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Macroinvertebrates and the Processing of Leaf Litter in a Tropical Stream[1]

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ABSTRACT

The processing of leaf litter in temperate streams has been the subject of numerous studies but equivalent tropical ecosystems have received little attention. The decomposition and macroinvertebrate colonisation of leaf litter was investigated using litter bags placed in a first-order rainforest stream over a 48 day period. Changes in leaf chemistry were also studied. Decay of the fresh, mixed-species litter was rapid (2.5 % day^{-1}) in comparison to that typically observed in temperate streams. The high water temperatures (21°C) at the study site are considered an important factor in the decay rate observed. Initially, average nitrogen content was high (3.5%). Content decreased to 3.1 percent after six days immersion and, thereafter, remained relatively constant. The consequent lack of evidence for microbial conditioning was attributed to species-specific differences in decay rate, giving rise to an overlapping sequence of conditioning and mineralisation of each leaf species within individual litter bags. Soluble polyphenols were largely leached from litter during the initial period of immersion. Constancy in remaining polyphenol content may be due to complexing with proteins and/or lignin compounds. The invertebrate community which colonised litter bags was dominated by insect groups and species richness was lower than that typical of many temperate streams. Colonisation dynamics differed among functional feeding groups: collector abundance increased on a linear basis whereas shredder and predator groups increased logarithmically. Despite differences in decay rate and taxonomic composition of the invertebrate community, the pattern of leaf litter utilisation and decay in the tropical stream studied was similar to that typically observed in temperate streams.

RESUMEN

Los detritos de plantas que se acumulan en el agua, son una importante fuente de energía para las comunidades de riachuelos forestales. El procesamiento del material vegetal en riachuelos ha sido bien estudiado en zona templadas, pero en los trópicos se le ha dado poca atención. La descomposición y colonización por macroinvertebrados del material vegetal, fue estudiada colocando hojas en bolsas de tela, en riachuelos forestales de bajo orden, durante 48 días. También se estudiaron los cambios químicos ocurridos en las hojas. La descomposición de mezclas de hojas frescas de varias especies fue rápida (2,5% por día) si se compara con la que ocurre en riachuelos de zona templada. Se considera que las altas temperaturas del agua (21°C) en el sitio de estudio, son un factor importante en la tasa de descomposición observada. Al inicio, el contenido promedio de nitrógeno fue alto (3,5%), pero decreció a 3,1% seis diás despues, para luego permenecer constante de ahí en adelante. La falta de evidencia de colonización microbial, fue atribuida a diferencias en la tasa de descomposición entre las especies de plantas, lo cual produjo una secuencia traslapada de condicionamiento y mineralización de las hojas dentro de cada bolsa. Los polifenoles solubles fueron en su mayoría lixiviados del material vegetal, durante el periodo inicial de inmersión. La constancia observada en el contenido restante de polifenoles puede deberse al enlazamiento con proteínas o ligninas. La comunidad de invertebrados que colonizó las bolsas fue dominada fue dominada por grupos específicos de insectos. La diversidad de especies fue menor que la observada en riachuelos de zona templada. La dinámica de colonización fue diferente entre los distintos grupos funcionales: la abundancia de colectores se incrementó linearmente, en tanto que la de desmenuzadores y depredadores se incrementó logarítmicamente. A pesar de las diferencias en la tasa de decomposición y la composición taxonómica de la comunidad de invertebrados, el patrón de utilización de la materia orgánica y su descomposición en el riachuelo tropical estudiado fue similar a aquello que es típica de riachuelos de zona templada.

Key words: aquatic macroinvertebrates; carbon: nitrogen ratios; Costa Rica; leaf decomposition; Neotropics; polyphenols; tropical rainforest streams.

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STREAM COMMUNITIES IN FORESTED CATCHMENTS ARE GENERALLY DEPENDENT on allochthonous organic matter as a trophic base. The shading effect of riparian vegetation effectively limits *in situ* primary production and inputs of reduced carbon compounds are, therefore, of primary importance in the energy budgets of forest streams (Cummins *et al.* 1973, Fisher & Likens 1973, Cummins 1974). There is a considerable body of literature concerning the processing of catchment-derived detritus within stream habitats (see Anderson & Sedell 1979, Cummins & Klug 1979, Webster & Benfield 1986, Maltby 1992 for reviews; also Kaushik & Hynes 1971, Petersen & Cummins 1973). Studies have been based primarily on midlatitude streams, especially those of North American and European deciduous forests. In contrast, tropical streams have received very little attention. Existing evidence suggests that tropical forest stream communities, like their temperate equivalents, rely heavily on terrestrially produced detritus as a major energy source (Fittkau *et al.* 1975, Henderson & Walker 1986, Walker 1987, Covich 1988). Although litter processing has been investigated in the tropics (see Padgett 1976; Stout 1980, 1989; Dudgeon 1982; Pearson *et al.* 1989; Irons *et al.* 1994) quantitative, community-based studies are still scanty. This study investigated the colonisation of mixed-species leaf litter bags by macroinvertebrates in a low order Costa Rican forest stream. Subsequent processing and associated changes in leaf chemistry were also studied.

