiaceae, Combretaceae among others, not yet identified. The mean surface area per randomly chosen, single leaf was 62.2 ± 24.7 cm^2 (n = 58, range = 24 - 125 cm^2); this corresponds to a mean dry weight of 0.87 ± 0.55 g/leaf (n = 60).

Recognition of morphotypes: All samples were examined, and all types were determined, by the author. After the several years that the program is in operation (WALKER, 1982, 1985) certain types of all groups are well recognized to generic, if not to species level, small adult insects (corixids, beetles) and later larval stages of larger insects probably to species level; youngest nymphs at best to family level unless the successive stages were known. The mostly extremely small chironomid larvae (FITTKAU, 1967; Table 8 in this paper), though, enter as only 8 types, and the number of morphotypes in the rotifers is certainly much below the number of real species. Protozoa below a diameter of ca 0.04 mm were classified as a single type (micro-Protozoa). Care was taken to judge doubtful cases with a bias towards underestimation. Some material is also lost when the baskets are collected and when the leaves are washed in alcohol with a brush. These reasons, and the fact that each morphotype recognized in the water samples counts for a single colonizer only, whilst these organisms are often breeding on the leaves, lead to an underestimate of the number of individuals per leaf as well. In short, the load of individuals and of morphotypes per leaf must be taken as minimal estimates. This is important for the consideration of biomass per area.

Evaluation of number morphotypes per series: Series of 12 samples were made rather than of 10 because of certain losses. Not all baskets were recovered at all times. In only two cases less than 10 baskets were found: 4- months - series, May 1986, 8 baskets; 2- months - series, April 1984, 9 baskets (the dates refer to retrieval, not to exposure). The number of morphotypes per series in the Tables is always calculated per 10 samples (i.e. 10 leaves). In case of 11-12 baskets, the new morphotypes appearing after the 10th sample were simply neglected. In the cases of 8-9 baskets, the mean number of new types appearing between the last 3 consecutively analysed samples was added per one sample missing.

Controls: Two types of controls were carried out: 1. Water controls: To find the morphotypes that entered the water samples with the river water, 10 bottles were set up, each with river water and with 4 quarter pieces of different leaf species that had been sterilized in boiling water. 2. Leaf controls: Litter leaves might carry small organisms or their propagules when picked up from the forest floor. Hence, 12 bottles were set up with heat- sterilized (40 min at boiling point in a water bath) Tarumãnzinho water and with one litter leaf each from the usual collection site.

After 1 month of incubation these control series were examined in the same way as the experimental water samples.

RESULTS

General pattern of colonization (Table 1)

After 1 - 2 weeks a certain maximum of individuals and morphotypes per leaf seems to be reached. The later decline should not be regarded as characteristic for a succession process; the 1- week series and one of the 2- week series are from the year 1985, when, for unknown reasons,

colonization was exceptionally intense. Between the first and the second day there is little increase in animal numbers and none in morphotypes. This indicates that the organisms are on the move: the rate of settling is roughly equal to the rate of quitting. After one week, though, leaves seem to become attractive, more organisms settle than leave, and after one month a certain equilibrium seems to be established; both, the number of individuals and of morphotypes stabilize. This means that the single leaf as a niche in this ecosystem is filled. Either newcomers cannot settle or the same number that settles, leaves. At this stage individual density is (0.5-1) individual/cm^2 of leaf tissue, and this is, it should be remembered (p.629), a minimal estimate. Species diversity per series, however, still increases. Significantly more types are recovered per series after 3-4 months than after 1-2 months ($P < 0.05$; X^2-test). Hence, diversity between leaves increases, while the pattern per single leaf remains roughly unaltered (for instance two leaves that loose a same morphotype are recolonized by two different morphotypes etc.).

Controls: In the water controls 9/10 bottles contained micro-protozoa; one bottle each was colonized by a single type of rotifer (Euchlanidae?), by a peritrich ciliate (Vorticella?) and by a micro- crustacean (Chydoridae). These 4 types make up 5-10% of the morphotypes per experimental series. We may thus safely conclude that the bulk of the types recovered had actually colonized the exposed leaf, or, at least, was attached to the leaf when it was lifted out of the water.

