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Breakdown of leaf litter in a neotropical stream

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Abstract.   We investigated the breakdown of 2 leaf species, *Croton gossypifolius* (Euphorbiaceae) and *Clidemia* sp. (Melastomataceae), in a 4th-order neotropical stream (Andean Mountains, southwestern Colombia) using leaf bags over a 6-wk period. We determined the initial leaf chemical composition and followed the change in content of organic matter, C, N, and ergosterol, the sporulation activity of aquatic hyphomycetes, and the structure and composition of leaf-associated aquatic hyphomycetes and macroinvertebrates. Both leaf species decomposed rapidly (k = 0.0651 and 0.0235/d, respectively); *Croton* lost 95% of its initial mass within 4 wk compared to 54% for *Clidemia*. These high rates were probably related to the stable and moderately high water temperature (19°C), favoring strong biological activity. Up to 2300 and 1500 invertebrates per leaf bag were found on *Croton* and *Clidemia* leaves after 10 and 16 d, respectively. Shredders accounted for <5% of the total numbers and biomass. Fungal biomass peaked at 8.4 and 9.6% of the detrital mass of the 2 leaf species, suggesting that fungi contributed considerably to leaf mass loss. The difference in breakdown rates between leaf species was consistent with the earlier peaks in ergosterol and sporulation rate in *Croton* (10 d vs 16 d in *Clidemia*) and the faster colonization of *Croton* by macroinvertebrates. The softer texture, lower tannin content, and higher N content were partly responsible for the faster breakdown of *Croton* leaves. The rapid breakdown of leaf litter, combined with a low influence by shredders, is in accordance with previous findings. The high fungal activity associated with rapid leaf breakdown appears to be characteristic of leaf processing in tropical streams.

Key words: tropical, decomposition, macroinvertebrates, shredders, aquatic hyphomycetes.

Allochthonous detritus, including leaf litter, is a main source of energy for woodland stream ecosystems (Wallace et al. 1997). Once in the stream, this detritus is subject to breakdown, i.e., a combination of physical and biological processes leading to size reduction, chemical transformation, and incorporation into the food web (Petersen and Cummins 1974, Webster and Benfield 1986, Maltby 1992). In temperate streams, both microfungi and shredders are important leaf decomposers (Maltby 1992, Gessner et al. 1999) because they convert a major part of plant detritus to CO_2, dissolved organic matter, fine particulate organic matter (FPOM), and living biomass. Some of these particulate fractions are further used by other macroinvertebrates, so they play an important role in the trophic dynamics of streams (Egglishaw 1964).

The abundant literature on leaf litter breakdown in temperate streams contrasts with the scarce information available from tropical rivers. Studies in low-order tropical streams generally report rapid breakdown of leaf litter compared to temperate rivers (Stout 1980, Dudgeon 1982, Benstead 1996). However, little is known about the absolute and relative importance of different decomposer types in the tropics, and the available literature leads to diverging conclusions. Pearson and Tobin (1989) in tropical Australia and Petersen (1984) in Jamaica attributed the rapid breakdown to a high activity of shredders. In contrast, Dudgeon (1982) observed that the higher invertebrate densities on a fast-decomposing leaf species were related to the higher abundance of the leaf-associated microflora, and thus shredders were of secondary importance. Aquatic hyphomycetes played a significant role in leaf litter breakdown in a Puerto Rican stream (Padgett 1976). Similarly, Dudgeon (1989) and Dudgeon and Wu (1999) in Hong Kong and Benstead (1996) in Costa Rica noted an under-representation of shredders in leaf-associated assemblages in comparison with their occurrence in temperate streams. In a regional comparison, Irons et al. (1994) suggested that shredding invertebrates were more important in leaf breakdown at high latitudes, whereas the contribution of microorganisms prevailed at low latitudes. These trends remain largely hypothetical, however, essentially because of the lack of substantial data on microbial processing. Ad-

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ditional data are needed using comparable methods to quantify both types of decomposers. The quantification of microbial, especially fungal, processing using specific methods has led to considerable progress in the understanding of the relative importance of different leaf decomposers in temperate woodland streams (Gessner et al. 1999), but these methods have, so far, not been applied to tropical stream ecosystems.

The aims of our study were to 1) compare the breakdown of 2 tree species differing in texture and chemical composition in a tropical upland forest stream, 2) characterize the leaf-associated assemblages of aquatic hyphomycetes and macroinvertebrates, and 3) gain insights into the relative importance of both types of decomposers in this stream.

Methods

Study site

The study was conducted in the Cabuyal, a 4th-order neotropical stream located in the Cauca region in southwestern Colombia, $\sim$ 100 km south of Cali (altitude: 1500 m, lat 2°79'N, long 76°53'W). The stream is a tributary of the Ovejas, which flows into the Cauca River. The average annual rainfall at the study site is $\sim$ 1900 mm (De Fraiture et al. 1997). The stream drains a 3200-ha watershed covered by a secondary forest and cultivated fields of manioc, plantain, coffee, maize, and red bean. This watershed is representative of forested hill land areas prevailing in Colombia. The riparian vegetation at the study site is dominated by *Bambusa vulgaris* Schrad. Ex J. C. Wendl, *Casearia arborea* (Rich.) Urb., *Clidemia* sp., *Coffea arabica* L., *Croton gossypifolius* Vahl, *Heliocarpus* sp., *Ocotea* sp., *Saccharum officinarum* L., and *Saurauia* sp. The stream bed, mostly made up of cobbles, leaf litter, and some large boulders, was shaded by riparian vegetation. Aquatic macrophytes were absent.