MATERIALS AND METHODS

STUDY SITE.—The study was conducted in an unnamed, first-order tributary of Quebrada Platanilla (altitude 675 m), Heredia Province, Costa Rica (10°17′N; 84°02′W), commencing on 16 July 1992. The study site was located within a private rainforest reserve on the Caribbean slope of the Cordillera Central. Annual mean temperature is 22°C (range 18–27°C). Annual rainfall averages 7500–8000 mm, with no pronounced dry season.

In order to minimise loss of litter bags during peak flow conditions, a pool (3–6 m wide) was chosen as the specific site of the study. Substrate varied from fine sand to large (70 cm maximum diam) boulders. Diurnal water temperature averaged 21°C during the study (range 20–21°C).

Vegetation in the catchment consists of premontane tropical rainforest (Premontane Perhumid Transition Life Zone; Holdridge *et al.* 1971) and includes approximately 500 canopy tree species. Few tree species are typically riparian in habit (A. Bien, pers. comm.). Of these, *Pachira aquatica* (Bombacaceae) and *Carapa guianensis* (Meliaceae) are the most abundant examples. Soils are extremely poor (pH < 5.0, soluble phosphorus barely detectable). The study site can be considered virtually pristine because of its protected nature and the absence of human activity within the catchment.

PREPARATION OF LITTER BAGS.—Litter bags (10 × 20 cm) were constructed from nylon mesh (8 × 6 mm) and cotton binding. Leaves were collected from the forest floor along a 3 km trail on the day the study commenced. Only leaves considered freshly fallen (*i.e.,* green and blemish-free) were chosen. After thorough mixing, leaves were picked blind and placed in litter bags (10 leaves per bag). Leaves were not selected on the basis of leaf or cuticle thickness, and no attempt was made to identify leaf species or enumerate leaf species richness in the litter bags. For practical reasons it was not possible to obtain initial weights of litter bag contents. In order to estimate the mean initial weight, thirty identical samples were dried and stored for subsequent weighing.

Small stones were added to each litter bag to ensure that contents were in contact with the stream bed. Litter bags were tied to 5 m lengths of nylon string at 50 cm intervals. Each length of string was secured at one end to riparian vegetation and placed in the stream parallel to the current.

COLLECTION AND PROCESSING OF LITTER BAGS.—Ten bags were subsampled after 3, 6, 12, 23, and 48 days by placing a small, fine-mesh net under each and cutting the attachment string. Litter bags were transferred to plastic bags and transported from the study site in stream water.

Invertebrates were subsequently washed from the leaves, sorted and preserved in 70 percent ethyl alcohol. Leaves and leaf fragments were placed in paper envelopes and dried. Macroinvertebrates were later counted and assigned to the highest possible taxonomic level (using letters to designate morphospecies). Where possible, insects were assigned to functional feeding group following Merritt and Cummins (1984). Leaves were dried at 100°C for 48 hours, cooled and weighed. The samples were then ground using a Moulinex grinder and passed through a 1 mm sieve.

ANALYSIS OF LITTER.—Polyphenols were extracted from 100 mg of ground leaves by boiling them in distilled water for 1 hour. Extracts were then filtered

