

An investigation of physical and biological processing of two species of leaf litter in Tai Po Kau Forest Stream, New Territories, Hong Kong

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With 12 figures and 4 tables in the text

Abstract

An investigation of the breakdown of two species of leaf litter, *Liquidambar formosana* and *Aleurites montana*, in Tai Po Kau Forest Stream, New Territories, Hong Kong, has been undertaken. Both species broke down rapidly and had disappeared by the 13th week of the study. *A. montana*, broke down more slowly than *L. formosana* and the latter lost considerably more weight due to leaching. Although the use of a novel exposure technique may have increased the rate of litter breakdown, it is suggested that high water temperatures (compared to temperate zone streams) were an important contributing factor. Patterns of fungal and bacterial abundance on the two types of litter differed; *L. formosana* supported larger microfloral populations and exhibited peaks in numbers of both types of microconsumers in the early stages of breakdown. By contrast, bacteria were initially dominant on *A. montana* leaves, fungi increasing in importance on the 5th week and declining subsequently. *L. formosana* supported more associated macroinvertebrates than *A. montana* and these exhibited an increase in abundance and diversity (\bar{d}) as breakdown progressed. No such trends were evident in *A. montana*-associated invertebrate populations. Laboratory experiments indicated that, when given a choice, a stream detritivore (the thiarid snail *Brotia hainanensis*) consumed significantly greater amounts of *L. formosana* — this may have been due to larger populations of associated microflora or inherent leaf palatability. The results were discussed with reference to leaf breakdown in temperate aquatic habitats. It was concluded that the tropical forest stream studied may be dependent upon inputs from the surrounding terrestrial environment to sustain existing community metabolism.

Introduction

The energy supply to freshwater consumers can be partitioned thuswise: the input of particulate and dissolved organic material of terrestrial origin, and autochthonous photosynthetic carbon fixation. In running waters the former is generally greater, and leaf litter is commonly a vital food source in forest streams (MINSHALL, 1967; KNÖPPEL, 1970; VANNOTE, 1969; FAHY, 1972; MECOM, 1972; FISHER & LIKENS, 1973). In above-ground terrestrial communities the bulk of biomass resulting from photosynthesis is not processed by herbivores; i. e., organic matter is produced in excess, and the ratio of primary production (P) to community respiration (R) is greater than 1. The excess of reduced

carbon compounds from the terrestrial landscape becomes available to lotic benthos via direct fall and lateral transport of litter (FISHER & LIKENS, 1973; DE LA CRUZ & POST, 1977; POST & DE LA CRUZ, 1977; DUDGEON, 1982 a), providing an energy subsidy to the aquatic habitat. As a consequence forest streams are generally characterized by P:R of less than 1 (HALL, 1972; FISHER & LIKENS, 1973; CUMMINS, 1974; DE LA CRUZ & POST, 1977; DUDGEON, in prep.).

Leaf litter processing in streams can be considered to operate on a community level (REICE, 1974) for it involves species populations from many phyla operating across trophic groupings. CUMMINS (1973; 1975) states that the role of macroinvertebrates in the overall structure of lotic habitats is the conversion of (mainly allochthonous) reduced carbon compounds into carbon dioxide. Apparently, the general macroinvertebrate functional categories (shredders, collectors, grazers and predators) simply serve as integrated storage bins for organic compounds, which are all eventually converted to carbon dioxide. A primary effect of linkages between consumer populations, and non-predatory consumers and their food, is the increase and decrease in particle size of their nutritional substance; a phenomenon associated with the breakdown (processing) of allochthonous detritus in lotic habitats. Clearly therefore, investigations of leaf decomposition in streams should take into account not only physical changes but should also attempt to assess changes in the macro- and microconsumer populations associated with the allochthonous material. Such an integration was one of the aims of the current study.

The importance of allochthonous organic matter to the energy budget of temperate zone woodland streams has been made abundantly clear in recent years (REICE, 1974, and references op. cit.) and, significantly, ROSS (1963) has shown that trichopteran evolutionary dispersal has been associated with changes in the eastern deciduous biome. Despite the importance of terrestrial carbon sources in temperate regions, comparatively little is known of their significance and processing, in tropical aquatic environments. There is evidence that terrestrial material is of considerable importance for the maintenance of consumer populations in Amazonian rainforest streams (KNÖPPEL, 1970; FITTKAU & KLINGE, 1973); detritus from floating 'water meadows' of emergent plants also having considerable importance for benthic organisms in this region (HOWARD-WILLIAMS & JUNK, 1976). Terrestrial material also makes an important contribution to the early development of tropical lakes (MCLACHLAN, 1974). Investigations carried out in Tai Po Kau Forest Stream have shown that a large standing stock of leaf litter is present in the stream bed at all seasons (DUDGEON, 1982 a) and that the P:R ratio in this habitat is less than 1 (DUDGEON, in prep.). Although PADGETT (1976) has demonstrated the importance of fungi in leaf breakdown in a stream in Puerto Rico, published work dealing with the processing of leaf litter at the community level in

tropical forest streams is lacking. A comparison of such phenomena in tropical and temperate environments would be expected to be of particular interest in view of the findings of SUBERKROPP et al. (1975) that temperature influences the rates of community processing of leaf litter.

