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Effects of different types of conditioning on rates of leaf-litter shredding by *Xiphocaris elongata*, a Neotropical freshwater shrimp

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Abstract. Temperate headwater streams with closed canopies rely on inputs of terrestrially derived organic matter to provide the major energy basis for their food webs. Microbial colonization, or conditioning, makes leaf litter more nutritional and palatable to stream detritivores, but few studies have investigated the relative importance of litter source to macroshredders in tropical streams. We determined the source (terrestrial, aquatic, or aerial), quantity, and species composition of allochthonous inputs into the Quebrada Prieta, a tropical headwater stream in Puerto Rico, as a first step toward understanding the importance of conditioning history to rates of tropical leaf-litter processing by decapod consumers. Fresh leaves of 4 common species of leaves were treated by exposing them to different conditions for 2 wk. These exposure treatments (conditioning histories) represented routes by which leaves might enter streams and included submersion (aquatic input), incubation on the streambank soil (terrestrial input), and suspension above the ground (aerial input). Conditioned leaves were placed in small experimental microcosms with or without shrimp (*Xiphocaris elongata*) for 20 d. Shrimp significantly increased the rate of decomposition of all leaf species independent of conditioning history. Conditioning history had little effect on breakdown rates independent of the presence of shrimp. One species (*Rourea surinamensis*) had faster mass loss when the leaves were conditioned as aquatic inputs rather than as terrestrial or aerial inputs. Our results indicate that conditioning history has little effect on the ability of some macroconsumers to alter detrital foodweb dynamics in tropical streams. Tropical stream ecosystems may function differently from temperate ecosystems because of the dominance of large detritivores such as shrimps.

Key words: *Xiphocarus elongata*, detrital processing, decompostion, food webs, microbial colonization, tropical streams, freshwater shrimp, litter processing.

Temperate-zone headwater streams depend on terrestrial leaf-litter inputs as a major source of organic C for their detritus-based food webs (Vannote et al. 1980, Wallace et al. 1997). In some cases, as much as 99% of the energy input is terrestrially derived (Fisher and Likens 1973). Leaf-litter inputs vary in timing, source, amount, and quality depending on climate and forest type (Pozo et al. 1997, Webster and Meyer 1997). In temperate deciduous forests, most of the litter falls in a relatively short period, and direct inputs of leaves from overhanging vegetation are more important than inputs of leaves from the ground (Winterbourn 1976, Pozo et al. 1997). However, downslope movement of leaves from the banks into the stream and downstream movement of leaves from within the stream channel also are substantial (Fisher and Likens 1973). Microbes colonize and condition leaf litter during both terrestrial and aquatic phases of downslope transport (Gessner and Chauvet 1994, Allan 1995, Gessner et al. 1999). Microbial colonization is important nutritionally and functionally because it alters the leaf substrate, increases palatability, and makes microbes an important dietary component for aquatic invertebrates (Cummins et al. 1973, Graça et al. 2005).

Once in the stream, leaves continue to break down as a consequence of physical abrasion during transport, continued colonization by microbes, and direct consumption by detritivorous invertebrates (Gessner et al. 1999). The process of breakdown results in

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particle size reduction (Crowl et al. 2002), chemical transformation, and incorporation into the food web (Webster and Benfield 1986, Gessner et al. 1999, Crowl et al. 2001, Robinson and Jolidon 2005). In temperate streams, both the microbial community and the invertebrate shredders are important in processing leaf litter (Gessner et al. 1999).

Much less is known regarding the relative importance of various leaf-litter processing mechanisms to decomposition rates in tropical streams and rivers (Stout 1980, Covich 1988, Benstead 1996, Graça et al. 2001, Wantzen et al. 2002, Larned et al. 2003). A number of differences between tropical and temperate streams are apparent from the few studies that have been published. First, inputs of allochthonous materials to temperate and tropical streams differ in their timing and sources. Litter inputs to tropical streams are more continuous and often consist of a higher proportion of fresh, green litter than inputs to temperate streams because tropical climates are aseasonal (or less seasonal) than temperate climates (Campbell et al. 1992, Pozo et al. 1997). Second, litter breakdown rates in tropical streams appear to be faster than those observed in most temperate streams (Stout 1980, Dudgeon 1982, Irons et al. 1994, Mathuriau and Chauvet 2002). The exact mechanisms responsible for the observed differences in breakdown rates between tropical and temperate streams are still unclear, especially with regard to leaf chemistry and secondary compounds (Stout 1989, Ostrofsky 1997, Wantzen et al. 2002) and the roles of the macro- and microbiota. In most studies, increased breakdown rates in tropical streams appeared to be related to higher abundances of leaf-associated microflora (Padgett 1976, Dudgeon 1982, Graça et al. 2001). These observations and an interregional comparison study led Irons et al. (1994) to suggest that warm temperatures cause microbial decomposition to be more important than shredder activity in tropical streams. Several authors have suggested that tropical streams possess fewer true shredder taxa than temperate streams, a pattern that lends further evidence for the greater importance of microbial breakdown than shredder activity in tropical streams (Dudgeon 1989, Dudgeon and Wu 1999, Dobson et al. 2002). However, other studies have suggested that shredder activities are important in leaf-litter breakdown rates in some tropical streams (Petersen 1984, Pearson and Tobin 1989, Crowl et al. 2001, Dobson 2004, Cheshire et al. 2005).

We addressed the relative influence of conditioning history of allochthonous inputs and direct consumption by a tropical freshwater shrimp (the dominant shredder in the stream) on breakdown rates of leaves in a tropical headwater stream. Our study asked the following questions: 1) What are the sources and dominant species of allochthonous litter inputs entering Quebrada Prieta, a tropical headwater stream? and 2) What are the relative importances of the shredding activity of the freshwater shrimp *Xiphocaris elongata* and the conditioning history (aquatic, terrestrial, or aerial) of the litter to breakdown rates?

Study Site

The Quebrada Prieta is a 2^{nd}-order tributary of the Quebrada Sonadora in the Espíritu Santo watershed of the Luquillo Experimental Forest in northeastern Puerto Rico (lat 18°18′N, long 65°47′W) (Covich et al. 1996). This subtropical rainforest stream is similar to many tropical streams in that it is disturbance-driven with relatively high water temperatures (20–26°C), heavy rainfall (mean annual precipitation = 360 cm), and low seasonality (Waide and Reagan 1996). The Quebrada Prieta originates at 550 m asl and flows through a closed canopy of mature 2^{nd}-growth rainforest, which is dominated by *Dacryodes excelsa* (Waide and Reagan 1996), until its confluence with the Sonadora at 310 m asl.