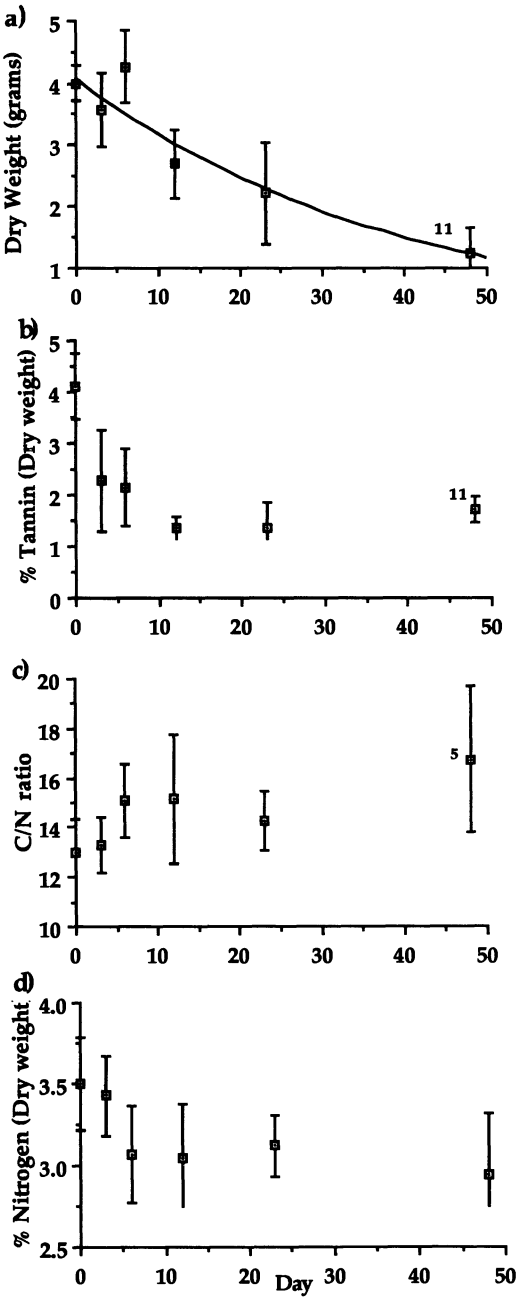

FIGURE 1. Change in (a), dry weight (b), percent soluble polyphenol content (measured as tannin), ($\bar{x}$ ± 1 SE, N = 30 at Day 0, N = 10 at other days unless specified) (c), C/N ratio and (d), percent total organic nitrogen of litter bag contents. ($\bar{x}$ ± 1 SE, N = 11 at Day 0, N = 6 at other days unless specified).

and made up to 50 ml volume. Polyphenol content was determined colorimetrically using reagent grade tannic acid as a standard (Allen 1974).

Carbon content was determined for 50 mg ground samples using a wet oxidation-titration technique (Allen 1974). Samples were boiled for 1 hour in an acid dichromate mixture and remaining dichromate subsequently titrated against a ferrous ammonium sulphate solution.

Total organic nitrogen was determined for 100 mg samples using the indo-phenol blue method after sulphuric acid-hydrogen peroxide digestion (Allen 1974).

ANALYSIS OF DATA.—Weight loss data were semilog transformed and decomposition rate, expressed as percent loss per day, calculated by fitting a linear model after checking for goodness-of-fit. For each sampling date, mean number and density (expressed as number per gram of leaf litter remaining) of invertebrates per bag were calculated for total invertebrates and for the two major functional feeding groups (shredders and collectors). Number of predators, species, and cumulative number of species was also calculated. Where statistically significant (P = 0.05), linear or logarithmic models were fitted to colonisation data.

RESULTS

DECAY RATE.—The exponential model $W_t = W_o^{e-kt}$ (where W_t is the amount of leaf litter remaining after time, t, of the initial amount W_o, and k is the processing coefficient) gave a highly significant fit (F value 71.94, P = 0.001) to the weight loss data. This model assumes that there is a constant fractional loss of the material present at any given time. The weight loss observed in this study, obtained from the processing coefficient k, was 2.5 percent of remaining leaf material per day (Fig. 1a). No immediate and dramatic weight loss due to leaching was observed in the initial period of the study. However, after 12 days, 32 percent of initial weight had been lost. The experiment was terminated after 48 days, at which time approximately 31 percent of initial weight of leaf litter remained.

Feeding activity, as indicated by stripping of mesophyll layers, was evident by day 6 of the study period. Case-building activity by calamoceratid caddis larvae was responsible for marked losses in leaf area throughout immersion. Cases were constucted from semicircles of leaf tissue cut from the edges of leaves. There was evidence for the selection of some leaf species for this purpose.

SOLUBLE POLYPHENOLS.—Initial levels of soluble polyphenols (measured as tannin) were moderate, with a mean content of 4.1 percent dry weight. Loss due to leaching in the first 3 days amounted to 44.8 percent of the initial content (Fig. 1b). High rates of loss continued until day 12 when a second phase, of little or no change in polyphenol content, was entered. Content remained at approximately 1.5 percent dry weight for the remainder of the study.

TOTAL ORGANIC NITROGEN (TON) AND C/N RATIO.—Carbon content remained relatively constant with very little difference between litter bags. The C/N ratio of litter bag contents (Fig. 1c) was therefore a negative function of TON content. Mean total organic nitrogen content was initially very high and the content also varied considerably between bags. The initial 6-days of immersion were characterised by a decrease in TON content (Fig. 1d). Although TON had increased slightly by day 23, the large differences in individual litter bag content persisted throughout immersion, making these differences statistically insignificant.

LITTER BAG FAUNA.—Macroinvertebrate colonisation of litter bags was rapid in the first 12 days of the study. Thereafter, rate of colonisation slowed and appeared to be reaching an asymptote by day 48 when the study was terminated (Fig. 2a). Density of colonising invertebrates (number per gram of leaf litter remaining) increased on a linear basis during the study (Fig. 2b).

The number of species (or morphospecies) present in the litter bags increased steadily in the first 23 days of the study (Fig. 2c). By day 48 species richness had declined. The cumulative species number curve (Fig. 2d) for all species recorded in litter bags during the course of the experiment was clearly reaching an asymptote by day 48.