The present study was initiated in an attempt to fill a significant gap in the literature, to evaluate the participation of elements of the stream biota in leaf breakdown and to measure the rates of processing of this material. Attention was centred upon two species of leaf commonly encountered in Tai Po Kau Forest, *Liquidambar formosana* HANCE (Hammamelidaceae) and *Aleurites montana* (LOUR.) WILS. (Euphorbiaceae). Both trees are deciduous although *A. montana* sheds the bulk of its leaves in October, one month earlier than *L. formosana* (DUDGEON, 1982 a). The foliage of these two species is dissimilar; the polymorphic leaves of *A. montana* are large and tough while those of *L. formosana* are relatively small, light and flimsy. Leaves of both species were incubated in Tai Po Kau Forest Stream for varying periods of time and the physical changes they incurred, as well as the associated microfloral and macro-invertebrate associations that they developed, were monitored. Laboratory studies were also carried out in parallel with the field investigations in order to measure the rate of leaching of organic material from the leaves. Additionally, experiments designed to assess the relative palatability of both types of leaf litter to a stream detritivore were undertaken.

Study Area

The study area was a shaded riffle reach of Tai Po Kau Forest Stream (altitude 200 m), New Territories, Hong Kong. The stream basin comprises pyroclastic rocks with intrusions of lava, the stream itself being surrounded by a mixture of undifferentiated colluvium consisting of boulders and fine interstitial material. The forest soils are acidic lateritic krasnozems supporting a vegetation made up of species which, with a few exceptions, are native to Southern China. The waters of Tai Po Kau Forest Stream are well buffered, soft and slightly acidic, with low conductivity but rather high concentrations of dissolved silicates. Further details of the study area and stream hydrology are presented elsewhere (DUDGEON, 1982 b).

Methods

Freshly fallen leaves of *Aleurites montana* and *Liquidambar formosana* were collected in Tai Po Kau Forest during October and November 1978, the months of peak abscission for each of these species respectively. Newly fallen leaves were easily distinguished from older ones by colour and texture, and only blemish-free litter was collected. The leaves were dried to constant weight and stored in sealed plastic bags prior to use.

As a measure of the rate of leaching of soluble compounds from litter in water, a number of preweighed and labelled bundles of 5 leaves of each species were placed in a

perspex trough with a permanent flow of chlorinated tap water ($22^{\circ}\text{C} \pm 2^{\circ}\text{C}$). Although the chlorine in the water probably inhibited the growth of microorganisms, small amounts of commercial disinfectant ("Lysol") were added to the system every 2 days thus ensuring that measured weight losses did not result from biotic processes. At varying intervals after immersion, bundles of leaves were removed from the water and oven-dried to constant weight at 70°C , and the weight loss due to leaching over time was calculated. BLACKBURN & PETR (1979) have measured this parameter in Erlenmayer flasks where the water was changed frequently. Other investigations of leaching from submerged leaves have involved the use of laboratory streams (KAUSHIK & HYNES, 1971; PETERSON & CUMMINS, 1974) but it is doubtful whether the use of more sophisticated apparatus than that employed in the present study would produce a significant increase in accuracy.

Leaves were exposed, *in situ*, in Tai Po Kau Forest Stream inside 20 cm lengths of PVC pipe, 10 cm in diameter. Preweighed amounts of one or other species of litter were placed inside each pipe and the ends sealed with 1 cm wire mesh. The choice of a suitable exposure technique is a critical problem in studies of leaf litter breakdown in aquatic environments (BENFIELD *et al.* 1979). Whole leaves or leaf discs have been incubated in bags (or boxes) of mesh with varying widths and incubated in the water of the habitat for varying periods of time (KAUSHIK & HYNES, 1968; HYNES & KAUSHIK, 1969; BÄR-LOCHER & KENDRICK, 1973 a, b; DE LA CRUZ & GABRIEL, 1974; HODKINSON, 1975; DE LA CRUZ & POST, 1977; POST & DE LA CRUZ, 1977; BRINSON, 1977; BLACKBURN & PETR, 1978; NEAVES, 1978; MEYER, 1980). Other workers have employed tethered leaves or loosely bound leaf packs (PETERSON & CUMMINS, 1974; REICE, 1974, 1977; SUBERKROPP *et al.* 1975; SUBERKROPP & KLUG, 1976; TRISKA & SEDELL, 1976). The former method has been criticized because of the possibility of decomposition rates being affected by the artificial confinement (PETERSON & CUMMINS, 1974) and BLACKBURN & PETR (1978) have shown that calculated rates of decomposition for a single species of leaf may vary considerably according to the mesh size of the litter bag used. A similar phenomenon has been recorded by BENFIELD *et al.* (1979). In contrast, the use of leaf packs introduces a different set of problems as the size of a leaf pack has a significant effect upon the rate at which it is broken down (REICE, 1974; BENFIELD *et al.* 1979). This may be due to differences in microclimate between internal and external leaves in packs with the outer leaves subject to the processes of sloughing and abrasion from which the other leaves are relatively protected. The inner leaves, on the other hand, would have a less free supply of oxygen thus affecting patterns of leaf breakdown by consumer organisms.

It is possible that leaves in the centre of leaf packs are 'stored' until such a time as they are exposed to processing factors (BENFIELD *et al.* 1979) so that the stream delays the availability of some portion of the species most 'preferred' by stream consumers (IVERSON, 1974) thus extending the time during which high quality food is available in the habitat (BENFIELD *et al.* 1979).