In the leaf controls 11 samples (92%) developed micro- protozoa; 9 (75%) contained one type of rotifer and 8 (67%) another type; one bottle contained a nematode and another bottle a third type of rotifer. All of these types were occasionally found to be frequent in the experimental samples. As the annual inundations cover the forest floor regularly, the 4 species are considered true colonizers

which survive the dry period in some form of egg or cyst.

Community structure

Table 2 shows that on the level of higher systematic taxa the composition of morphotypes remains surprizingly constant. This faunal stability is also evident from the low values of the variance (s^2) between series of equal exposure time. As a rule $s^2 \leq \bar{x}$, which means that, in the three years of sampling, variation was rather less than random. The only indication of true succession is the increase of the percent oligochetes with increased exposure time. This trend is confirmed in Table 3; the number of oligochete types per series increases as well. Most other groups increase their number of types during the first 2 weeks only, from then on they vary little and inconsitently, although most have their maxima after 3 or 4 months, which results in the significant increase of morphotypes shown for Table 1.

While the qualitative composition of the fauna is relatively stable, the frequency of occupation may vary greatly (Table 4). The variance (s^2) is in most cases considerably larger than the mean number of leaves occupied ($\bar{x}$); hence, a group that was found to be frequent at one time may be rare at another. Only the oligochetes and the nematodes spread out slowly and consistently with exposure time. This is not necessarily due to slow movement, most naidids, for instance, are rather better swimmers than the chironomids. With the exception of the Acari, the Gastrotricha and of some insect orders, all groups are invariably frequent. (The only rare organisms were the Tardigrada, they occurred once and are mentioned in Table 3). Most Trichoptera, Ephemeroptera and Odonata appeared inearly developmental stages. The Odonata were all Libellulidae and hence, obligatory predators. Obviously, they habe both, food and shelter in the habitat of submerged litter. (The larger stages are collected by other methods and are categorized

Table 2 - Composition of morphotypes in mean % ($\bar{x} \pm s$) per series. n = number series. In general $s^2 \leq \bar{x}$.
! this series is from the year 1985 with exceptionally high population numbers; see Table 5.

Group \ Exposure time	1 day n= 7		2 days n= 2		1 week n= 1	2 weeks n= 2		1 month n= 4		2 months n= 2		3 months n= 1	4 months n= 1
	$\bar{x}$	± s	$\bar{x}$	± s	x	$\bar{x}$	± s	$\bar{x}$	± s	$\bar{x}$	± s	x	x
Protozoa	39.0	4.2	35.2	8.8	22.9	33.3	2.5	29.6	5.3	23.5	1.8	31.3	19.1
Rhabdocoela	12.0	3.4	12.4	3.6	10.0	12.9	5.6	10.3	2.9	11.9	1.2	8.8	14.7
Nematoda	2.5	1.7	3.5	0.5	1.4	1.5	0	2.4	0.7	3.1	0.9	1.3	1.5
Rotifera	16.2	6.4	12.6	0.6	8.6	15.1	4.4	19.4	3.9	12.8	1.9	16.3	22.1
Gastrotricha	5.0	2.7	1.5	1.5	1.4	3.7	2.2	3.6	2.1	5.3	1.3	5.0	4.4
Oligochaeta	2.5	1.8	2.2	2.2	2.9	5.3	0.8	6.4	1.3	7.9	1.2	8.9	7.4
Acari	2.8	1.4	2.2	2.2	5.7	6.9	3.9	3.6	1 3	6.5	2.5	5.0	5.9
Micro-crustacea	11.6	4.0	14.8	2.8	14.3	15.2	3.3	13.6	3.9	16.5	3.5	16.3	20.6
Insecta	8.8	2.7	15.6	3.6	28.6!	6.9	2.4	10.0	3.2	13.1	2.5	11.4	6.0

Table 3 - Mean number of recognized morphotypes per series. n = number series. * includes one species of Tardigrada.