Xiphocaris elongata, a freshwater shrimp, is the most abundant macroinvertebrate in the Quebrada Prieta, and occurs at most elevations in the Luquillo streams (Covich and McDowell 1996). It often reaches densities $>6/m^2$ (Crowl et al. 2001, March et al. 2002). *Xiphocaris elongata* is a shredder, particle feeder, and predator (Covich et al. 1999), and plays an important role in the breakdown of leaf litter and nutrient cycling in these tropical streams (Crowl et al. 2001, 2002).

Methods

Allochthonous inputs

Allochthonous leaf-litter inputs were quantified within the Quebrada Prieta to determine dominant riparian species entering the study stream and the sources of the litter. Species composition and biomass of allochthonous inputs were quantified from litter captured in traps in 3 source areas: terrestrial bank runoff (terrestrial), overhanging vegetation (aerial), and downstream transport (aquatic). Litter traps were placed in 4 different study reaches. Terrestrial inputs were quantified from one triangular bank trap (galvanized wire-mesh, 0.35-m^2 openings, total volume = 350 cm^3) placed on each stream bank (slopes varying from 40–60°) with the openings oriented upslope to capture terrestrial inputs. Aerial inputs were quantified from plastic-mesh nets (1-cm^2 mesh size, total area = 2.1 × 1.3 m) suspended 2 m above the stream by cotton ropes tied to each corner of the net and attached to the nearest adjacent trees. Aquatic inputs were quantified from 2 triangular submerged traps (same construction as bank traps) placed at the upstream end of each study reach with the openings oriented upstream.

All organic matter captured in the traps was collected weekly from 2 June to 28 July 2003. Leaves of *Prestoea montana*, an important riparian species to this tropical montane community, can reach sizes as great as 1 to 3 m long × 0.5 m wide. Thus, these leaves sometimes exceeded the size of our traps, and large single leaves could have biased a sample towards this species. When *P. montana* leaves were partially touching the traps, the leaf area that covered the mouth of the trap was cut and retained and the rest of the leaf was discarded. Organic matter was transported to the lab, air dried for 48 h, and identified to species. Following identification, organic matter was separated by species, oven dried at 55°C for 48 h, and weighed to determine dominant species composition and to compare the relative contributions of litter inputs from each input source.

Input source/conditioning history

Fresh green leaves were used in our experiments instead of fallen brown leaves because a high % of litter biomass (64.6 ± 4.8%) collected in the stream consisted of green or yellow leaves, indicating that leaves were displaced from trees by wind or rain before natural abscission occurred. This composition was consistent throughout the collection period, including weeks without heavy winds.

Leaves of 4 of the most common riparian species entering the study reaches (the trees *Dacryodes excelsa* and *Manilkara bidentata*, the palm *Prestoea montana*, and the vine *Rourea surinamensis*), were picked from the trees, air dried overnight, placed in nylon mesh bags, and exposed in the stream, on the stream bank soil, or suspended above ground from an overhanging tree for 2 wk. These placements were intended to mimic the conditioning history that leaves from each of the 3 major sources of leaf litter entering the streams would experience. At the end of the 2-wk conditioning period, the leaves were removed from the bags, dried at room temperature for 12 h, and cut into 2.6-cm-diameter leaf discs using a cork corer. All leaf discs were weighed and placed in laboratory microcosms for shrimp feeding trials.

Shrimp feeding trials

Feeding trials were done to determine if the species/conditioning history of leaves and presence/absence of the dominant macoinvertebrate shredder (*X. elongata*) influenced the decomposition rate of the leaves. Shrimp were captured using baited wire-mesh funnel traps (Covich et al. 1996) in the Quebrada Sonadora and were starved for 24 h before the trials. The trials were run in small microcosms (plastic boxes, 31.2 × 17.2 × 10 cm). Microcosms were filled with 2.2 L water and allowed to stand with aeration for 24 h. At the beginning of the feeding trial, 5 leaf discs were randomly placed into each microcosm so that each microcosm had one leaf species with one conditioning history. Each leaf species/conditioning history treatment was replicated 6×. Five *X. elongata* (14.8 ± 0.08 mm, mean carapace length ± 1 SD) were placed in 4 of the 6 replicate microcosms in each treatment, and the remaining 2 replicates in each treatment were used as controls (no shrimp). One randomly chosen leaf disc was removed from each microcosm every 4 d. Discs were frozen for 24 h to eliminate further breakdown, oven-dried at 55°C for 48 h, and weighed. If the microcosm contained shrimp, one shrimp was removed at the same time each leaf disc was removed to maintain equal resource availability throughout the experimental period. All fecal material was siphoned from each container every 1 to 3 d to eliminate this material as a potential food source.

Data analysis

Data were analyzed using SAS (version 8.0, SAS Institute, Cary, North Carolina). Analysis of variance (ANOVA) was used to compare amounts of allochthonous inputs among sources (bank trap, aerial net, submerged trap). Analysis of covariance (ANCOVA) was used to compare the effects of shrimp and conditioning history on leaf mass loss and decomposition rates.

A standard negative exponential model, $m_t = m_0 e^{-kt}$, where m_t is final mass, m_0 is initial mass, and t is time (d) was used to calculate decomposition rate (k). However, to enhance the robustness of the ANCOVAs, the decomposition equation was linearized to

$$\ln(m_t) = \ln(m_0) - kt.$$

Two sets of ANCOVA analyses were used. In the 1st set, each leaf species was analyzed separately with conditioning history as the main effect and days as the covariate, and separate analyses were run with and without shrimp. The fraction of mass remaining each day was used as the response variable. These comparisons allowed us to determine the effect of conditioning history on breakdown rates without the dominant macroshredder (microbial breakdown only) and to determine whether conditioning history affected shrimp consumption rates. In the 2nd set of ANCOVAs, each leaf species was analyzed separately with conditioning history and shrimp presence/absence as main effects and days as the covariate. The fraction of mass remaining was used as the response variable. This analysis allowed us to determine the direct effect of shrimp consumption on leaf breakdown separately from the effect of conditioning history. We separated the analyses into components that addressed the individual questions regarding shrimp and conditioning to provide straightforward, easily interpretable results. We considered *p*-values <0.05 highly significant and *p*-values <0.10 marginally significant. Our justification is based on our observation that those treatment effects with *p*-values between 0.05 and 0.10 often are still biologically significant. Three-way ANCOVAs could have been used to address all questions simultaneously, but we still would have had to use a statistical approach to decompose pairwise comparisons to interpret the results.