Separation into functional feeding groups revealed considerable differences between the colonisation dynamics of shredders and collectors. Colonisation by shredders was rapid in the first 12 days. Thereafter, numbers per bag steadily declined (Fig. 3a). Shredder density data revealed that numbers per gram of leaf litter remained relatively constant after the initial period of rapid colonisation

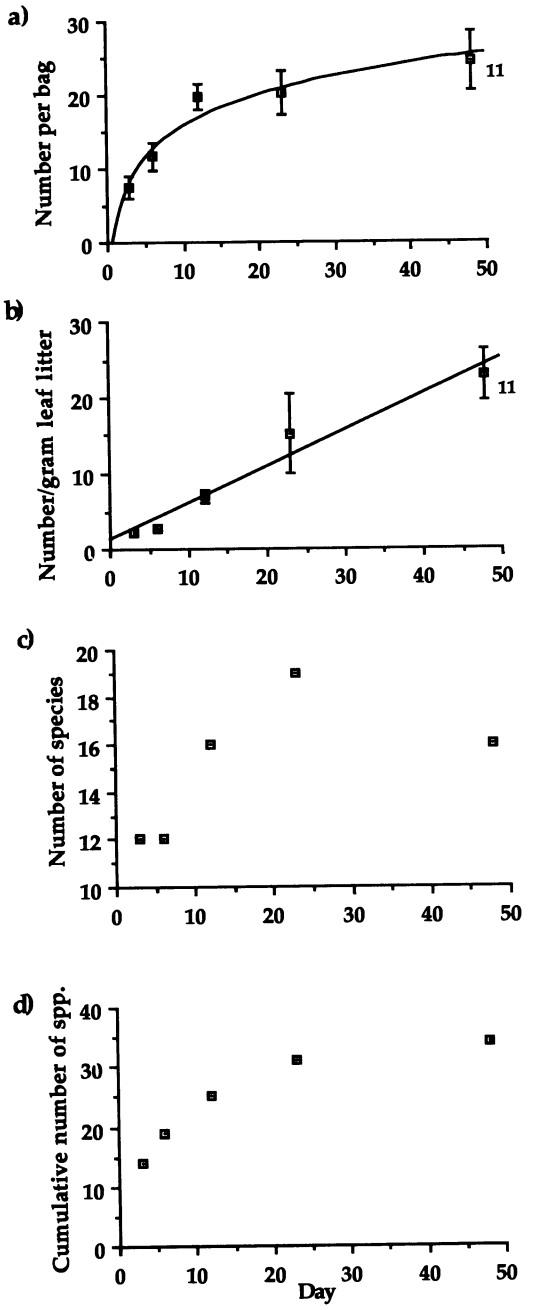

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FIGURE 2. (a) Number of macroinvertebrates per litter bag. Fitted logarithmic curve ($N_t = 5.39, t^{0.43}$ where N_t is the number of macroinvertebrates at time t, F-value = 27.09, $P = 0.014$) (b), density of macroinvertebrates (number per gram of leaf litter remaining) in litter bags. Fitted regression line ($D_t = 1.22 + 0.47t$ where D_t is the density of macroinvertebrates at time t, F-value = 72.58, $P = 0.003$), ($\bar{x} \pm 1$ SE, $N = 10$ unless specified) (c), number of morphospecies recorded at each sampling date and (d), cumulative number of morphospecies recorded in the litter bags during the study period (Chironomidae excluded, see text).