Average stream width and depth were determined over a 50-m long riffle. Discharge was measured using an HP 302 flow meter. The chemical composition of stream water was determined using standard procedures (APHA 1989). The water chemistry and physical characteristics of the study site are presented in Table 1.

TABLE 1. Physical characteristics of the study site and chemical composition of the stream water (range determined on 6 occasions between March 1997 and August 1998).

Parameter	Range
Width (m)	3–5
Depth (cm)	5–25
Discharge (m³/s)	0.14–0.86
Suspended solids (mg/L)	4.5–31.4
Temperature (°C)	18–27.5
Dissolved oxygen (mg/L)	6.6–7.2
pH	6.0–7.1
Conductivity (µS/cm)	34–59
Alkalinity (CaCO$_3$) (mg/L)	15.8–31.5
N-NO$_3^-$ (mg/L)	0.08–0.17
N-NO$_2^-$ (mg/L)	<0.0003–0.01
P-PO$_4^{3-}$ (mg/L)	<0.001–0.0442

Experimental setup

A litter breakdown study was conducted during the dry season from 1 August to 14 September 1999. Leaves of 2 contrasting tree species were used: *Croton gossypifolius* (Euphorbiaceae) with thin, soft, and hairy leaves and *Clidemia* sp. (Melastomataceae) with thick, tough, and glabrous leaves. Freshly fallen leaves of both species were collected from the riparian forest floor. Color and texture were used to distinguish fresh leaves from old ones. Leaf petioles were removed and leaves enclosed in nylon mesh bags (15 × 20 cm, 7-mm-mesh openings) the same day as collection. Forty-two bags, each containing 7 ± 0.01 g of fresh leaves, were placed in the stream within a 50-m long × 4-m wide riffle. Leaf bags were individually tied to iron rods driven into the substratum and placed under similar conditions of current velocity and turbulence. Three replicate samples of each species were randomly removed after 3, 10, 16, 23, 29, 36, and 43 d. Upon collection, each leaf bag was placed into a plastic bag containing stream water and put into an icebox. In addition, 3 samples per species were collected on day 0 for determination of initial leaf dry mass and chemical composition.

Macroinvertebrate sampling and determination

In the laboratory, the leaf material was carefully rinsed in running tap water, with the associated macroinvertebrates retained on a 300-

μm-mesh screen. Macroinvertebrates were preserved in 2% formalin, and later sorted using a dissecting microscope and identified mostly to genus with the help of identification keys (e.g., Roldán 1996). Chironomidae and Oligochaeta were identified only to family and class levels, respectively. All individuals were counted, grouped by taxa, dried at 105°C for 24 h and weighed to the nearest 0.1 mg. Taxa were assigned to functional-feeding groups (FFG) according to Merritt and Cummins (1996). Chironomids were considered to be collectors because most of the individuals identified from subsamples belonged to this FFG. Oligochaeta contain various FFG, but because they were not further identified they were not placed into any particular group.

Fungal determinations

A total of 23 leaf discs was cut from the leaf material of each bag with a 1-cm diameter cork borer. Ten discs were incubated statically at 20°C in Erlenmeyer flasks containing 30 mL of filtered stream water to induce sporulation. After 48 h, discs were removed and the conidial suspension preserved with formalin (final concentration: 2%). Aliquots of the conidial suspension were filtered on Whatman cellulose nitrate membrane filters (5 μm porosity). Each filter was stained with a 60% lactic acid: 0.1% Trypan blue solution (Iqbal and Webster 1973) and examined microscopically ($\times$ 200 magnification) to determine the total number of conidia produced per mg of leaf ash-free dry mass (AFDM) and identify the aquatic hyphomycetes. Ten other leaf discs were used for ergosterol analysis as an indicator of fungal biomass (Gessner and Schmitt 1996). These leaf discs were preserved in vials containing 10 mL of methanol and stored in a freezer until analyzed. Ergosterol was extracted by 30 min refluxing in alcoholic base, purified by solid-phase extraction, and quantified by high pressure liquid chromatography (Gessner and Schmitt 1996). The remaining 3 leaf discs were dried at 105°C for 24 h and weighed to determine the dry mass of the 23 leaf discs.

Determination of leaf mass loss and chemical composition

The remaining leaf material was dried at 105°C for 24 h and weighed. This mass was added to that of the corresponding 23 leaf discs to calculate the total leaf mass loss of each sample. The leaf material was then ground in a mortar and the organic matter content was determined on aliquots by ignition for 2 h at 550°C. Carbon and N contents of leaves were determined using a NA2100 Thermoquest CHN analyzer.

The initial tannin content was estimated as protein-precipitating potential using a radial diffusion assay described in Hagerman (1987) as modified in Gessner and Chauvet (1994). Initial leaf cellulose and lignin content was determined gravimetrically following the procedure of Goering and Van Soest (1970). All determinations were done on 3 replicate samples.

Data analysis

The loss in leaf AFDM through time was fitted to an exponential model $m_t/m_o = e^{-kt}$ where m_t is the mass remaining at time t, m_o is the initial mass, and k is the breakdown rate constant (Boulton and Boon 1991). Breakdown rates were estimated by nonlinear regression ($k \pm$ asymptotic SE) and slopes, calculated by linear regression on log-transformed data, were compared using ANCOVA (Zar 1984). Numbers and biomass of macroinvertebrates, fungal biomass, and conidial production over the first 29 d were tested for normality (those not normally distributed were log transformed) and compared using ANOVA. Statistical analyses were conducted using Systat 5.2.1 (L. Wilkinson. 1990. Systat: the system for statistics, Systat Inc., Evanston, Illinois).