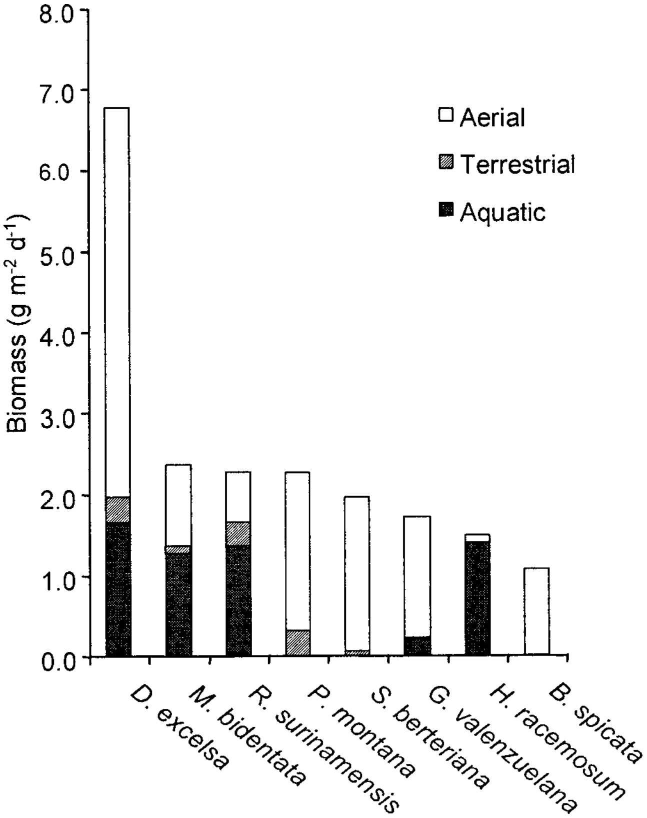

FIG. 1. Allochthonous input rates of leaf litter from common plant species (*Dacryodes excelsa, Manilkara bidentata, Rourea surinamensis, Prestoea montana, Sloanea berteriana, Guettarda valenzuelana, Homalium racemosum,* and *Byrsonima spicata*) in the Luquillo Experimental Forest based on biomass in aerial, terrestrial, and aquatic litter traps.

Results

Allochthonous inputs

The 4 most abundant (biomass) species of leaf litter found in the aquatic traps were *D. excelsa, Homalium racemosum, R. surinamensis,* and *M. bidentata. Dacryodes excelsa, R. surinamensis,* and *P. montana* were most common in the terrestrial traps, and *D. excelsa, P. montana, Sloanea berteriana,* and *Guettarda valenzuelana* were most abundant in the aerial traps (Fig. 1). Across all sampling methods, *D. excelsa* was by far the most abundant (6.8 g m^{-2} d^{-1}). *Manilkara bidentata, R. surinamensis,* and *P. montana* were also common (by biomass) leaves entering stream litter pools. On a daily basis, inputs were highest from aerial sources (13.0 g m^{-2} d^{-1}), intermediate (5.9 g m^{-2} d^{-1}) by aquatic transport, and lowest (1.0 g $m^{-2}d^{-1}$) from terrestrial sources (Fig. 1).

Leaf breakdown and shrimp feeding

In the absence of shrimp, conditioning history did not significantly affect leaf breakdown rate of D. excelsa, M. bidentata, P. montana, or R. surinamensis (Table 1). *Rourea surinamensis*, an understory vine, did show a marginally significant conditioning-history effect (ANOVA, $p = 0.08$; Table 1). Leaves that were placed in the stream for 2 wk (aquatic conditioning) lost mass slightly faster than leaves with other conditioning histories. When shrimp were present, breakdown rates were independent of conditioning history for all leaf species (Table 1). The fraction of mass remaining decreased significantly and exponentially as a function of time but independent of conditioning history.

Dacryodes excelsa (Fig. 2A–C), M. bidentata (Fig. 3A–C), P. montana (Fig. 4A–C), and R. surinamensis (Fig. 5A–C) leaves lost significantly more mass in the presence of shrimp than in the absence of shrimp,

TABLE 1. Analysis of variance table for the feeding experiment comparing the effects of conditioning history (aquatic, terrestrial, or aerial) on leaf breakdown rates for 4 abundant species of leaves in Luquillo Experimental Forest in the presence and absence of shrimp.

	No shrimp		Shrimp	
Leaf spp.	*F*	*p*	*F*	*p*
Dacryodes excelsa	0.03	0.9718	0.56	0.5723
Manilkara bidentata	0.55	0.5827	0.63	0.5337
Prestoea montana	0.71	0.4981	0.18	0.8332
Rourea surinamensis	2.69	0.0844	0.12	0.8884