In the present study leaves were exposed in PVC pipe placed in the stream with their long axes parallel to the direction of current flow. The 1 cm mesh of the wire closing the ends of the pipe was large enough to ensure that the flow of water through the pipe was sufficient to exclude the possibility of decomposition rates being affected by confinement. The number of leaves placed in each pipe varied according to species but the surface area exposed was approximately the same in each case. The actual amount of litter placed in the pipes was carefully controlled so as to avoid excessive disruption of water flow. Estimates of leaf breakdown from this study were considered to represent the 'optimum' possible in Tai Po Kau Forest Stream, mimicking decomposition in a lotic habitat where the supply of dissolved oxygen to decomposers/consumers is not

limiting. The exposure of litter in this way had the added advantage that the walls of the pipe did not allow the passage of light thus preventing the growth of periphytic algae on the leaf surfaces (recorded by IVERSON, 1973). This avoided possible confusion in the interpretation of some results, a problem encountered by TRISKA & SEDELL (1976) during an investigation of leaf decomposition. The elimination of periphyton from litter substrates ensured that macroinvertebrates associated with such material were utilizing it as a food source or shelter rather than as a convenient foraging ground for algae.

Leaf containers were first placed in the stream in mid-December 1977, and were retrieved 1, 2, 3, 4, 5, 7, 9 and 11 weeks later. On each occasion at least one container of leaves of each species was removed and replaced with another filled with undecomposed tissue. Wherever possible additional containers were removed in order to obtain replicate values for the parameters measured. Each container was enclosed in a plastic bag before removal from the stream. In the laboratory 5 discs were cut from each species of leaf with a flamed cork borer and transferred to separate sterile bottles containing 10 ml of autoclaved tap water (the general characteristics of which were similar to those of Tai Po Kau Forest Stream). The bottles were shaken vigorously for 5 minutes and allowed to stand overnight. The resulting suspensions were used to make dilutions for viable counts of microorganisms. When plating was completed, the leaf discs used in the preparation of the inoculum were oven-dried so that the numbers of bacteria and fungi, as determined by plate counts, could be expressed per g dry weight of leaf tissue.

Plating was undertaken in an inoculation room previously sterilized by irradiation for at least 12 hours, and the plates incubated at 20–22 °C. Initially, an incubation period of 7 days, as used by SUBERKROPP & KLUG (1976), was employed but it was difficult to count colonies at the end of this time due to their rapid rate of growth and spread. Consequently, counting was carried out 5 days after plating. The bacterial growth substrate was yeast extract agar (0.3% yeast extract, 0.5% peptone and 1.5% agar) which is closely similar to the PYG agar used by SUBERKROPP & KLUG (1976). They record that, of a number of media (including leaf extract agar), PYG agar gave the highest total viable counts, colony diversity and pigmentation for aquatic bacteria. Fungal counts were made using potato dextrose agar (PDA: 20% potato infusion, 2% dextrose and 1.5% agar) with the addition of streptomycin (30 µg/ml) (pers. comm. Dr. I. J. HODGKISS, Department of Botany, Hong Kong University) to prevent bacterial development. Microscopic examination of the microflora growing on agar with added streptomycin revealed that the great majority of them were fungi. It should be emphasized that the methods used for determination of microfloral abundance in this study are by no means perfect. However it is considered that they were sufficient to enable comparisons of abundance of microflora at various stages of leaf decomposition and between different types of litter.

After the removal of a sample of leaf tissue for the estimation of microbial numbers, the remaining material was carefully washed in running water and the associated invertebrates retained with a 200 µm mesh net. The animals were preserved in 70% ethanol while the leaf tissue was oven-dried to constant weight. Samples of this material were ashed to determine percentage of organic carbon; PETERSON & CUMMINS (1974) state that ashing causes negligible carbonate loss from litter. As the percentage of organic matter in freshly fallen samples of *Liquidambar formosana* and *Aleurites montana* was determined at the start of the study, thus the change in organic matter attributable to in-stream processing of litter could be estimated. Macroinvertebrates were sorted and enumerated, and numbers of animals per g dry weight of leaf tissue were calculated (after the weight of the tissue used for microfloral analysis had been added to that of the remainder of the leaf material). Estimates of macrofaunal diversity (\bar{d}) on decomposing

leaf litter were made with a diversity index based on the Shannon-Weiner function (WILHM, 1970) using a computer program modified from that of CAIRNS & DICKSON (1972).

The relative 'palatability' of *Liquidambar formosana* and *Aleurites montana* litter to stream invertebrates was investigated using the detritivorous prosobranch snail *Brotia hainanensis* (BROT 1872) (Thiaridae) which is abundant in Tai Po Kau Forest Stream. Firstly, the rate of consumption of each species of leaf litter by a population of snails was measured by placing a quantity of previously soaked leaves of one or other species into a tank containing a known number of snails. The experimental tanks were well aerated and supplied with an undergravel filter and a substratum of well washed stream sand and rocks. The snails were allowed to feed ad libitum for 7 days after which time the partially skeletonized leaf tissue was removed from the experimental tanks, dry weighed, and ashed to determine the percentage of organic matter. This procedure was repeated 5 times for each species of leaf after which the experimental snails were killed and dry weighed. Results were expressed according to the dry weight of each species of leaf consumed per g dry weight of snail per week. On only one occasion was more than 50% of the available leaf material consumed and thus it was assumed that the calculated feeding rates were applicable to populations of snails in a habitat where food was freely available.