Results

Leaf chemical composition

The initial percentages of leaf C for *Croton* and *Clidemia* were similar (Table 2). Nitrogen content of *Croton* was initially higher than *Clidemia*. Both leaf species exhibited a pronounced N increase (Fig. 1), which resulted in consistent decreases in C:N ratios (data not shown). Initial cellulose and lignin contents were higher in *Croton* than in *Clidemia*. In contrast, the initial tannin content was higher in *Clidemia* than in *Croton* (Table 2).

TABLE 2. Initial content of C, N, cellulose, lignin, and tannins (% of dry mass ± SE), and the C:N ratio of *Croton* and *Clidemia* leaves.

Constituent	*Croton*	*Clidemia*
C	46.4 ± 0.3	45.2 ± 0.3
N	1.91 ± 0.05	1.25 ± 0.04
C:N	24.3 ± 0.8	36.3 ± 1.3
Cellulose	22.1 ± 0.9	12.4 ± 1.4
Lignin	26.4 ± 0.5	16 ± 0.2
Tannins	1.13 ± 0.04	1.88 ± 0.11

Leaf breakdown

A rapid mass loss occurred within the first 3 d of immersion (14 and 25% for *Clidemia* and *Croton*, respectively) (Fig. 2). The subsequent mass loss slowed down for *Clidemia* during the following 13 d and then increased. Breakdown continued to be rapid for *Croton*. Only 5% of the AFDM of *Croton* and 46% of *Clidemia* remained after 29 d of immersion. *Croton* ($k = 0.0651 \pm 0.0083$/d) exhibited a significantly (ANCOVA, $p < 0.001$) higher breakdown rate than *Clidemia* ($k = 0.0235 \pm 0.0027$/d).

Leaf-associated fungi

At the beginning of the study, both leaf species contained low amounts of ergosterol (0.12 and 0.06 μg/mg in *Croton* and *Clidemia*, respectively) (Fig. 3A). Concentrations then increased rapidly with peak values of 0.46 and 0.53 μg/mg AFDM at 10 and 16 d in *Croton* and *Clidemia*,

FIG. 2. Mass loss (mean % ash-free dry mass [AFDM] ± SE) of *Croton* and *Clidemia* leaves during breakdown in the Cabuyal.

FIG. 3. Mean (± SE) concentration of ergosterol (A) and mean (± SE) conidial production (B) in *Croton* and *Clidemia* leaves.