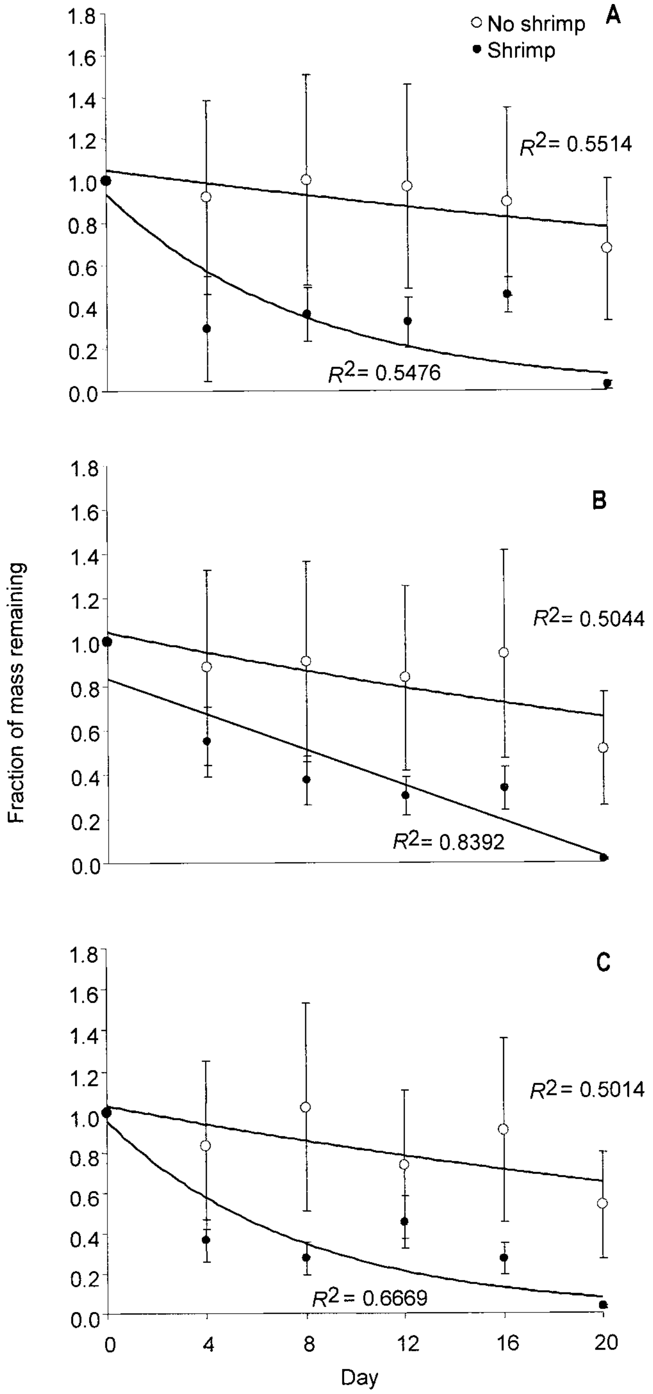

FIG. 2. *Dacryodes excelsa* breakdown rates with shrimp (treatment) and without shrimp (control). A.—Aquatic conditioning. B.—Aerial conditioning. C.—Terrestrial conditioning.

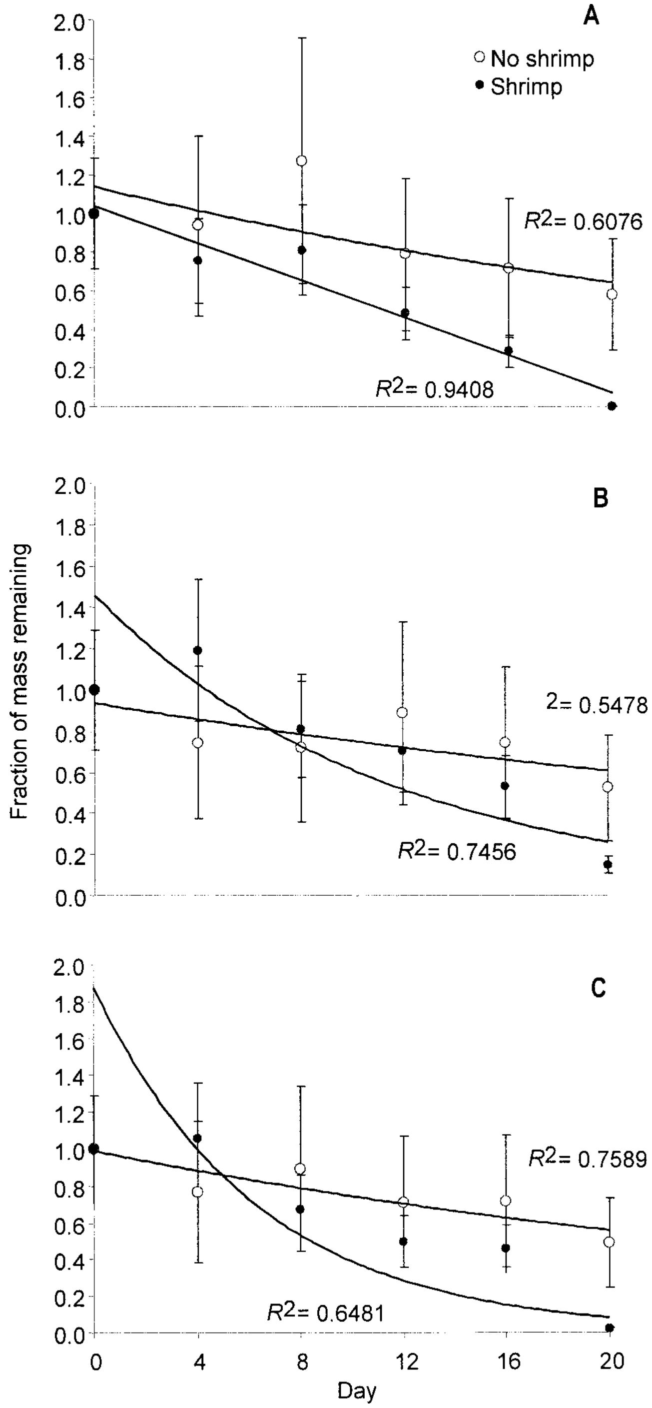

FIG. 3. *Manilkara bidentata* breakdown rates with shrimp (treatment) and without shrimp (control). A.—Aquatic conditioning. B.—Aerial conditioning. C.—Terrestrial conditioning.

regardless of conditioning history or leaf species (Table 2). The single exception was *M. bidentata* leaves that were aerially conditioned (Fig. 3B); this species showed no overall treatment effect (ANCOVA, $p = 0.7332$). In 10 of the 12 treatment combinations, a significant time × treatment (shrimp) effect suggested that the rate of mass loss was significantly higher in the presence of shrimp than in the absence of shrimp (Table 2). Only *P. montana* with aquatic and aerial conditioning histories had similar breakdown rates in shrimp-present and shrimp-absent treatments (Fig. 4A, B). For all 12 treatment combinations, significantly less leaf biomass remained by the end of experiment when shrimp were present than when they were not. Across conditioning histories, *k* values for all 4 species were 1 to 2 orders of magnitude higher in the presence of shrimp than in the absence of shrimp (Table 3).

Discussion

Allochthonous inputs

The abundance of *D. excelsa*, the characteristic species of the Tabonuco forest type, from all litter sources (aerial, terrestrial, and aquatic) suggests that this dominant forest community species is also one of the most important in terms of riparian litter inputs into the stream. Over the 2 mo sampling period, total inputs averaged 6.8 g dry mass/d, almost 3× higher than any other species. Tabonuco (*D. excelsa*) was, by far, the most abundant species in the aerial and terrestrial traps (Fig. 1). The vine *R. surinamensis* was one of the most abundant species in the terrestrial traps, a pattern that can be explained by the frequent presence of juveniles on the banks. Palm leaves (*P. montana*) were the 2nd-most abundant species collected in our aerial traps. Palms are abundant along the Prieta, but only a few leaves contribute to the overall detritus input directly because most leaves remain attached to the trunk and decompose above ground. Palms also can intercept the upper-canopy leaf fall from taller species, thereby delaying or preventing upper-canopy leaves from falling to the ground or entering the stream. These delays can create a wide array of variously decomposed leaf litter that enters the ground or stream litter during storms (Covich 1988).