In order to compare the rate of consumption of different species of leaves in situations where the consumer has a choice of foodstuffs, populations of *Brotia hainanensis* in laboratory tanks were presented with presoaked *Liquidambar formosana* and *Aleurites montana* leaves of known dry weight in approximately equal proportions. After a feeding period of 7–14 days, the remaining leaf material was dry weighed and the percentage of available material consumed, as well as the dry weight of leaves consumed per g dry weight of snail per week, was calculated for each type of litter. This procedure was repeated 7 times with 2 groups of experimental snails which were subsequently killed and dry weighed.

Results

Laboratory investigations of the rate of weight loss of leaf litter in the laboratory showed that there were marked differences between species (Fig. 1). After 1 day, *Liquidambar formosana* leaves had lost 14.5% of their original weight while *Aleurites montana* had lost only 6.3%. Weight loss of *L. formosana* was fairly slight after the initial large loss until just before the 20th day when it began to increase with 72.1% and 57.8% of the original weight remaining after the 26th and 50th days of immersion respectively. In contrast, *A. montana* lost only 10% additional weight after the initial drop of 6.3% during the first 24 hours. Thus on day 26, 84.4% of the original leaf weight remained and this had only fallen by 1.2% on the 50th day.

An exponential function has often been used to describe the weight loss of decomposing leaves in aquatic environments (PETERSON & CUMMINS, 1974; NEAVES, 1978; BENFIELD et al. 1979; MEYER, 1980). This model assumes that there is a constant fractional loss of the material present at any given time, in comparison with a linear loss model which assumes a constant fractional loss of the initial mass with time. As was the case in the investigation carried out by

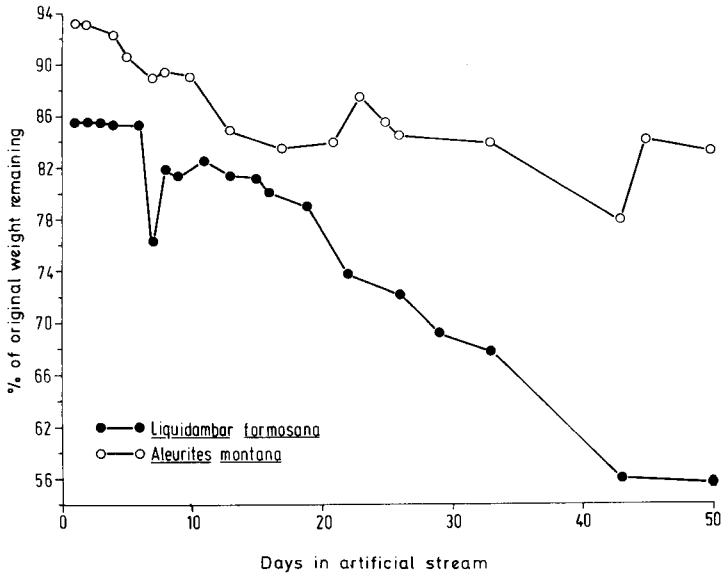


Fig. 1. Percentage of the original weight of leaves of *Liquidambar formosana* and *Aleurites montana* remaining after increasing length of exposure in an artificial laboratory stream.

BLACKBURN & PETR (1979), weight loss in this study did not follow an exponential function and, as can be seen by comparisons of weight loss due to leaching, varied between the two types of litter examined. Consequently, the exponential decay model was not used.

Changes in the pattern of weight loss of *L. formosana* and *A. montana* litter during incubation in Tai Po Kau Forest Stream did not display the same interspecific differences shown in Fig. 1. Both species lost over 20% of their original dry weight in the first week; subsequently weight loss of *L. formosana* was almost linear falling to a mean value of 10% of the original dry weight remaining by the 11th week. (Fig. 2). In contrast, *A. montana* lost relatively little weight between weeks 1 and 4 (inclusive). Subsequently loss speeded up with only 17.6% of the original tissue remaining by the 11th week (Fig. 3). Comparing the pattern of variation in the percentage of organic matter in both types of litter (Figs. 2 and 3). *A. montana* showed no marked variation in this parameter over the course of the study ranging between 93.9 and 87.8%. These values are not significantly different from the percentage of organic matter (89.77 ± 2.38) in freshly fallen leaves of this species. In contrast, the percentage of organic matter of *L. formosana* litter fell from the prestream level of $85.37 \pm 1.55\%$ to 75.3% after one week in the stream. The organic matter content rose subsequently and peaked at 86.8% in the 7th week. Further decomposition caused a fall to 78.2% at the end of the study.

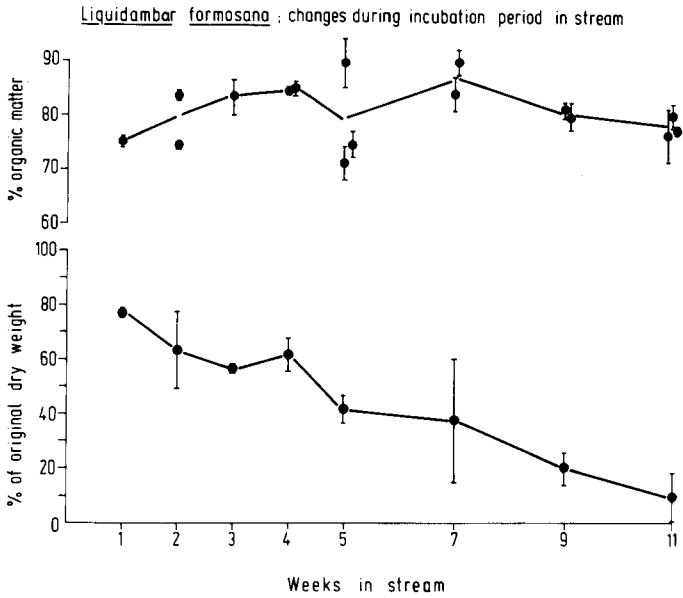


Fig. 2. Percentage of the original weight and the percentage of organic matter of leaves of *Liquidambar formosana* with increasing length of exposure in Tai Po Kau Forest Stream. Points on the graph represent mean values \pm S.D.