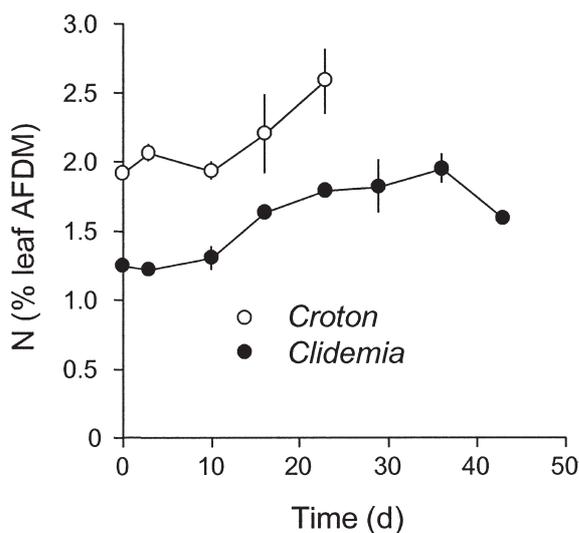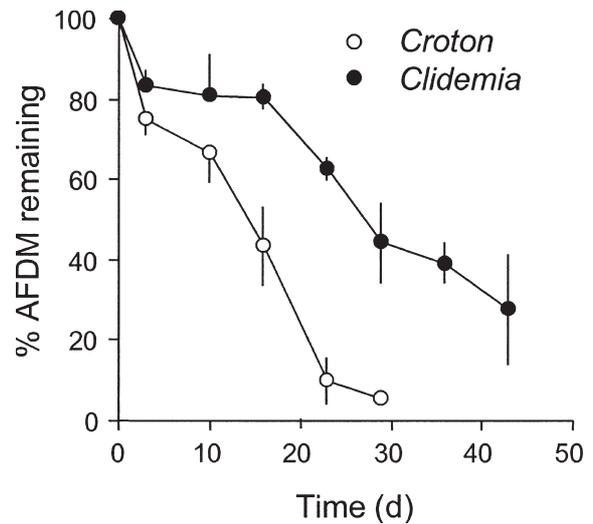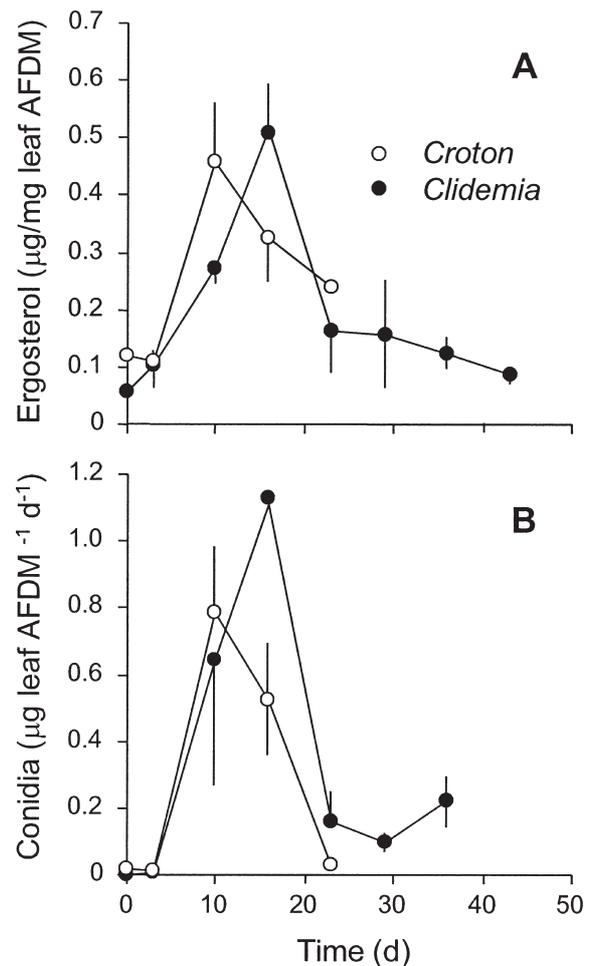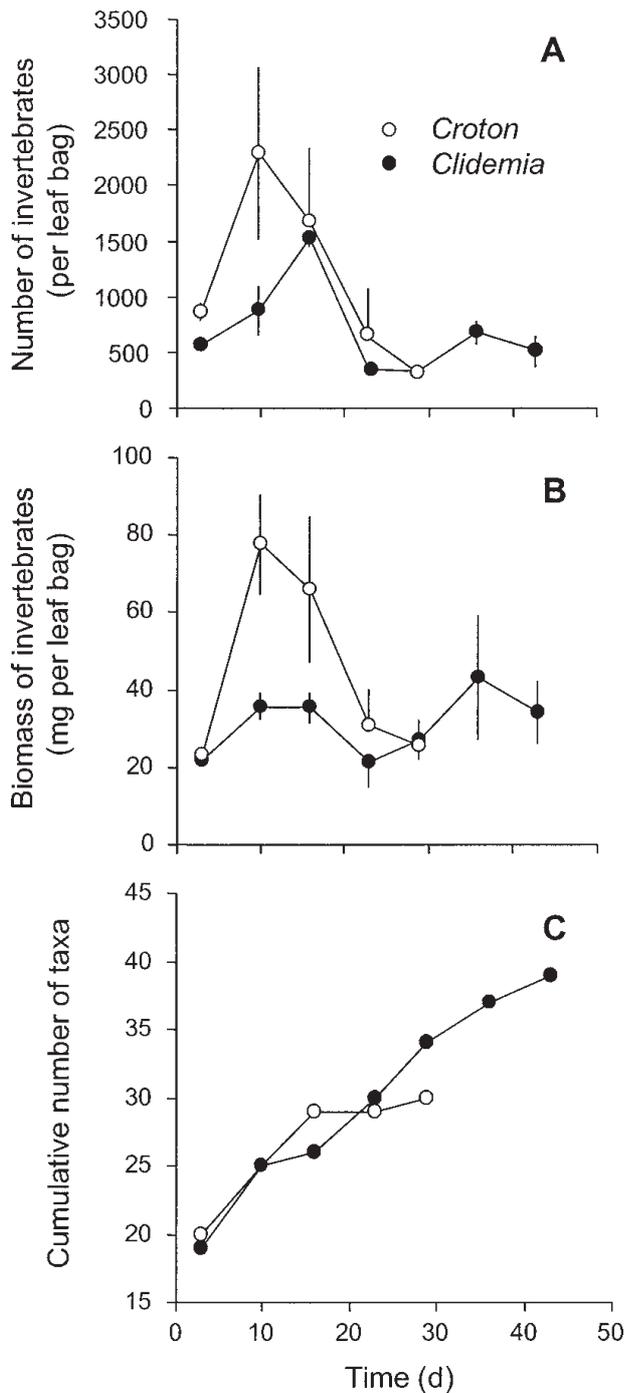FIG. 1. Nitrogen content (mean % ash-free dry mass [AFDM] ± SE) of *Croton* and *Clidemia* leaves.

FIG. 4. Mean (± SE) density (A) and mean (± SE) biomass (B) of macroinvertebrates, and cumulative number of macroinvertebrate taxa (C) colonizing *Croton* and *Clidemia* leaves.

respectively. Peaks in ergosterol occurred at relatively low leaf mass loss (Fig. 2), and were followed by rapid ergosterol decreases concomitantly with high leaf mass loss for both species. Sixteen taxa of aquatic hyphomycetes were identified from sporulating *Croton* and *Clidemia* leaves (Table 3). Nine of them each contributed

>1% of the total conidial production cumulated over the study period. *Flagellospora curvula* Ingold on *Croton* and *Alatospora acuminata* Ingold and *Lunulospora curvula* Ingold on *Clidemia* contributed to >½ of the produced conidia (Table 3). Conidial production on both leaf species followed the same temporal pattern as ergosterol, although with more marked initial increases and subsequent decreases (Fig. 3B). Peaks of 0.8 and 1.1 conidia μg leaf $AFDM^{-1}$ d^{-1} were reached on *Croton* and *Clidemia* after 10 and 16 d, respectively.