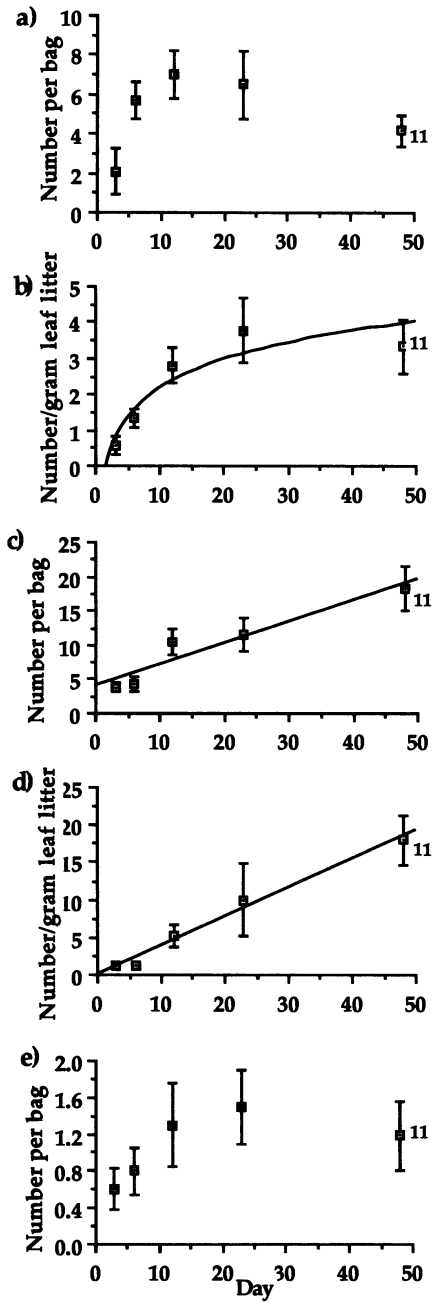

FIGURE 3. Change in (a), number of shredders in litter bags (b), density of shredders (number per gram of leaf litter remaining) in litter bags. Fitted logarithmic curve ($D_t = 0.374, t^{0.66}$ where D_t is the density of shredders at time t, F-value = 14.23, $P = 0.03$) (c), number of collectors in litter bags. Fitted regression line ($N_t = 3.96 + 0.31t$ where N_t is the number of collectors at time t, F-value = 30.92, $P = 0.01$) (d), density of collectors (number per gram of leaf litter remaining) in litter bags. Fitted regression line ($D_t = 0.06 + 0.38t$ where D_t is the density of collectors at time t, F-value = 194.62, $P = 0.001$) (e), number of macroinvertebrate predators in litter bags. ($\bar{x} \pm 1$ SE, $N = 10$ unless specified).

TABLE 1. *Composition of litter bag fauna in study stream, 1992 (Co = collector/gatherer, Sh = shredder, Fi = filterer, Pi = piercer, Sc = scraper, Pr = predator).*

Taxon	Total	Percent composition	Feeding group
Bivalvia	2	0.2	Fi
Amphipoda	6	0.7	Sc/Sh
Ephemeroptera			
Thraulodes sp. A	249	29.9	Co
Paraleptophlebiidae sp. A	4	0.5	Co
Ulmeritus sp. A	2	0.2	Co
Tricorythides sp. A	83	9.6	Co
Trichoptera			
Triplectides flintorum	138	16.0	Sh
Leptoceridae sp. A	5	0.6	Pr
Leptoceridae sp. B	2	0.2	?
Leptoceridae sp. C	3	0.3	?
Leptoceridae sp. D	1	0.1	?
Calamoceratidae sp. A	135	15.7	Sh
Hydropsychidae sp. A	2	0.2	Co/Fi
Hydroptilidae sp. A	4	0.5	Pi
Polycentropodidae sp. A	2	0.2	Co/Fi
Odonata			
Zygoptera sp. A	4	0.5	Pr
Zygoptera sp. B	1	0.1	Pr
Zygoptera sp. C	17	2.0	Pr
Zygoptera sp. D	6	0.7	Pr
Zygoptera sp. E	1	0.1	Pr
Zygoptera sp. F	1	0.1	Pr
Zygoptera sp. G	3	0.3	Pr
Zygoptera sp. H	1	0.1	Pr
Plecoptera			
Anacroneuria sp. A	4	0.5	Pr
Coleoptera			
Elminthidae adult sp. A	1	0.1	Co/Sc
Coleoptera larva sp. A	3	0.3	?
Coleoptera larva sp. B	2	0.2	?
Coleoptera larva sp. C	2	0.2	?
Coleoptera larva sp. D	2	0.2	?
Coleoptera larva sp. E	1	0.1	?
Hemiptera			
Naucoridae sp. A	6	0.6	Pr
Diptera			
Tabanidae sp. A	2	0.2	Co
Chironomidae spp.	161	18.7	Co
Oligochaeta	2	0.2	Co
Platyhelminthes	3	0.3	Pr
Total individuals	862		

(Fig. 3b). Number and density of collectors both increased on a linear basis throughout the study (Figs. 3c and 3d). Rates of increase in number and density were similar.

The pattern of predator colonisation was broadly similar to that of the shredder group (Fig. 3e). Colonisation was rapid and numbers increased until day 23. By the end of the study, however, numbers were clearly declining.

For reasons of taxonomic difficulty no attempt was made to assign bivalves, amphipods, oligochaetes, and platyhelminthes to morphospecies. Numerically these groups were of little importance, accounting for 1.4 percent of the litter bag fauna. Although the chironomids were of numerical importance (18.7% of macroinvertebrates), similar problems prevented morphospecies assignment in this group. Excluding these groups, thirty species or morphospecies colonised the litter bags during the course of the study (see Table 1). Of these, four taxa constituted 71.2 percent of the individuals: two shredder caddis species, *Triplectides flintorum* (16%) and Calamatoceridae sp. A (15.7%), and two collector/gatherer mayfly species, *Thraulodes* sp. A (29.9%) and *Tricorythides* sp. A (9.6%).

DISCUSSION

In contrast to many investigations of leaf litter processing, a sharp decrease in initial weight due to immediate loss of leachates was not observed in this study. This pattern of weight loss was possibly a function of the fresh, undried nature of the leaves used. Recent work has outlined the effect of preexposure drying (a procedure adopted for practical reasons in many studies) on leaching (Gessner & Schwoerbel 1989, Bärlocher 1991, Gessner 1991). These studies indicate that drying, by damaging the cuticle layer or destroying leaf cell integrity, gives rise to an artificially rapid loss of soluble compounds and, consequently, the established view of rapid leaching as a characteristic component of the breakdown process is now in doubt. In addition, many tropical plants have leaves with very thick cuticles, an adaptation which prevents leaching by high rainfall and which acts as a deterrent to some herbivores. These factors may explain the relatively slow initial weight loss observed in this study.