Exposure time / Organisms	1 day n= 7	2 days n= 2	1 week n= 1	2 weeks n= 2	1 month n= 4	2 months n= 2	3 months n= 1	4 months n= 1	Total in Σn= 20 series
Protozoa	18	14.5	16	22.0	18.8	16.0	25	13	46
Rhabdocoela	5.3	5.0	7	8.5	6.5	7.0	7	10	25
Nematoda	1.1	-	1	1.0	1.5	2.0	1	1	4
Rotifera	8.6	6.0	6	10.0	12.3	8.0	13	15	30
Gastrotricha	2.6	1.0	1	2.5	2.2	3.0	4	3	8
Oligochaeta	1.1	1.5	2	3.5	4.0	4.5	7	5	9
Acari	1.0	1.5	4	4.5	* 3.2	3.5	4	4	12
Micro-crustacea	4.7	7.5	10	10.0	8.5	10.5	13	14	23
Insecta	4.0	8.0	20	4.0	6.5	7.5	9	4	39

Table 4 - Percent leaves occupied by systematic group as mean ($\bar{x} \pm s$) of n series of 10-12 leaves each. ! 8 leaves only. In general $s^2 > \bar{x}$.

Exposure time / Organisms	1 day n= 7 $\bar{x} \pm s$		2 days n= 2 $\bar{x} \pm s$		1 week n= 1 x	2 weeks n= 2 $\bar{x} \pm s$		1 month n= 4 $\bar{x} \pm s$		2 months n= 2 $\bar{x} \pm s$		3 months n= 1 x	4 months ! n= 1 x
Protozoa	96.2	6.3	100.0	0	80	95.0	5.0	95.4	4.6	88.5	11.5	100	87.5
Rhabdocoela	59.3	21.2	75.8	15.8	70	85.0	15.0	93.3	7.1	83.0	17.0	100	100.0
Nematoda	26.7	14.4	21.7	11.7	40	40.0	30.0	48.3	15.4	52.8	1.6	63.7	57.1
Rotifera	84.1	13.6	72.5	2.5	70	100.0	0	90.8	9.3	67.5	23.5	100	87.5
Gastrotricha	42.4	22.0	20.8	20.8	10	45.0	25.0	43.0	25.6	35.7	8.4	54.5	37.5
Oligochaeta	15.2	14.4	16.7	16.7	20	55.0	25.0	73.8	18.8	59.3	13.8	100	85.7
Acari	21.4	15.9	12.5	12.5	40	50.0	30.0	39.3	8.1	19.6	1.4	36.4	62.5
Micro-crustacea	56.7	20.4	70.0	30.0	100	80.0	20.0	77.0	14.3	89.5	1.5	81.8	100.0
Chironomidae	74.5	28.4	75.8	15.8	100	100.0	0	97.7	4.0	92.0	8.0	81.8	100.0
Trichoptera	1.6	3.9	21.7	11.7	30	35.0	15.0	9.2	5.9	20.1	1.9	-	12.5
Ephemeroptera	31.1	24.0	25.0	25.0	60	15.0	15.0	43.3	24.8	29.1	10.9	54.5	57.1
Odonata	6.0	7.4	4.2	4.2	50	25.0	25.0	7.5	8.3	-	-	9.1	14.3
Other insects	10.2	14.6	9.2	0.8	20	-	-	14.6	11.4	4.6	4.6	-	-

as "macrofauna"; these data are not presented in this paper).

Sources of variation

Variation between years (Table 5): For unknown reasons the frequency of individuals may vary considerably between years. While the number of morphotypes per leaf remains roughly constant after an initial period of colonization (see also Table 1), all series in 1985 show exceptionally high population numbers, particularly the chironomids.

Opportunistic colonization: The initial colonization process is obviously a function of the actual abundance of organisms in the area. The leaves exposed in 1985 for 24-48 hours are colonized by more individuals of more morphotypes (Tab. 5). Specific opportunistic behaviour is shown in Table 6 for the Gastrotricha, the Ephemeroptera and the microcrustacea: what happens to be frequent at the time (1-month series) is colonizing more intensely (1- day series). The opportunistic effect of colonization may either mask or simulate patterns of succession in studies with insufficient data.