Leaf-associated macroinvertebrates

Both leaf species were rapidly colonized by macroinvertebrates, reaching 862 and 567 individuals per leaf bag on *Croton* and *Clidemia*, respectively, after only 3 d (Fig. 4A). Peaks of 2290 and 1528 individuals occurred after 10 and 16 d. Both species exhibited the same pattern with a strong decrease after the early peak in colonization. The average number of individuals was always higher, although nonsignificantly, on *Croton* than on *Clidemia* (Fig. 4A). *Croton* supported the highest biomass of macroinvertebrates ($p = 0.03$), peaking at 78 mg per leaf bag after 10 d (Fig. 4B). The biomass of organisms associated with *Clidemia* showed less variation, with values ranging from 22 mg after 3 d to 43 mg after 36 d.

Croton had a lower number of taxa than *Clidemia* (Fig. 4C). Macroinvertebrate taxa and their relative abundances are listed in Table 4. The assemblage structure of macroinvertebrates on both leaf types was broadly similar, being composed of Diptera (78.8% on *Croton*, 64.7% on *Clidemia*), Ephemeroptera (6.6 and 14.9%), Oligochaeta (5.4 and 7.8%), Trichoptera (5.3 and 5.9%), and Coleoptera (3.2 and 5.4%). These 5 taxa represented ~90% of the total numbers. Chironomidae were predominant at 75.2% and 61.2%, respectively, followed by *Leptohyphes* (5.8 and 12.8%), Oligochaeta (5.4 and 7.8%), *Heterelmis* (2.9 and 4.9%), and *Simulium* (2.5 and 2.2%). Figure 5 shows changes in individual numbers of these 8 dominant taxa during the course of the study. The number of chironomids was high by day 3; it then increased to 1870 ind./bag after 10 d on *Croton* and 1179 ind./bag after 16 d on *Clidemia*, and declined thereafter (Fig. 5F). Simuliids colonized both leaf types very rapidly; maximum densities were found on

TABLE 3. Relative abundance of identified taxa of aquatic hyphomycetes sporulating on *Croton* and *Clidemia* leaves (% of total conidial production cumulated over the study period).

Taxon	*Croton*	*Clidemia*
Alatospora acuminata Ingold	2.8	27.9
Anguillospora longissima? (Sacc. and Syd.) Ingold	<0.1	<0.1
Articulospora atra? Descals	<0.1	<0.1
Campylospora chaetocladia Ranzoni	0.8	1.1
Flagellospora curvula Ingold	48.4	4.5
Heliscella stellata (Ingold and Cox) Marvanová and S. Nilsson	<0.1	<0.1
Heliscus submersus Hudson	10.7	7.0
Heliscus tentaculus Umphlett	<0.1	<0.1
Lunulospora curvula Ingold	13.4	31.6
Mycocentrospora sp.	<0.1	<0.1
Nawawia filiformis Nawawi (Marvanová)	2.1	0.1
Tetracladium marchalianum de Wildeman	2.0	0.7
Phalangispora constricta? Nawawi and Webster	4.6	15.5
Tripospermum camelopardus Ingold, Dann and McDougall	13.3	–
Tripospermum sp.	<0.1	<0.1
Triscelophorus konajensis? Sridhar and Kaveriappa	<0.1	<0.1

day 3, and numbers decreased thereafter (Fig. 5H).

The overall functional composition of invertebrate assemblages on *Croton* and *Clidemia* was similar (data not shown). Both leaf types were dominated by collectors (96 and 93%, respectively) and, to a lesser extent, predators (3.9 and 5%). Shredders represented only 0.2 and 0.8% on *Croton* and *Clidemia*, respectively. On a mass basis, the same dominance of collectors (71.7 and 69.2% on *Croton* and *Clidemia*, respectively), followed by predators (27.1 and 23.2%), and a low biomass of both shredders and scrapers (<5% on both leaf types) were observed.

Discussion

Leaf breakdown

Both leaf species decomposed very rapidly in the Cabuyal. The breakdown rate of *Croton* (0.0651/d) is amongst the highest rates reported in the literature. Breakdown rates in the Cabuyal were generally higher than those reported from previous studies conducted under comparable conditions in other tropical streams (Dudgeon 1982, Benstead 1996, Dudgeon and Wu 1999, O'Connor et al. 2000). Similar or even higher rates have been reported for various tree leaf species decomposing in Costa Rican streams (Stout 1980), but these rates were calculated using % leaf area loss, which probably overestimates mass loss. Our results are thus consistent with previous observations that leaf breakdown rates are typically higher in tropical streams than in temperate ones (Irons et al. 1994, Benstead 1996).

There is some evidence that the high temperature (19°C) in our stream played a role in controlling leaf-associated biological activity. When calculated on a degree-day basis, i.e., eliminating the effect of temperature, breakdown rates (0.0034 and 0.0012/degree-day on *Croton* and *Clidemia*, respectively) were similar, although still slightly higher, to those reported for other leaf species from mid latitudes (Irons et al. 1994; EC, unpublished data).

Leaf quality

The fast leaf breakdown observed in our study may have been caused by differences in leaf quality related to the initial chemical composition and texture of the leaves. Initial mass loss of both leaf species was higher than that commonly reported from colder, high-latitude streams, and is generally attributed to the leaching of soluble compounds. Leaching seems to be enhanced in tropical streams (Covich 1988). However, unlike in the present work, previous studies in tropical streams often used predried instead of fresh leaves, which can greatly enhance leaching (Gessner 1991, Taylor and Bär-

TABLE 4. Relative abundance of macroinvertebrate taxa associated with *Croton* and *Clidemia* leaves (% of total numbers cumulated over the study period). Co = collectors, Shr = shredders, Pr = predators, Scr = scrapers, Pi = piercers, ? = functional-feeding group (FFG) unknown, * = FFG not determined, – = absent.