As in many other studies (Petersen & Cummins 1974, Bunn 1988, Pearson *et al.* 1989) weight loss data fitted an exponential model. This model assumes that there is a constant fractional loss of the leaf litter present at any given time, in comparison with a linear model which assumes a constant fractional loss of the initial mass with time. The loss of 2.5 percent day^{-1} is rapid in comparison to most studies, and the processing rate can be considered particularly fast given the mixed-species nature of the litter bags. Species-specific differences in leaf breakdown rates are well documented (Petersen & Cummins 1974, Padgett 1976). Petersen and Cummins (1974) found a "hierarchy of species along a processing continuum" and separated leaf species into three categories, according to rate of processing. Species with a processing coefficient, k, of greater than 0.01 day^{-1} were placed in the "fast" group. Although species-specific differences in decay rate were obvious in individual litter bags, the diverse multispecies assemblages used in this study had an overall processing coefficient of 0.025 day^{-1}, suggesting that the fast processing rate was not determined solely by species composition of the litter bags. Dudgeon (1982) concluded that the rapid processing rate in a subtropical Hong Kong stream was largely due to high ambient temperature, and it seems likely that high temperature, in comparison to temperate streams, was an important contributing factor in this study. High water temperature would give rise to rapid microbial conditioning of leaf litter, with a potential, subsequent increase in the rate of consumption by the shredder community. Recently however, Irons *et al.* (1994) have hypothesized that the relative importance of insect and microbial communities in leaf litter breakdown exhibits an approximately inverse relationship along latitudinal (*i.e.,* thermal) gradients, the microbial community being the more important consumers in low-latitude, relatively warmer streams. It seems likely, therefore, that microbial activity was mainly responsible for the observed litter breakdown.

Change in soluble polyphenol content of leaf litter provides insight into the loss of an important group of secondary defence compounds and, in addition, indicates loss of other mobile components (Gessner 1991). Polyphenols were leached rapidly as expected in the initial period of the study. Thereafter content remained stable. This stability suggests that a certain fraction of these compounds existed in complexes that were resistant to leaching at ambient water temperatures. Phenolic compounds, such as tannins, are known to complex with lignin and proteins, thereby forming very stable, resistant compounds (Suberkropp *et al.* 1976). It seems likely that this complexing process was responsible for the observed constancy in polyphenol content during the latter part of the study period. Phenolic compounds and condensed tannins are potential inhibitors of biotic litter processing (Stout 1989). How-

ever, this and two recent temperate studies (Ostrofsky 1993, Campbell & Fuchshuber 1995) have revealed little correlation between polyphenol levels and breakdown rates. Presumably, any effects of phenolic compounds and condensed tannins on litter processing are, under certain field conditions, swamped by other factors.

Nitrogen content remained relatively constant after the initial decrease. Microbial colonisation of leaf litter generally gives rise to an increase in nitrogen content. Although a lack of any sequential increase in nitrogen was observed in a similar tropical study (Padgett 1976), the results obtained are thought to be due to the mixed-species nature of the leaves used in this study. In such taxonomically diverse leaf assemblages, species-specific differences in decay rates would give rise to an overlapping sequence in conditioning, and subsequent mineralisation, of individual leaves. As a result, no single peak in microbial nitrogen would be observed. That increases in nitrogen content of litter are typically observed only in single-species accumulations supports this explanation. Consequently, the lack of evidence for microbial conditioning is believed to be an artefact of the method used in this study.

A ratio of carbon to nitrogen of approximately 10:1 is considered optimal for the decomposition of organic material (Alexander 1977). The initial C/N ratio of leaf litter approached this value, but subsequently increased with immersion, indicating a decline in nutritional quality. Despite this decline, the C/N ratio remained at a level which can be considered relatively low, indicating that the high quality of the leaf litter as a food resource was sustained throughout the study. Percentage carbon content of leaf litter remained almost constant during the study period and, consequently, C/N ratio remained a negative function of nitrogen content.

Benthic invertebrate density was extremely low in comparison to that typical of similar streams in temperate latitudes (pers. obs.). High densities of benthic invertebrates in tropical forest streams are, evidently, associated almost exclusively with natural leaf litter assemblages (Henderson & Walker 1986, Walker 1987). Colonisation of litter bags was, however, immediate and rapid. Separation of colonising invertebrates into functional feeding groups enabled comparisons of colonisation dynamics to be made. Since literature concerning some groups is scarce, assignment to trophic groups is tentative. In addition, Covich (1988) has stressed the prevalence of omnivory in tropical stream communities, which also makes assignment to trophic groups difficult. Nevertheless, the two major groups (shredders and collectors) showed very different colonisation patterns. Response from the shredder community was initially rapid. Shredders rely on a food resource which typically occurs in discrete patches, *i.e.,* areas of reduced current and on the upstream side of physical obstructions. Rapid location and colonisation of leaf accumulations is expected for this group. The subsequent decline in shredder abundance after day 12 seemed a function of decreasing amounts of leaf litter remaining in the litter bags. Shredder density data revealed that numbers per gram of leaf litter remained constant during the latter part of the study period. The balance of shredder immigration and emigration was, therefore, strongly dependent on the mass of leaf litter remaining. Degree of conditioning could also have been an important factor. The results suggest that natural leaf packs in tropical streams represent a food resource which is relatively short-lived. Thus, the completion of insect larval stages may necessitate the successive location and colonisation of such litter assemblages.