Water level: Water level, surprizingly, seems to have no effect on abundance and composition of the microfauna in the litter habitat (Table 6). On March 19th water depth over the baskets was 1.4-1.6 m, the 1- month series was exposed in February in ca 0.5 m depth. Until May 15th the water rose to 3.3-5.0 m; the 1- and 4- months series were exposed into 1.5 m depth. Yet, there is no difference between the data of the two periods. From April to August the water is virtually stagnating in this area, there is no perceivable surface flow. Yet, oxygen does not seem to be a limiting factor. TUNDISI et al (1984) showed that, in a central amazonian blackwater lake, Lago Cristalino, nocturnal mixing reaches into a depth of 3-4 m. This process, and the steady influx from the cooler streams draining the adjacent

Table 5 - Variation between years. Exposure time: d = day(s), w = week(s), m = month. * calculated for 10 leaves per series.

Year 1984					Year 1985				
Exposure time; retrieval date	Chiro-nomids per leaf	Total individuals per leaf	Types per leaf	Types per series*	Chiro-nomids per leaf	Total individuals per leaf	Types per leaf	Types per series*	Exposure time; retrieval date
1 d 16.III. 18.V.	0.9	6.7	5.7	28 ± 7.0	13.1	22.2	8.8	46.5 ± 3.5	13.III. 17.IV. 1 d
2 d 16.III.	1.7	7.6	5.1	25	14.7	32.4	10.3	60	14.III. 2 d
1 w -	-	-	-	-	14.3	55.8	11.1	70	20.III. 1 w
2 w 11.IV.	7.6	26.1	14.8	67	64.4	97.6	16.0	65	26.III. 2 w
1 m 25.IV.	13.2	26.3	13.6	67	49.9	69.2	13.6	61	16.IV. 1 m

Table 6 - Opportunistic colonization and true succession; single series of 1986 only. % T = percent morphotypes; L.C. = number of leaves colonized per 10 leaves; * opportunistic pattern. Succession: + = increase, - = decrease and 0 = no consistent trend of colonization; (+) = doubtful pattern.

Organisms	18. and 19.III retrieved						14. and 15.V retrieved				Succession	
	1 day		1 month		4 months		1 month		1 day			
	% T	L.C.	% T	L.C.	% T	L.C.	% T	L.C.	% T	L.C.	% T	L.C.
Protozoa	38.6	9	21.7	9	19.1	9	34.4	10	39.2	10	-	0
Rhabdocoela	11.4	5	6.7	8	14.7	10	9.4	10	11.8	7	0	(+)
Nematoda	2.3	3	1.7	7	1.5	6	3.1	4	3.9	2	0	(+)
Rotifera	18.2	9	23.3	8	22.1	9	21.9	10	23.5	9	0	0
Gastrotricha	4.5	2	5.0	5	4.4	4	6.3	*9	9.8	*6	0	0
Oligochaeta	4.5	3	6.7	9	7.4	9	4.7	6	0	0	+	+
Acari	2.3	3	5.0	5	5.9	6	1.6	3	0	0	+	+
Micro-crustacea	11.4	*7	10.0	*7	20.6	10	14.1	6	5.9	4	(+)	(+)
Ephemeroptera	4.5	*6	6.7	*8	1.5	6	1.6	1	3.9	2	0	0

terra firme, seem to allow for non- limiting oxygen levels.

Colonization by Chironomidae and Oligochaeta (Table 7)

Chironomids and oligochetes are of special interest for several reasons. Firstly, they consitute perhaps the most significant fraction of microfaunal biomass in the habitat of submerged litter, and they are the staple food of benthic predators such as shrimps, aquatic insects and small fish (KENSLEY and WALKER, 1982; HENDERSON and WALKER, 1986; WALKER in press). Secondly, most of them are scrapers and shredders of litter leaves and as such are the principal mechanical decomposers which produce the fine detritus that is carried downstream into the larger rivers and lakes (WALKER, 1985; HARGRAVE, 1975). Lastly, the oligochetes are the only group that shows, so far, a clear pattern of succession.