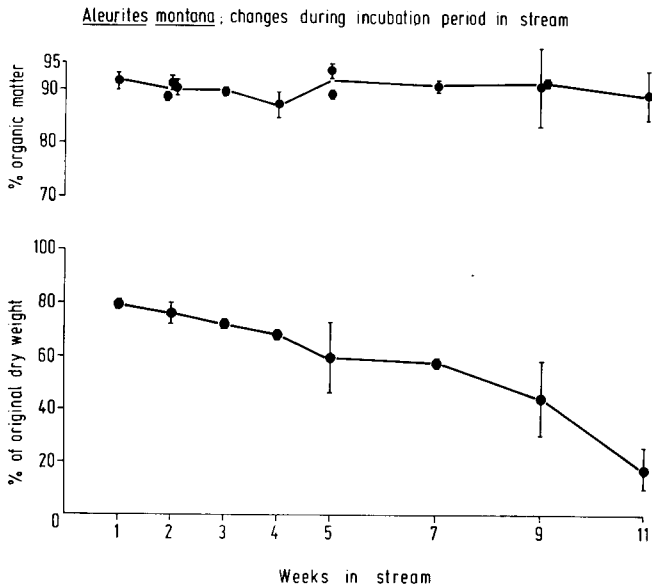


Fig. 3. Percentage of the original weight and the percentage of organic matter of leaves of *Aleurites montana* with increasing length of exposure in Tai Po Kau Forest Stream. Points on the graph represent means values \pm S.D.

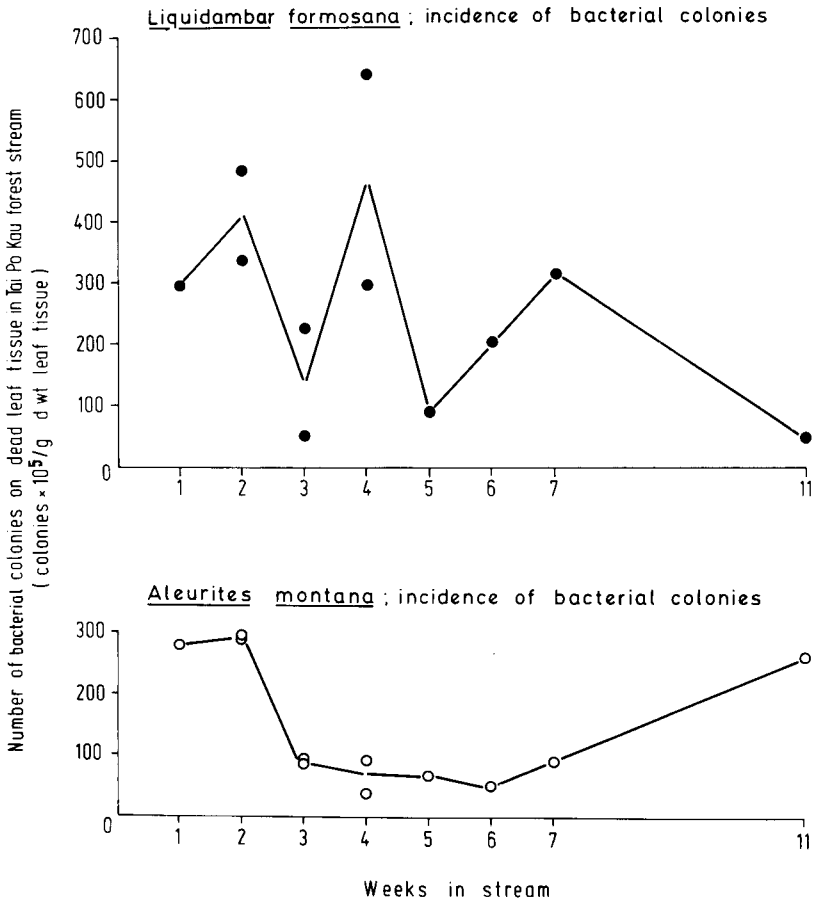


Fig. 4. Changes in the numbers of bacteria associated with *Liquidambar formosana* and *Aleurites montana* leaves with increasing length of exposure in Tai Po Kau Forest Stream. The occurrence of duplicate points for the same time interval indicates that determinations of microbial abundance were carried out on separate occasions 4–6 weeks apart.

Considerable variation in the numbers of bacteria on decomposing litter were noted. However, there appeared to be a general trend toward large numbers of bacteria in the early stages of leaf processing (during the first 2 weeks in the case of *A. montana* and the first 4 weeks for *L. formosana*) with a decline in abundance in the later stages (Fig. 4). There is some indication that a secondary increase in bacterial numbers occurred toward the latter stages of processing of *A. montana*, as seen on the 11th week. Apart from this occasion however, bacteria were comparatively much more numerous on *L. formosana* litter during the decomposition period.