Our observation that inputs from aerial (overhanging vegetation) sources are greater than from terrestrial (bank transport) sources is consistent with other findings (Cillero et al. 1999). The flow of organic matter into terrestrial bank traps is correlated with bank slope (Ractliffe et al. 1995), suggesting that significant terrestrial inputs would be expected only for deeply incised stream sections with steep bank slopes. Our sampling areas in the Luquillo Long-Term Ecological Research (LTER) site have moderate to steep (30–60%) slopes (Crowl et al. 2001, Covich et al. 2003), which are characteristic of the Quebrada Prieta.

Terrestrial leaf litter in the Luquillo Experimental Forest is broken down by basidiomycetes, and networks of fungal hyphae can hold litter in place even on steep slopes (Lodge and Asbury 1988). The effectiveness of this mechanism for retaining leaf litter and preventing its movement into stream channels is dependent on the continuously moist conditions in these aseasonal climates. When droughts do occur, fungal growth decreases and leaf litter accumulates so that pulses of litter can enter stream channels during initial stages of storm flows.

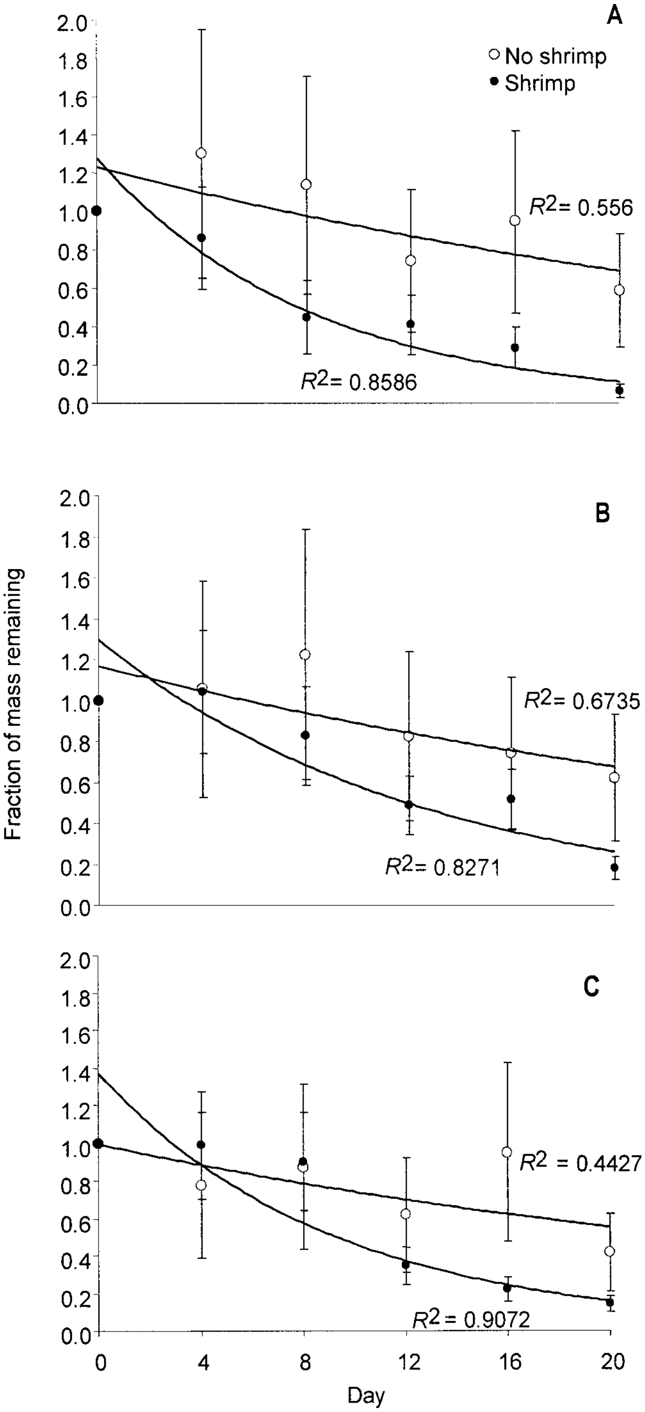

FIG. 4. *Prestoea montana* breakdown rates with shrimp (treatment) and without shrimp (control). A.—Aquatic conditioning. B.—Aerial conditioning. C.—Terrestrial conditioning.