Potential detritivores not recorded in the litter bags (because of mesh size) include the fish and crab species present in the stream (pers. obs.). These groups were assumed to have partial access to the contents of the litter bags, and their contribution to litter processing in the stream studied is not known but may have been significant (Wooton & Oemke 1992).

In contrast to the shredder group, abundance and density of collector species both increased on a linear basis throughout the study. This linear increase suggests that colonisation by this group was 1) a more passive process than that of the shredder community, and 2) independent of the amount of leaf litter remaining in the litter bags. It seems possible that collector abundance was indirectly linked to decay rate via the production of fine particulate organic matter (FPOM) by shredders within the litter bags. Richardson (1992) compared patterns of colonisation in natural and artificial (polyester cloth) leaf packs. Collector abundance was a function of the amount of accumulated fine particulate detritus contained within leaf packs. In the present study, however, correlation analysis revealed no relationship between collector abundance and the two potential correlates of *in situ* FPOM production: dry weight of leaf litter remaining and shredder abundance. This lack of linkage may indicate the importance of detritus which is derived from outside leaf assemblages, as opposed to detritus produced by *in situ* decay.

The pattern of predator colonisation was similar

to that of the shredder group. As stated above, tropical stream invertebrates are, typically, only found at high densities within accumulations of leaf litter, and natural leaf litter assemblages represent concentrated patches of prey in an environment which is otherwise characterised by low prey density. This is supported by the rapid colonisation of litter bags by predatory invertebrates. By the end of the study period, however, the number of predators had declined despite increasing numbers of prey, possibly as a result of the decreasing amounts of leaf litter present in the litter bags. This decrease may indicate the importance of leaf litter as a microhabitat for predators in the stream studied.

A marked feature of the litter bag community was its dominance by insects, both numerically and in terms of number of species. In this respect the stream community was similar to those of temperate latitudes, as well as those found in the subtropical streams of Hong Kong (Dudgeon 1987). During sorting of the litter bag community, assignment of morphospecies status erred towards caution. As a consequence, estimation of the species richness of the litter bag community may be conservative. The results indicate that invertebrate species richness at the study site was low in comparison to that typical of low-order streams at temperate latitudes. The cumulative species number curve can be likened to a species-sample curve, although the possibility of succession, as well as the effect of decreasing amounts of litter in the bags, must be taken into account. Clearly, the curve approached an asymptote, suggesting that most species in the leaf litter community were recorded. The taxonomic composition of the community also differed from typical temperate streams in the relative importance (as indicated by number of representative species) of certain insect orders. Number of Coleoptera and Odonata species was particularly high. By contrast, the Plecoptera were under-represented. Covich (1988) states that the taxonomic composition of neotropical stream communities is characterised by high endemicity of certain groups coupled with a paucity of species in others, giving rise to species richness which may be no higher than that of temperate latitudes. The results of the present study support this view. Despite observed differences in stream community structure, it is clear that community function was similar in every respect to those of temperate stream ecosystems.

In conclusion, the processing of catchment-derived leaf litter at the study site was rapid in comparison to that typically observed for temperate streams. The role of high ambient water temperature can be considered of primary importance in the control of the processing rate observed through its effect on microbial conditioning and, consequently, consumption by detritivorous invertebrates. The low C/N ratio of the leaf litter, indicating high food quality, may have been an additional factor in the determination of litter palatability. Rapid macroinvertebrate colonisation of litter bags was observed, indicating the importance of leaf litter as a microhabitat for tropical stream invertebrates. The leaf litter community at the study site was dominated by insects and, evidently, of lower species richness than that typical of many temperate streams.

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LITERERATURE CITED

ALEXANDER, M. 1977. Introduction to soil microbiology. J. Wiley & Sons, New York, U.S.A.

ALLEN, S. E. (Ed.) 1974. Chemical analysis of ecological materials. Blackwell Scientific Publications, Oxford, U.K.

ANDERSON, N. H., AND J. R. SEDELL. 1979. Detritus processing by macroinvertebrates in stream ecosystems. Ann. Rev. Entom. 24: 351–377.

BÄRLOCHER, F. 1991. Fungal colonisation of fresh and dried leaves in the River Teign (Devon, England). Nova Hedwigia 52: 349–357.