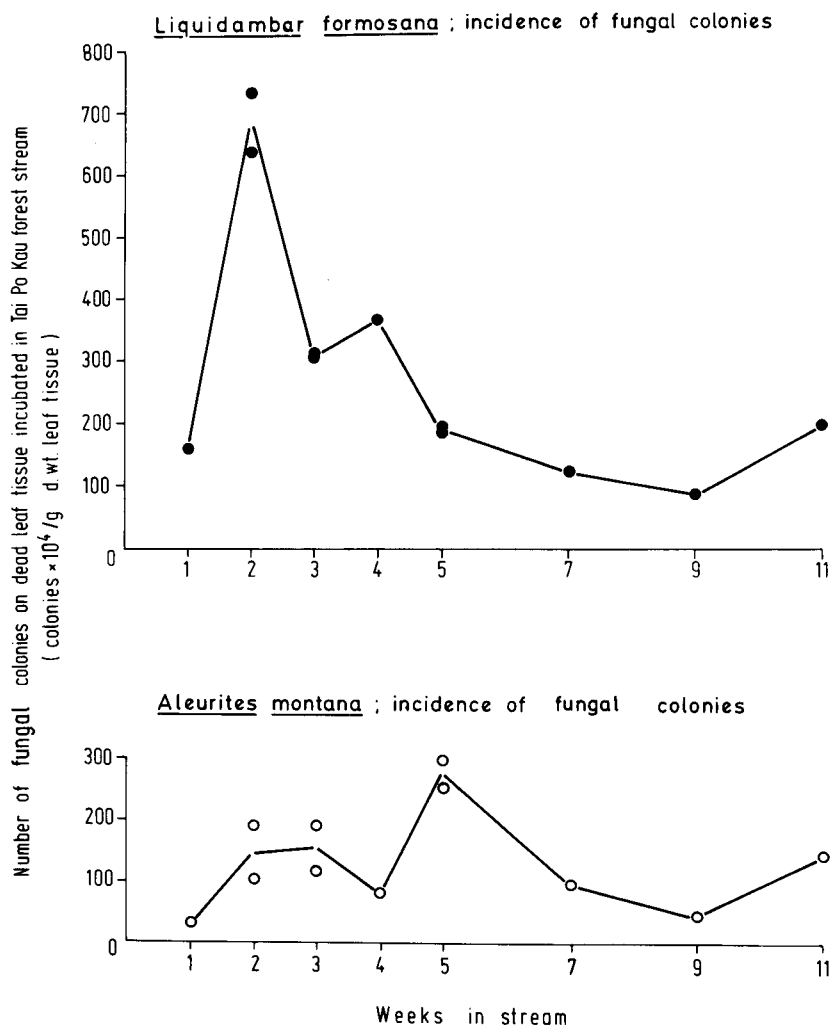


Fig. 5. Changes in the numbers of fungi associated with *Liquidambar formosana* and *Aleurites montana* leaves with increasing length of exposure in Tai Po Kau Forest Stream. The occurrence of duplicate points for the same time interval indicates that determinations of microbial abundance were carried out on separate occasions 4–6 weeks apart.

Clear differences in the abundance and pattern of succession of fungi on the two types of litter were evident (Fig. 5). There was a marked peak in the numbers of fungi on *L. formosana* leaves in the early part of the incubation period, and on the second week there were approximately 6 times more fungi on this litter than on *A. montana*. After this time the numbers of fungi on *L.*

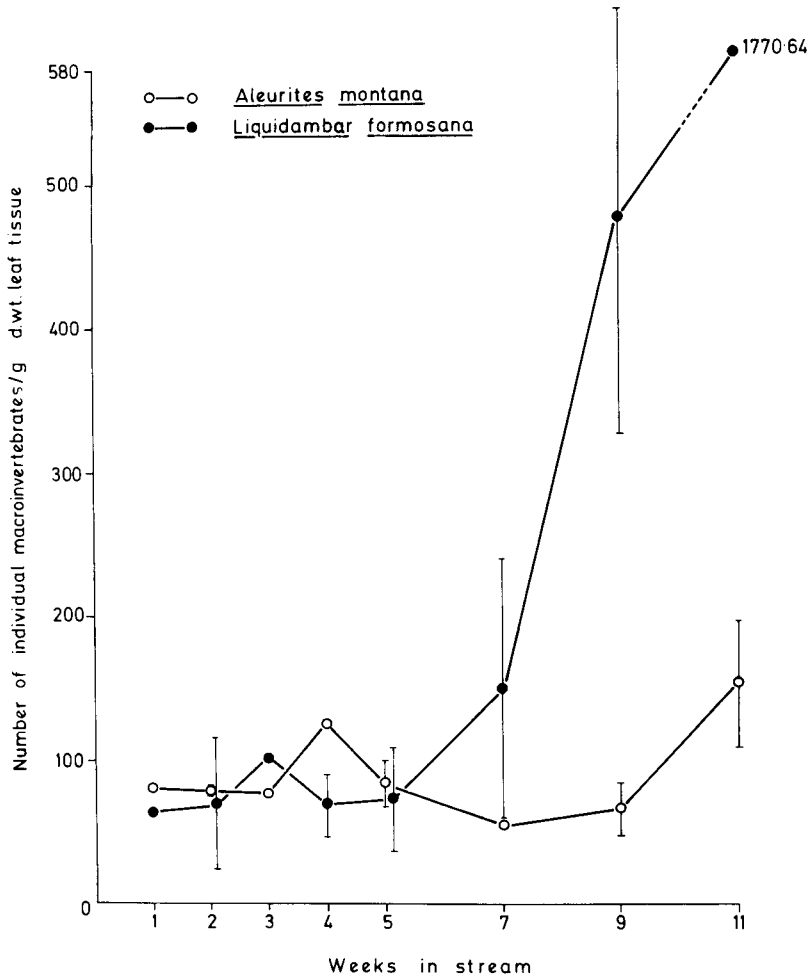


Fig. 6. The number of macroinvertebrates (mean \pm S.D.) associated with *Liquidambar formosana* and *Aleurites montana* leaves with increasing length of exposure in Tai Po Kau Forest Stream.

formosana fell steeply and between the 7th and 11th weeks there was only a two fold difference in fungal abundance between the two types of litter.