Practically 100% of leaves that are submerged for at least one week carry an average of 21 chironomid larvae. This is the balance of a dynamic system: each day a fraction quits to pupate, each day a fraction falls victim to predation. Freshly submerged leaves are colonized at a rate of 3.4 chironomids/leaf day until the leaf is fully occupied (this mean includes the 25% not occupied). This is input from oviposition and from the fraction of larvae that circulate between already colonized substrates and that has to find a new "niche". This balance indicates that food is not limiting for the predators during the period of rising waters, and that leaf space might be the limiting factor for the resource organisms. The large standard deviations (i.e. $s^2 > \bar{x}$) indicate that the distribution of chironomids is clumped in time (s between several series n_{10}) as well as in space (s between leaves in a single series): at different periods chironomids are more or less abundant, and different leaves are colonised with different intensity, either because different leaves may be more or less attractive and/or

Table 7 - Colonization by Chironomidae and Oligochaeta. T = number of morphotypes. n_{10} , n_{20} = number of series assessed with 10 and 20 leaves each, respectively. s = standard deviation between series, in case of single series, between 10 ± 2 leaves.

Time of exposure	Chironomidae				Oligochaeta		Leaves mined		
	Individuals/leaf $\bar{x}$ ± s	n_{10}	Leaves colonized %	T/Series	Leaves colonized %	% ± s		n_{20}
1 day	5.3 ± 5.2	7	74.5	1.1	15.2	-		
2 days	8.2 ± 6.5	2	75.8	1.5	16.7			
1 week	14.3 ± 8.8	1	100	2.0	20.0	-		
2 weeks	36.0 ± 28.4	2	100	3.5	55.0	-		
1 month	23.6 ± 16.1	4	97.7	4.0	73.8	26.3	7.9	10
2 months	7.1 ± 1.9	2	92.0	4.5	59.3	22.9	5.2	12
3 months	11.6 ± 11.7	1	81.8	7.0	100	60.0	11.1	10
4 months	23.3 ± 19.1	1	100	5.0	85.7	55.6	15.3	8

because whole egg masses may land on a single leaf.

Body size of chironomids: Table 8 shows that the mean size of chironomids increases within the first month ($P < 0.01$ between 24h and 1 months, t- test), and again between the first month and any longer exposure period ($P < 0.05$, t- test). Predominantly smaller stages colonize newly submerged leaves; presumably they stay on the leaves and grow larger. The relative increase of the standard deviation (s in %) means greater variability; smallest stages keep colonizing older leaves with already more mature larvae. Most species seem to be very small (pupae < 2mm long); the largest individual in the series in Table 8 was 6 mm long.

Leaf mining and surface loss; This is not a study on litter decomposition, but a few data that relate to the ecology of the colonizing micro- fauna are given below. After 4 months a total of only 4 leaves in the 8 baskets (= 2.5% of leaves) were fractionated beyond recognition. The remaining leaves had, on the average per basket, lost 3-10% of their surface. Thus, after 3-4 months a fraction of the colonizing fauna has to find new substrate to settle.

After one month, leaf mining by chironomids and, to a lesser extent by oligochetes, reaches appreciable intensity. The number of morphotypes and of individuals were not determined, but one species of chironomid, not found on the leaf surface, seems to be the dominant miner. These organisms drill through the epidermis and rasp through the mesophyll and the hyphae of the decomposing fungi, without, however, causing any loss of leaf surface. After 4 months more than half of the leaves are mined; the mean leaf area with the mesophyll removed in this way varies from 10-40% between baskets (these values include leaves not mined, i.e. they refer to total leaf area per basket). Leaf mining and colonization of the mesophyll is thus, perhaps, the most obvious characteristic of faunal succession on decomposing, submerged litter leaves.

The most outstanding feature of the microfauna in

Table 8 - Mean body length (in mm) of chironomids on leaves exposed for various periods in 1986. N = number of chironomids measured; n = number series of 10 ± 2 leaves each.