Taxon	Croton	Clidemia	FFG
TURBELLARIA			
Dugesiidae	<0.1	0.2	Pr
OLIGOCHAETA	5.4	7.8	*
MOLLUSCA			
Aroapyrgus?	<0.1	0.1	Scr
Ancylidae	–	0.2	Scr
Physa	<0.1	0.2	Scr
ACARINA			
Hydracarina	0.7	0.6	Pr
EPHEMEROPTERA			
Lachlania	0.1	0.2	Co
Thraulodes	0.1	0.4	Co
Leptohyphes	5.8	12.8	Co
Haplohyphes	–	<0.1	Co
Tricorythodes	<0.1	<0.1	Co
Americabaetis	0.4	1.0	Co
Baetodes	0.2	0.5	Scr
ODONATA			
Hetaerina	<0.1	0.1	Pr
Brechmorhoga	–	<0.1	Pr
PLECOPTERA			
Anacroneuria	0.1	0.2	Pr
COLEOPTERA			
Dryops	–	<0.1	Shr
Heterelmis	2.9	4.9	Co
Microcylloepus	0.2	0.4	Co
Cylloepus	–	<0.1	Co
Hexanchorus	<0.1	<0.1	?
Macrelmis	–	<0.1	Co
Phanocerus	–	<0.1	Co
Xenelmis	–	<0.1	Co
Anchytarsus	–	<0.1	Shr
TRICHOPTERA			
Helicopsyche	–	<0.1	Scr
Atopsyche	1.3	1.0	Pr
Mortoniella	<0.1	<0.1	Scr
Nectopsyche	0.2	0.7	Shr
Oecetis	0.4	1.0	Pr
Metrichia	<0.1	<0.1	Pi
Leptonema	0.8	0.8	Co
Smicridea	2.4	2.1	Co
LEPIDOPTERA	<0.1	–	Shr

TABLE 4. Continued.

Taxon	Croton	Clidemia	FFG
DIPTERA			
Limoniidae	–	<0.1	Pr
Chironomidae	75.2	61.2	Co
Ceratopogonidae	<0.1	–	Pr
Simulium	2.5	2.2	Co
Chelifera	0.5	0.3	Pr
Hemerodromia	0.6	1.0	Pr
Wiedemannia	<0.1	–	Pr
Suragina	–	<0.1	Pr
Total number of taxa			
Total number of organisms	30 17,325	39 14,965	

locher 1996). In our study, therefore, processes other than leaching better explain the mass loss during the initial stages of leaf breakdown. The faster breakdown of *Croton* relative to *Clidemia* was correlated with a higher initial N content, which translates into a lower C:N ratio and faster colonization by fungi. Such relationships were also noted by Kaushik and Hynes (1971), Suberkropp et al. (1976), Pearson and Tobin (1989), and Stout (1989).

Tannins, which are considered to be defensive compounds against microbial colonization (Stout 1989), were initially lower in the *Croton* leaves. Although questionable in some situations (Campbell and Fuchshuber 1995), an inhibitory effect of tannins has commonly been reported (e.g., Cameron and LaPoint 1978). Differences in tannin concentrations of 10 leaf species decomposing in a Costa Rican stream were apparently responsible for differences in leaf breakdown rates that spanned one order of magnitude (table 2 in Irons et al. 1994). The tannin content of *Clidemia* and *Croton* was relatively low when compared with other tropical leaf species (Stout 1989), which suggests that tannins played a minor role in the observed difference in breakdown of these 2 species.

The higher lignin content of *Croton* relative to *Clidemia* did not translate into a slower breakdown for this species, although lignin is one of the best indicators of leaf breakdown (Gessner and Chauvet 1994). Despite their higher lignin content, *Croton* leaves had thinner cuticles and a softer texture, which led to a mode of leaf disintegration contrasting to that of *Clidemia*. The rapid maceration of *Croton* leaves, combined

with the turbulent water flow, continuously released FPOM. In *Clidemia*, the epidermis peeled off and the leaf tissue was divided into layers, and thus was retained longer within the leaf bags.

Contribution of fungi

Fungal biomass and activity associated with decomposing leaves has rarely been assessed in tropical streams. Our study showed that leaf litter was rapidly colonized by fungi, attaining a biomass (as ergosterol) as high as in temperate streams (Gessner 1997, Gessner et al. 1997). The conidial production of aquatic hyphomycetes also was high and followed the same temporal pattern as reported for temperate streams (Gessner 1997). This result suggests that aquatic hyphomycetes dominated fungal assemblages in the present tropical stream as they do in temperate ones. Consequently, the ergosterol-to-biomass conversion factor determined for this group of fungi (5.5 mg/g fungal dry mass; Gessner and Chauvet 1993) is applicable to our study. Calculations showed that fungal biomass attained 8.4 and 9.6% of the detrital mass of *Croton* and *Clidemia* leaves, respectively, falling within the range determined for medium- to fast-decomposing leaf species in temperate streams (Gessner 1997).