There were clear differences in the numbers of macroinvertebrates associated with each species of leaf litter (Fig. 6). *A. montana* showed little change in the density of macroinvertebrate colonizers from the first (83 individuals/g dry weight of litter) to the 9th week (69 individuals/g dry weight of litter). The highest density (156 individuals/g dry weight of leaf tissue) was recorded on the 11th week. The numbers of macroinvertebrates associated with *L. formosana* litter were similar to those of *A. montana* until the 7th week when they

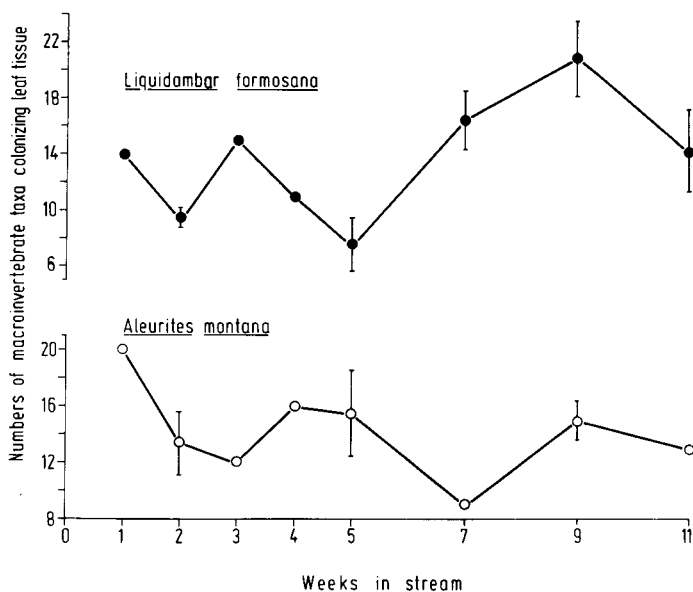


Fig. 7. The number of macroinvertebrate taxa (mean \pm S.D.) associated with *Liquidambar formosana* and *Aleurites montana* leaves with increasing length of exposure in Tai Po Kau Forest Stream.

increased markedly, continuing to rise until the end of the study when a density of 1771 individuals/g dry weight of litter was recorded.

The numbers of macroinvertebrate taxa colonizing both types of litter showed no predictable variation with time (Fig. 7), with the largest number of taxa (20) being the same in each case. This peak was attained during the first week by *A. montana* and in the 9th by *L. formosana*. The diversity (\bar{d}) of the litter associated macroinvertebrates showed a tendency to increase with duration of exposure time (Fig. 8) although *A. montana* displayed an early peak \bar{d} value after only 1 week of in-stream exposure.

A total of 46 taxa of macroinvertebrates, mostly insects, were recorded decaying litter in Tai Po Kau Forest Stream (Table 1). 33 taxa were common to both species of litter, 36 taxa occurring on *A. montana* leaves and 43 on *L. formosana*. Not all of the taxa were common and some were only recorded on 1 or 2 occasions. Those found on only one type of litter (3 on *A. montana*, 10 on *L. formosana*) were representatives of scarce taxa and were never common. A logarithmic transformation of the numbers of individuals in the commoner macroinvertebrate taxa colonizing unit weights of litter are shown in Figs. 9–11. Larval Chironomidae (Diptera) (excluding Tanypodinae) were the most abundant taxon, but systematic difficulties precluded attempts to sort them to species. The numbers of Chironomidae on *A. montana* remained fairly stable