Exposure time	Mean body length $\bar{x} \pm s$		s in %	N	n
24 h	0.93	0.52	56.4	111	3
1 month	1.23	0.57	46.5	84	1
2 months	1.71	0.99	57.7	132	1
3 months	1.43	0.95	66.4	115	1
4 months	1.53	0.77	50.3	154	1

the litter habitat of the Tarumãzinho is the constancy of the number of morphotypes and, to a lesser extent, of individuals per leaf. This seems to agree with the MacARTHUR-WILSON (1963) equilibrium model as discussed by CAIRNS (1982) for freshwater protozoan communities which colonize small pieces of exposed, artificial substrates (= "islands"). After a characteristic period the number of species that leaves the island equals the number of species that is settling on it; the, "island", in our case, being the single leaf.

The few remarkable characteristics of succession are the consistent increase of types and individuals of oligochetes per leaf, leaf mining by chironomids and oligochetes and the increase of species diversity between leaves.

The observations on leaf mining and surface loss indicate that the rate of underwater decomposition of leaf litter in acid amazonian waters is not slower than the rate in streams of the temperate zone, which is 0.2-1.75%/day (SAUNDERS, 1975). A daily mean of 0.274% results in 100% per year: decomposition then balances the rate of litter fall, which amounts to 6.7 t/ha.yr (FRANKEN et al., 1979), 5.3 t of which are leaves only (ADIS et al., 1979). These are measures of dry weight determined for the inundation forest of the Rio Negro. With a mean leaf weight of 0.87 g (p.629) we arrive at an annual input of 611 leaves/m^2, i.e. at roughly 2 leaves/m^2.day.

The following measures aloow for an approximate calculation of the standing wet microfaunal biomass:

Minimum number of colonizable leaves/m^2 in the sampling area = 396 (author's determinations by quadrat sampling).

Mean leaf area = 62.2 cm^2 (p.629), occupied by 30-60 individuals, 21 being chironomids and 2 other insects, thus leading to a density of 0.5-1.0 organisms per cm^2 of leaf tissue. ROBERTSON et al. (this volume), who counted the number of individuals of the micro- Crustacea and the Rotifera

as well, arrive at 1.7 organisms/cm^2.

Chironomid volume (our own measures) = approximately 234.10^5 μm^3 ≈ 0.024 mg (1 μm^3 = 10^{-9} mm^3);

Weight of 1 ostracod = 0.08 mg, and of 1 nematode = 0.05 mg (REISS, 1977, Rio Cuieiras, black water, Amazonia); 1 Paramaecium caudatum = 6.10^{-4} mg (FENCHEL and FINLAY, 1983).

We thus arrive at a total number of 9128 smallest insect larvae per m^2 (90% being chironomids) with a wet weight of ca 220 mg; the rest of the fauna adds at least another 10-20%, thus totalling roughly 250 mg. This value is 1000 times higher than IRMLER'S (1975) value for the total benthic biomass per m^2 in the lower course of the Tarumãnzinho. However, his samples were taken in the more muddy-sandy substratum with less litter and furthermore, he worked with a bottom dredge. Dredge samples do not allow for the detection of smallest, fragile organisms, and some of the larger ones (shrimps, Odonata) escape before the dredge hits the ground and closes, as pointed out by the author himself. With the same method REISS (1977) recovered 5282 individuals/m^2, weighing 1.16 g (wet weight), in the Rio Cuieiras (black water, Central Amazonia). JUNK (1972) collected a total of 13.000 individuals in 0.064 m^3 wire net boxes with wool shavings, which were exposed (floating) for one month in the igapó of the Rio Negro. This corresponds to a layer of 6.4 cm over 1 m^2. Excluding the Protozoa, the results given in this paper, complemented by the more complete counts by ROBERTSON et al. (this volume), lead to a minimal estimate of microfaunal density of 11.000-40.000 individuals/m^2 in the litter habitat of the Tarumãnzinho during rising waters. Together with the macrofauna, the data of which are not yet evaluated, the figures are expected to rise considerably, especially with regard to biomass. The shrimps, for example, have a density of 10/m^2 during rising waters in our sampling area (WALKER and FERREIRA, 1985).

The results so far obtained support the suggestion

made by HENDERSON and WALKER (1986) that amazonian black waters may be richer in animal biomass than earlier estimates indicate (FITTKAU et al., 1975).

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