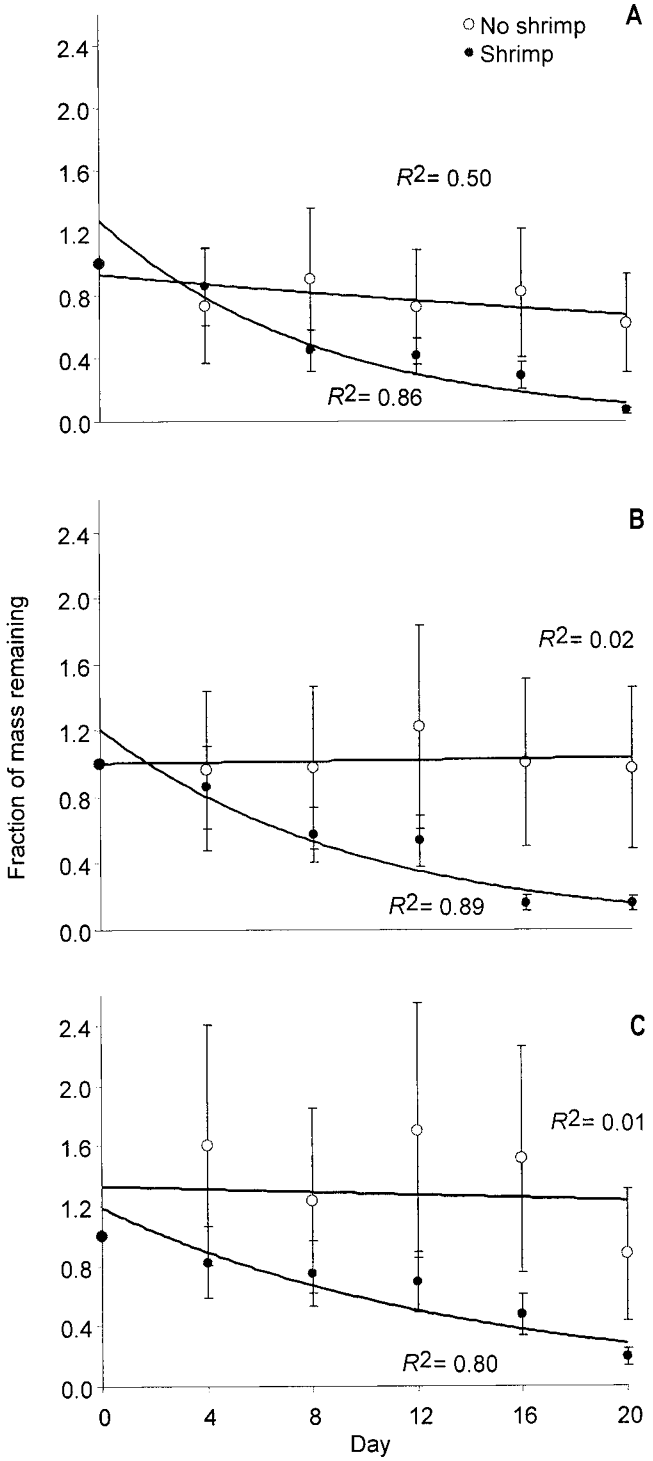

FIG. 5. *Rourea surinamensis* breakdown rates with shrimp (treatment) and without shrimp (control). A.—Aquatic conditioning. B.—Aerial conditioning. C.—Terrestrial conditioning.

Leaf breakdown and shrimp processing

Preferential feeding on conditioned leaves is well documented for shredder species from both temperate (Bärlocher and Kendrick 1973, Arsuffi and Suberkropp 1989, Graça et al. 1993, 2001) and tropical streams (Irons et al. 1994, Graça et al. 2001). Results from experiments designed to determine the importance of microbial processing typically find a synergistic response between conditioning and the presence of shredders (Wright and Covich 2005a, b). That is, leaves that have been microbially processed are broken down faster by shredders than those that have not. We did not measure microbial biomass or chemical changes among conditioning treatments, but we did quantify changes in leaf mass over time. This approach allowed us to compare breakdown rates with and without shrimp among conditioning treatments. Our results provide no support for the notion that conditioning affects shrimp processing rates, at least for green leaves over short periods of time. Rather, conditioning history had almost no effect on leaf consumption rates by *X. elongata*, the most abundant leaf consumer in these streams.

In temperate streams, microbial biomass on leaves usually peaks at ~4 wk (Hieber and Gessner 2002). Relative to experiments in temperate streams, 2 wk is a short time for conditioning, but Mathuriau and Chauvet (2002) found that microbial biomass on leaves peaked by day 10 in a tropical Colombian stream. We were working in a very moist warm forest, and the presence of a white fungus on the terrestrially conditioned leaves and aquatic hyphomycetes on the aquatically conditioned leaves provided direct evidence that conditioning did occur in our study. Two weeks was adequate to mimic conditioning history of most green/yellow leaves entering these streams.

The relative contribution of microbes vs macroinvertebrate shredders to leaf decomposition usually is evaluated by correlating the biomass of each decomposer group with the measured breakdown rates of senescent leaves (Baldy et al. 1995, Hieber and Gessner 2002). Such a comparison is not possible for this ecosystem, where our primary macroinvertebrate shredder is a relatively large, highly mobile consumer that does not colonize the food substrate. Our approach of measuring biomass loss rates in the presence and absence of the dominant shredder should provide a direct estimate of the relative importance of macroconsumers vs microbes. Rates of mass loss were significantly higher when shrimp were present than when decomposition was a result of microbial activity only. In most cases, <30% of the leaf mass was lost by

TABLE 2. Analysis of covariance table for the feeding experiment comparing the effects of the presence or absence of shrimp (treatment) on leaf breakdown rates of 4 species of leaves with 3 conditioning histories (aquatic, terrestrial, or aerial).

Riparian species	Conditioning history	Effect	*F*	*p*
Dacryodes excelsa	Aerial	Time × treatment	7.83	0.0086
		Treatment	53.41	0.0001
	Aquatic	Time × treatment	3.4	0.0704
		Treatment	49.15	0.0001
	Terrestrial	Time × treatment	3.39	0.0747
		Treatment	42.22	0.0001
Manilkara bidentata	Aerial	Time × treatment	3.28	0.0793
		Treatment	0.12	0.7332
	Aquatic	Time × treatment	3.89	0.0573
		Treatment	14.36	0.0006
	Terrestrial	Time × treatment	7.39	0.0105
		Treatment	4.18	0.0492
Prestoea montana	Aerial	Time × treatment	1.51	0.2284
		Treatment	4.59	0.0399
	Aquatic	Time × treatment	1.85	0.1835
		Treatment	13.95	0.0007
	Terrestrial	Time × treatment	9.54	0.0041
		Treatment	5.90	0.0209
Rourea surinamensis	Aerial	Time × treatment	13.79	0.0008
		Treatment	29.93	0.0001
	Aquatic	Time × treatment	20.26	0.0001
		Treatment	33.31	0.0001
	Terrestrial	Time × treatment	5.39	0.0268
		Treatment	45.36	0.0001

day 20 in the absence of the shredders, whereas >90% was lost when shrimp were present. We cannot comment on the actual role of microbial processing on the leaves in this experiment, but we can infer that shrimp are much more effective in consuming the material and processing it than are microbes alone.

Our breakdown rates (Table 3) are among the highest published values. When shrimp were present, breakdown rates for *M. bidentata* averaged 0.2563/d, and all other leaves showed breakdown rates of ≥0.1/d. *Xiphocaris elongata*, while certainly functioning as a shredder, also consumes leaves at the same rate as the most efficient terrestrial herbivores.