BUNN, S. E. 1988. Processing of leaf litter in a northern jarrah forest stream, Western Australia: I. Seasonal differences. Hydrobiologia 162: 201–210.

CAMPBELL, I. C., AND L. FUCHSHUBER. 1995. Polyphenols, condensed tannins, and processing rates of tropical and temperate leaves in an Australian stream. J. N. Am. Benthol. Soc. 14: 174–182.

COVICH, A. P. 1988. Geographical and historical comparisons of neotropical streams: biotic diversity and detrital processing in highly variable habitats. J. N. Am. Benthol. Soc. 7: 361–386.

CUMMINS, K. W. 1974. Structure and function of stream ecosystems. Bioscience 24: 631–641.

———, R. C. PETERSEN, F. O. HOWARD, J. C. WAYCHECK, AND V. I. HOLT. 1973. The utilisation of leaf litter by stream detritivores. Ecology 54: 336–345.

———, AND M. J. KLUG. 1979. Feeding ecology of stream invertebrates. Ann. Rev. Ecol. Syst. 10: 147–172.

DUDGEON, D. 1982. An investigation of physical and biotic processing of two species of leaf litter in Tai Po Kau Forest Stream, New Territories, Hong Kong. Arch. Hydrobiol. 96: 1–32.

———. 1987. The ecology of a forest stream in Hong Kong. Arch. Hydrobiol., Ergeb. Limnolog. 28: 449–454.

FISHER, S. G., AND G. E. LIKENS. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecol. Monogr. 43: 431–439.

FITTKAU, E. J., V. IRMLER, W. J. JUNK, F. REISS, AND G. W. SCHMIDT. 1975. Productivity, biomass and population dynamics in Amazonian waterbodies. *In* F. B. Golley and E. Medina (Eds.). Tropical ecological systems; Trends in terrestrial and aquatic ecological research, pp. 289–311. Springer-Verlag, Berlin.

GESSNER, M. O. 1991. Differences in processing dynamics of fresh and dried leaf litter in a stream ecosystem. Freshwater Biol. 26: 387–398.

———, AND J. SCHWOERBEL. 1989. Leaching kinetics of fresh leaf-litter with implications for the current concept of leaf processing in streams. Arch. Hydrobiol. 115: 81–90.

HENDERSON, P. A. AND I. WALKER. 1986. On the leaf litter community of the Amazonian blackwater stream Tarumazinho. J. Trop. Ecol. 2: 1–17.

HOLDRIDGE, L. R., W. C. GRENKE, W. H. HATHAWAY, T. LIANG, AND J. A. TOSI, Jr. 1971. Forest environments in tropical life zones: a pilot study. Pergamon Press, New York, U.S.A.

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

KAUSHIK, N. K. AND H. B. N. HYNES. 1971. The fate of dead leaves that fall into streams. Arch. Hydrobiol. 68: 465–515.

MALTBY, L. 1992. Detritus processing. *In* P. Calow and G. E. Petts (Eds.). The rivers handbook (Volume I), pp. 331–353. Blackwell Scientific Publications, Oxford, U.K.

MERRITT, R. W., AND K. W. CUMMINS. 1984. An introduction to the aquatic insects of North America, 2nd Edition. Kendall/Hunt Publications, Iowa.

OSTROFSKY, M. L. 1993. Effect of tannins on leaf processing and conditioning rates in aquatic systems: An empirical approach. Can. J. Fish. Aquat. Sci. 50: 1176–1180.

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

PEARSON, R. G., R. K. TOBIN, R. E. W. SMITH, AND L. J. BENSON. 1989. Standing crop and processing of rainforest litter in a tropical Australian stream. Arch. Hydrobiol. 115: 481–498.

PETERSEN, R. C., AND K. W. CUMMINS. 1973. Leaf processing in a woodland stream. Freshwater Biol. 4: 343–368.

RICHARDSON, J. S. 1992. Food, microhabitat, or both? Macroinvertebrate use of leaf accumulations in a montane stream. Freshwater Biol. 27: 169–176.

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

———. 1989. Effects of condensed tannins on leaf processing in mid-latitude and tropical streams: A theoretical approach. Can. J. Fish. Aquat. Sci. 46: 1097–1106.

SUBERKROPP, K., G. L. GODSHALK, AND M. J. KLUG. 1976. Changes in the chemical composition of leaves during processing in a woodland stream. Ecology 57: 720–727.

WALKER, I. 1987. The biology of streams as part of Amazonian forest ecology. Experientia 43: 279–287.

WEBSTER, J. R., AND E. F. BENFIELD. 1986. Vascular plant breakdown in freshwater ecosystems. Ann. Rev. Ecol. Syst. 17: 567–594.

WOOTON, J. T. AND M. P. OEMKE. 1992. Latitudinal differences in fish community trophic structure, and the role of fish herbivory in a Costa Rican stream. Environ. Biol. Fishes. 35: 311–319.