Croton exhibited peaks in fungal biomass and sporulation after only 10 d, i.e., by the time ⅓ of the leaf mass had disappeared, a finding similar to those reported for other fast-decomposing leaf species such as alder in temperate streams (Gessner 1997). The peak for *Croton* may have occurred even earlier because of the rapid mycelial development by these fungi (Suberkropp 1991) and may have been missed by our sampling schedule, explaining why at 10 d fungal biomass was slightly lower for *Croton* than *Clidemia*. Calculations based on an average fungal growth efficiency of 0.35 (net production efficiency from table 3 in Suberkropp 1991) indicated that fungal biomass at 10 d on *Croton* and 16 d on *Clidemia* contributed from 72% to > 100% of leaf mass loss, respectively. The latter estimate obviously indicates some imprecision in our determinations or the growth efficiency coefficient, or the use of non-leaf organic matter by fungi. Overall, these high values suggest that fungi incorporated a major part of the leaf litter during early breakdown. The pronounced increase in leaf-associated N is an indication that fungi also were involved in N immobilization.

Overall, the composition of the fungal assemblage was similar to that found in Puerto Rico (Padgett 1976, Santos-Flores and Betancourt-López 1997) and, to a lesser extent, southern Asia (Sridhar and Kaveriappa 1988, Au et al. 1992). Leaf-associated fungal assemblages of our study included several aquatic hyphomycete species with typical tropical distributions (Hyde 1997). In terms of conidial production, fungal assemblages, however, were dominated by 3 widespread species commonly found in temperate streams: *Alatospora acuminata*, *Flagellospora curvula*, and *Lunulospora curvula* (Webster and Descals 1981). Apart from the tropical species, the fungal assemblages were thus close to those found in subtropical southeastern North America (Suberkropp and Chauvet 1995) and summer assemblages in temperate lowland rivers (Chauvet 1991). The stable and moderately high water temperature prevailing in the Cabuyal was close to that occurring in these subtropical and temperate regions, at least in some seasons, suggesting that temperature may influence aquatic hyphomycete assemblages in a similar way among different geographic regions. This finding provides further indication that temperature is a prime factor in the spatial and temporal dynamics of these aquatic fungi (Suberkropp 1984, Gessner et al. 1993).

Role of macroinvertebrates

In contrast to fungi, macroinvertebrates appeared to play a minor role in leaf breakdown in our study stream. Although numerically abundant, they represented a moderate biomass that never exceeded 40 mg/g leaf mass. They colonized leaf litter rapidly, however, which is in accordance with observations made by Dudgeon (1982) in Hong Kong and Stewart (1992) in South Africa. The high initial occurrence of aquatic invertebrates appeared associated with leaf fungal dynamics. For instance, *Croton* leaves, which exhibited the fastest breakdown and fungal colonization and the highest N accumulation, also supported the fastest and highest colonization by macroinvertebrates. This result indicates that *Croton* was probably more palatable than *Clidemia*. However, *Clidemia*, requiring a longer breakdown time and thus providing a more durable substrate for the benthic

Number of invertebrates per leaf bag

Time (d)
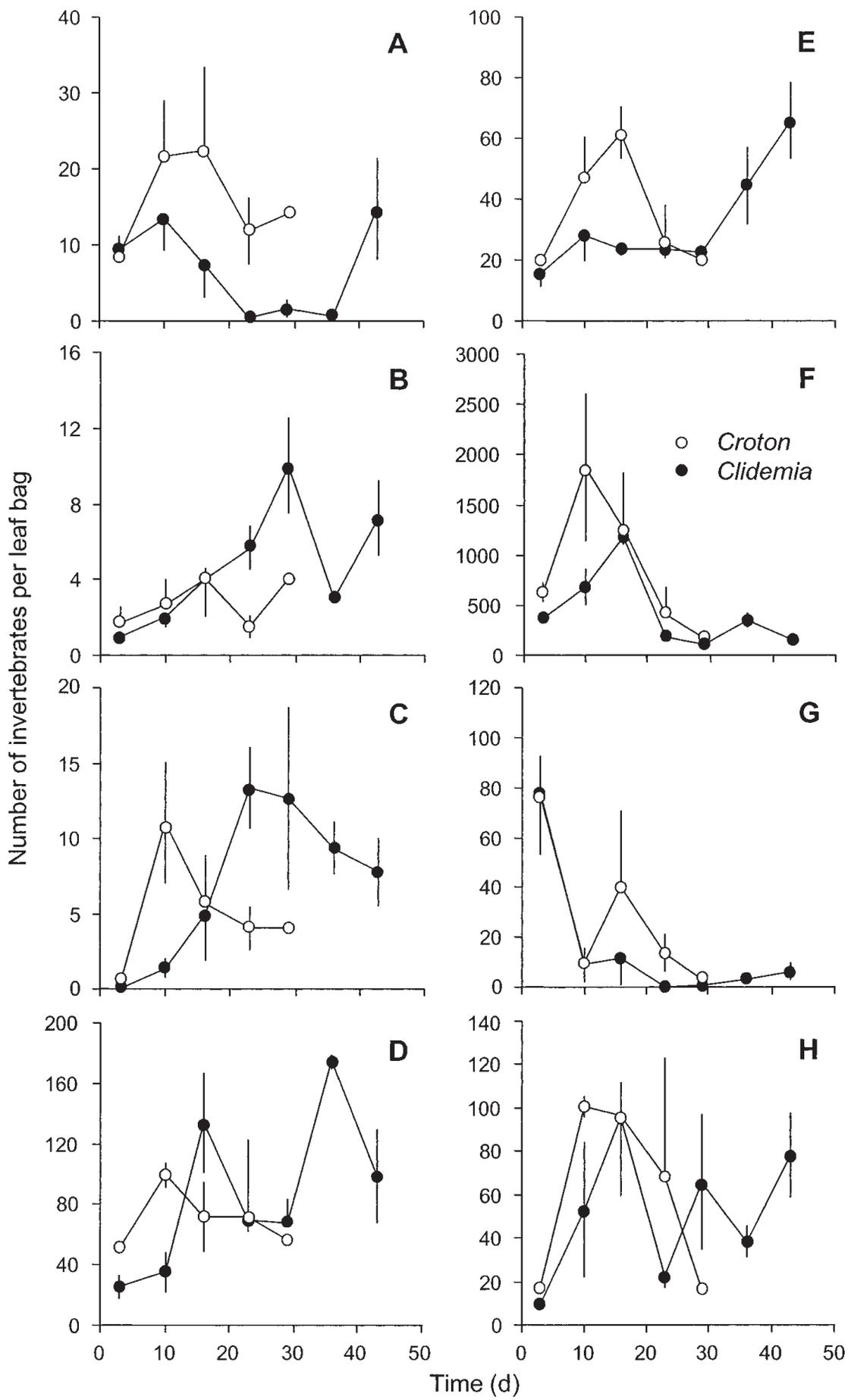
fauna, supported a more diverse macroinvertebrate assemblage. Four of the 5 dominant taxa (i.e., Chironomidae, *Leptohyphes*, *Heterelmis*, and *Simulium*), which constituted 86.4 and 81.1% of the total fauna colonizing *Croton* and *Clidemia* leaves, respectively, belong to the collector feeding group. Shredders, mainly represented by the genus *Nectopsyche*, accounted for only 0.2 and 0.8% of the total macroinvertebrate assemblage on *Croton* and *Clidemia*, respectively. The same patterns have been reported in other studies in tropical streams (Benstead 1996, Pringle and Ramírez 1998, Rosemond et al. 1998, Dudgeon and Wu 1999).