Whether shredders consume leaf material directly as an energy source or enhance breakdown of leaves secondarily while consuming bacteria and fungi has a long history of debate in the aquatic literature (see Gessner et al. 1999 for a review). For most ecosystems, shredders are relatively small invertebrates, typically insect larvae or amphipods, that cannot manipulate large leaves. In this tropical ecosystem, the shrimp shredders are relatively large and physically capable of using the wide size range of available leaf litter. Previously estimated values of consumption rates between 10 and 80% of biomass/d (Hieber and Gessner 2002) are well within the realm of our observed consumption rates. The shrimp used in this experiment averaged 0.2 g dry mass. If we use a consumption rate of 0.4 mg leaf mass consumed per mg body mass of the consumer per day (Hieber and Gessner 2002), we would estimate a consumption rate of 80 mg shrimp^{-1} d^{-1}. Shrimp actually consumed an average of 3.8 mg shrimp^{-1} d^{-1} of *M. bidentata*, the leaf type that lost mass fastest. We have initiated a study to measure growth and assimilation rates of shrimp feeding on microbially colonized leaves and on unconditioned leaves to directly assess the importance of leaf material as a direct energy source for these macroconsumers.

Whether shredders are absent from tropical stream ecosystems also has received considerable discussion in the literature (sensu Dobson et al. 2002). Data from Hong Kong (Dudgeon 1989, Dudgeon and Wu 1999),

TABLE 3. Mean leaf decomposition rates (*k*) for leaf species with and without shrimp. Values were obtained by fitting a least-squares best-fit regression to the natural log of the % mass remaining regressed against time (d).

	No shrimp		Shrimp	
Riparian Species	*k*	SE	*k*	SE
Dacryodes excelsa	0.0181	0.0026	0.1729	0.0183
Manilkara bidentata	0.0278	0.0042	0.2563	0.0305
Prestoea montana	0.0219	0.0041	0.1347	0.0194
Rourea surinamensis	0.0019	0.0042	0.1180	0.0161

Costa Rica (Pringle and Ramírez 1998, Rosemond et al. 1998), New Guinea (Yule 1996), and Kenya (Dobson et al. 2002) all suggest very low abundance or richness of shredder taxa. One hypothesis is that high temperatures and high microbial community activities may render detritus an unpredictable, low-availability resource, but many estimates of standing stock biomass of coarse particulate organic matter in tropical ecosystems have suggested otherwise (Dobson et al. 2002, Crowl et al. 2002). These data indicate that the definition of the shredder functional group may need to be expanded to include additional taxa for those tropical streams that are dominated by omnivorous decapods. Decapods may be one of the most important shredders because of their large body sizes (relative to aquatic insects and amphipods) and broad feeding habitats. When they are locally abundant, decapods may significantly alter the detrital pathway by greatly increasing detrital breakdown rates to levels well above rates caused by microbial activity alone, thereby altering the dynamics of the entire detrital food web.

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Literature Cited

Allan, J. D. 1995. Stream ecology: structure and function of running waters. Chapman and Hall, London, UK.

Arsuffi, T. L., and K. Suberkropp. 1989. Selective feeding by shredders of leaf-colonizing stream fungi: comparison of macroinvertebrate taxa. Oecologia (Berlin) 79:30–37.

Baldy, V., M. O. Gessner, and E. Chauvet. 1995. Bacteria, fungi and the breakdown of leaf litter in a large river. Oikos 74:93–102.

Bärlocher, F., and B. Kendrick. 1973. Fungi and food preferences of *Gammarus pseudolimnaeus*. Archiv für Hydrobiologie 72:501–526.

Benstead, J. P. 1996. Macroinvertebrates and the processing of leaf litter in a tropical stream. Biotropica 28:367–375.

Campbell, I. C., K. R. James, B. T. Hart, and A. Devereaux. 1992. Allochthonous coarse particulate organic material in forest and pasture reaches of two south-eastern Australian streams. I. Litter accession. Freshwater Biology 27:341–352.

Cheshire, K. L., L. Boyero, and R. G. Pearson. 2005. Food webs in tropical Australian streams: shredders are not scarce. Freshwater Biology 50:748–769.

Cillero, C., I. Pardo, and E. S. Lopez. 1999. Comparisons of riparian vs. over stream trap location in the estimation of vertical litterfall inputs. Hydrobiologia 416:171–179.

Covich, A. P. 1988. Geographical and historical comparisons of neotropical streams: biotic diversity and detrital processing in highly variable habitats. Journal of the North American Benthological Society 7:361–386.

Covich, A. P., T. A. Crowl, S. L. Johnson, and M. Pyron. 1996. Distribution and abundance of a tropical freshwater shrimp along a stream corridor: response to disturbance. Biotropica 28:484–492.

Covich, A. P., T. A. Crowl, and F. N. Scatena. 2003. Effects of extreme low flows on freshwater shrimps in a perennial tropical stream. Freshwater Biology 48:1199–1206.

Covich, A. P., and W. H. McDowell. 1996. The stream community. Pages 433–460 *in* D. P. Reagan and R. B. Waide (editors). The food web of a tropical rain forest. University of Chicago Press, Chicago, Illinois.

Covich, A. P., M. A. Palmer, and T. A. Crowl. 1999. Role of benthic invertebrate species in freshwater ecosystems. BioScience 49:119–127.

Crowl, T. A., A. P. Covich, F. N. Scatena, R. Phillips, M. J. Townsend, and D. K. Vinson. 2002. Particulate organic matter dynamics in tropical headwater streams: a comparison of biotic and abiotic factors. Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie 28:923–927.

Crowl, T. A., W. H. McDowell, A. P. Covich, and S. L. Johnson. 2001. Freshwater shrimp effects on detrital processing and nutrients in a tropical headwater stream. Ecology 82:775–783.

Cummins, K. W., R. C. Petersen, F. O. Howard, J. C. Wuycheck, and V. I. Holt. 1973. The utilization of leaf litter by stream detritivores. Ecology 54:336–345.

Dobson, M. 2004. Freshwater crabs in Africa. Freshwater Forum 21:3–26.

Dobson, M., A. Magana, J. M. Mathooko, and F. K. Ndegwa. 2002. Detritivores in Kenyan highland streams: more evidence for the paucity of shredders in the tropics. Freshwater Biology 47:909–919.

Dudgeon, D. 1982. An investigation of physical and biological processing of two species of leaf litter in Tai Po Kau forest stream, New Territories, Hong Kong. Archiv für Hydrobiologie 96:1–32.

DUDGEON, D. 1989. The influence of riparian vegetation on the functional organization of four Hong Kong stream communities. Hydrobiologia 179:183–194.