Collectors, which feed on FPOM, are not able to directly participate in the rapid breakdown of leaves. They use leaf litter as a substratum and leaf fragments as a food resource. Using artificial and natural leaf packs, Richardson (1992) and Dudgeon and Wu (1999) concluded that leaves are principally used as a food source, although some collectors colonized artificial leaves. In our study, *Simulium* clearly used leaves as a substratum. *Leptohyphes*, *Heterelmis*, and *Americabaetis* collected fine suspended solids retained on leaf surfaces together with leaf decomposition products. Similarly, scrapers such as gastropods, which feed on biofilm, used leaves as traps for algae and FPOM. Leaves in this tropical stream thus have a triple function, depending on the invertebrate taxa and the state of leaf breakdown: they acted as a substratum, a trap for drifting FPOM and sediment, and a source of C and nutrients.

The low proportion of shredders indicated that these animals only weakly influenced the breakdown of both leaf species. Assuming a relatively high consumption rate of 1.0/d (e.g., Hieber and Gessner 2002) and applying it to the peak shredder biomass, i.e., 2.6 and 3.0 mg/g leaf mass for *Clidemia* at 43 d and *Croton* at 29 d, respectively, the contribution of shredder feeding activity would be 0.26 to 0.30% of leaf mass loss per day. Such a low rate, i.e., 0.0026 to 0.0030/d, explains a minor part of total leaf mass loss (0.0235–0.0651/d), even during late stages of breakdown. Predators like *Brechmor-*

hoga (Odonata), *Oecetis* (Trichoptera), and *Anacroneuria* (Plecoptera) may have influenced leaf breakdown indirectly by affecting shredders (Oberndorfer et al. 1984, Malmqvist 1993), but this effect was probably limited because of the low abundance of predators (<5% of total number of macroinvertebrates).

Given that the food base of many tropical macroinvertebrates remains partly unknown, we cannot preclude that several invertebrates presently categorized as collectors or scrapers may actually behave as shredders during some stages or periods. Such opportunistic feeding behavior and shifts in food regime are not typical of tropical streams, but they appear to be in line with Covich's (1988) conclusions about the dominance of generalized consumers in food webs of small neotropical streams. Several chironomids that accumulated on the leaves had a visible mining influence and, although not considered to be shredders, may have participated in leaf fragmentation (Rosemond et al. 1998). A similar exploitation of decomposing leaves by tubificid Oligochaeta has been reported from a temperate river (Chauvet et al. 1993).

In conclusion, our results suggest that invertebrate-mediated leaf breakdown in our tropical study stream was low, especially in comparison with that occurring in streams at higher latitudes. In contrast, aquatic hyphomycetes developed abundantly on leaves, suggesting that these fungi were important in litter breakdown, similar to temperate streams. These observations partially support previous hypotheses and findings regarding latitudinal patterns in leaf litter breakdown (Irons et al. 1994), i.e., both low shredder involvement and high microbial processing at low latitude. Whether the only moderately high temperature related to the high elevation of our study stream limited fungal development (peak fungal biomass < 10%) is unknown. However, even at the high temperatures prevailing in lowland tropical streams, we expect fungal biomass not to exceed the high values reported for fast-decomposing leaf species in cold, high-latitude streams (e.g., 16% of leaf detrital mass; Gessner 1997). Future research

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Fɪɢ. 5.   Mean (± SE) density of dominant macroinvertebrate taxa colonizing *Croton* and *Clidemia* leaves. A.—*Atopsyche*. B.—*Nectopsyche*. C.—*Oecetis*. D.—*Leptohyphes*. E.—*Heterelmis*. F.—Chironomidae. G.—*Simulium*. H.—Oligochaeta.

should examine the specific effect of temperature on microbial leaf decomposition. In this respect, the role of bacteria, which could be more sensitive to temperature than fungi, deserves particular attention.

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