DUDGEON, D., AND K. K. Y. WU. 1999. Leaf litter in a tropical stream: food or substrate for macroinvertebrates? Archiv für Hydrobiologie 146:65–82.

FISHER, S. G., AND G. E. LIKENS. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecological Monographs 43:421–439.

GESSNER, M. O., AND E. CHAUVET. 1994. Importance of stream microfungi in controlling break down rates of leaf litter. Ecology 75:1807–1817.

GESSNER, M. O., E. CHAUVET, AND M. DOBSON. 1999. A perspective on leaf litter break down in streams. Oikos 85:377–384.

GRAÇA, M. A. S., F. BÄRLOCHER, AND M. O. GESSNER. 2005. Methods to study litter decomposition: a practical guide. Springer–Verlag, New York.

GRAÇA, M. A. S., C. CRESSA, M. O. GESSNER, J. J. FEIO, K. A. CALLIES, AND C. BARRIOS. 2001. Food quality, feeding preferences, survival and growth of shredders from temperate and tropical streams. Freshwater Biology 46: 947–957.

GRAÇA, M. A. S., L. MALTBY, AND P. CALOW. 1993. Importance of fungi in the diet of *Gammarus pulex* and *Asellus aquaticus* I. Feeding strategies. Oecologia (Berlin) 93:139–144.

HIEBER, M., AND M. O. GESSNER. 2002. Contribution of stream detrivores, fungi, and bacteria to leaf breakdown based on biomass estimates. Ecology 83:1026–1038.

IRONS, J. G., M. W. OSWOOD, J. R. STOUT, AND C. M. PRINGLE. 1994. Latitudinal patterns in leaf litter breakdown: is temperature really important? Freshwater Biology 32: 401–411.

LARNED, S. T., R. A. KINZIE, A. P. COVICH, AND C. T. CHONG. 2003. Detritus processing by endemic and non-native Hawaiian stream invertebrate: a microcosm study of species-specific effects. Archiv für Hydrobiologie 156: 241–254.

LODGE, D. J., AND C. E. ASBURY. 1988. Basidiomycetes reduce export of organic matter from forest slopes. Mycologia 80:888–890.

MARCH, J. G., C. M. PRINGLE, M. J. TOWNSEND, AND A. I. WILSON. 2002. Effects of freshwater shrimp assemblages along an altitudinal gradient of a tropical island stream. Freshwater Biology 47:1–14.

MATHURIAU, C., AND E. CHAUVET. 2002. Breakdown of leaf litter in a neotropical stream. Journal of the North American Benthological Society 21:384–396.

OSTROFSKY, M. L. 1997. Relationship between chemical characteristics of autumn-shed leaves and aquatic processing rates. Journal of the North American Benthological Society 16:750–759.

PADGETT, D. E. 1976. Leaf decomposition by fungi in a tropical rainforest stream. Biotropica 8:166–178.

PEARSON, R. G., AND R. K. TOBIN. 1989. Litter consumption by invertebrates from an Australian tropical rainforest stream. Archiv für Hydrobiologie 116:71–80.

PETERSEN, R. C. 1984. Detritus decompositon in endogenous and exogenous rivers of a tropical wetland. Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie 22:1926–1931.

POZO, J., E. GONZALEZ, J. R. DIEZ, J. MOLINERO, AND A. ELOSEGUI. 1997. Inputs of particulate organic matter to streams with different riparian vegetation. Journal of the North American Benthological Society 16:602–611.

PRINGLE, C. M., AND A. RAMÍREZ. 1998. Use of both benthic and drift sampling techniques to assess tropical stream invertebrate communities along an altitudinal gradient, Costa Rica. Freshwater Biology 39:359–373.

RACTLIFFE, S. G., B. R. DAVIES, A. S. STEWART, AND C. D. SNADDON. 1995. The influence of discharge on entrainment of bank litter in a headwater stream. Archiv für Hydrobiologie 134:103–117.

ROBINSON, C. T., AND C. JOLIDON. 2005. Leaf breakdown and the ecosystem functioning of alpine streams. Journal of the North American Benthological Society 24:495–507.

ROSEMOND, A. D., C. M. PRINGLE, AND A. RAMÍREZ. 1998. Macroconsumer effects on insect detritivores and detritus processing in a tropical stream. Freshwater Biology 39:515–523.

STOUT, J. R. 1980. Leaf decomposition rates in Costa Rican lowland tropical rainforest streams. Biotropica 12:264–272.

STOUT, J. R. 1989. Effects of condensed tannins on leaf processing in mid-lattiude and tropical streams: a theoretical approach. Canadian Journal of Fisheries and Aquatic Sciences 46:1097–1106.

VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130–137.

WAIDE, R. B., AND D. P. REAGAN. 1996. The rainforest setting. Pages 1–13 *in* D. P. Reagan and R. B. Waide (editors). The food web of a tropical rain forest. University of Chicago Press, Chicago, Illinois.

WALLACE, J. B., S. L. EGGERT, J. L. MEYER, AND J. R. WEBSTER. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277:102–104.

WANTZEN, K. M., R. WAGNER, R. SETFELD, AND W. J. JUNK. 2002. How do plant-herbivore interactions of trees influence coarse detrital processing by shredders in aquatic ecosystems of different latitudes? Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie 28:815–821.

WEBSTER, J. R., AND E. F. BENFIELD. 1986. Vascular plant breakdown in freshwater ecosystems. Annual Review of Ecology and Systematics 17:567–594.

WEBSTER, J. R., AND J. L. MEYER. 1997. Organic matter budgets for streams: a synthesis. Pages 141–161 *in* J. R. Webster and J. L. Meyer (editors). Stream organic matter budgets. Journal of the North American Benthological Society 16.

WINTERBOURN, M. J. 1976. Fluxes of litter falling into a small beech forest stream. New Zealand Journal of Marine and Freshwater Research 10:399–416.

WRIGHT, M. S., AND A. P. COVICH. 2005a. The effect of macroinvertebrate exclusion on leaf breakdown rates in a tropical headwater stream. Biotropica 37:403–408.

WRIGHT, M. S., AND A. P. COVICH. 2005b. Relative importance of bacteria and fungi in a tropical headwater stream: leaf decomposition and invertebrate feeding preference. Microbial Ecology 49:536–546.

Yule, C. M. 1996. Trophic relationships and food webs of the benthic invertebrate fauna of two aseasonal tropical streams on Bougainville Island, Papua New Guinea. Journal of Tropical Ecology 12:517–534.

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