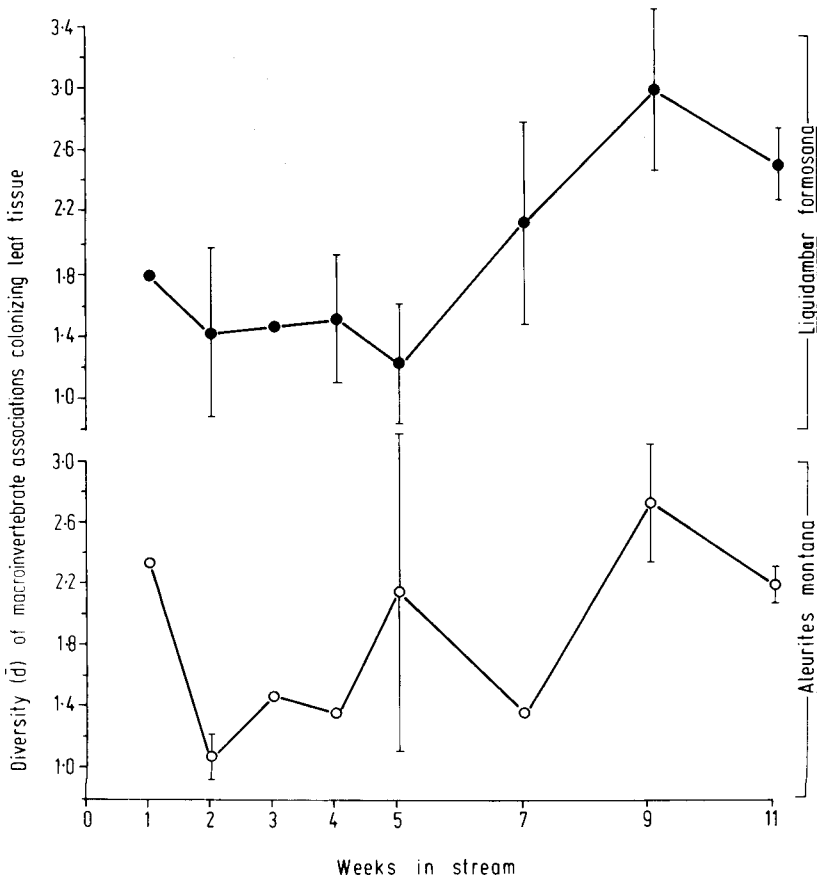


Fig. 8. The diversity (\bar{d}) of macroinvertebrates associated with *Liquidambar formosana* and *Aleurites montana* leaves with increasing length of exposure in Tai Po Kau Forest Stream.

with a small increase on the 11th week. After 5 weeks, the numbers of chironomids on *L. formosana* increased, peaking on the 11th week (Fig. 9). Baetidae (Ephemeroptera) varied greatly in abundance over time, both within and between the different types of leaf litter (Fig. 10). All 3 of the baetid taxa collected were more abundant on *L. formosana* litter. The numbers of *Baetis* T₁ and *Baetis* T₂ on this litter remained relatively constant until the 7th week and then increased. *Pseudocloeon* T₁ was rare until week 9 when a relatively large number of these nymphs were recorded on both types of litter, their abundance further increasing on the 11th week.

As was the case for Baetidae, the numbers of *Ephemerella* T₂ (Ephemeroptera: Ephemerellidae) increased with in-stream exposure time of *L. formosana* litter. This trend was less marked for *A. montana* leaves. The numbers of *Ephe-*

Table 1. The macroinvertebrate taxa associated with decomposing *Aleurites montana* and *Liquidambar formosana* litter in Tai Po Kau Forest Stream, Hong Kong. Individuals were identified to the lowest taxonomic rank possible and distinct morphotypes within the same rank were assigned letters and numbers by way of designation.

Gastropoda	Trichoptera
<i>Brotia hainanensis</i> (BROT)	<i>Chimarra</i> T ₁
Acarina	<i>Hydropsyche</i> T _A †
Hydrachnellae spp. indet.	<i>Hydropsyche</i> T _B
Ostracoda	<i>Hydropsyche</i> sp.
Cypridae sp. T ₁ †	<i>Hydropsyche</i> genus indet. Ch
Copepoda	<i>Cheumatopsyche</i> T ₁
Cyclopoidea sp. indet.	<i>Cheumatopsyche</i> dB †
Decapoda	<i>Cheumatopsyche</i> sp.
<i>Caridinea lanceifrons</i> (YU)	<i>Pseudoneureclipsis</i> TA ₁
<i>Macrobrachium hainanense</i> (PARISI) †	<i>Stenopsyche</i> cf. <i>angustata</i> MARTYNOV
Ephemeroptera	<i>Psilotreta</i> T ₁
<i>Baetis</i> T ₁	<i>Anisocentropus</i> T ₁
<i>Baetis</i> T ₂	Calamoceratidae genus indet. T ₁ †
<i>Baetis</i> T ₃	cf. <i>Mystacides</i> sp. †
<i>Pseudocloeon</i> T ₁	<i>Hydroptila</i> sp. *
<i>Pseudocloeon</i> T ₂	Coleoptera
<i>Epeorus</i> T ₁	cf. <i>Dineutes</i> sp. †
<i>Ecdyonurus</i> T ₁	Hydrophilidae genus indet. T ₁
<i>Thalerosphyrus</i> T ₁	<i>Helodes</i> T ₁ †
<i>Choroterpes</i> T ₁	<i>Psephenus</i> T ₁ †
<i>Ephemerella</i> T ₁	Diptera
<i>Ephemerella</i> T ₂	Tanypodinae
<i>Caenis</i> T ₁	Chironomidae (excluding
Odonata	Tanypodinae)
<i>Mnias mneme</i> RIS	<i>Simulium</i> T ₁
<i>Heliogomphus sinicus</i> (CHAO)*	
Plecoptera	
<i>Leuctra</i> T ₁ *	
<i>Amphinemura</i> T ₁	
Nemouridae sp. indet. †	
Perlidae spp.	

* Associated with *Aleurites montana* only.

† Associated with *Liquidambar formosana* only.

merella T₁ on both types of litter tended to increase with time but this was not the case for *Ecdyonurus* T₁ (Ephemeroptera: Heptageniidae) where the numbers of nymphs on *L. formosana* litter fluctuated markedly. Nymphs of the leptophlebiid *Choroterpes* T₁ (representing a fourth family of ephemeropterans) showed a general trend toward increased numbers over time on *L. formosana* leaves. In contrast, these animals were abundant on *A. montana* litter during the early part of the study and subsequently became scarce.

Two plecopteran taxa were found associated with leaf litter in Tai Po Kau Forest Stream. One taxon, referred to as Perlidae, comprised an assortment of (generally small) perlid nymphs which could not be consistently assigned species designations. These animals did not colonize *L. formosana* litter until the fourth week of exposure but subsequently increased in numbers (Fig. 12). They were quite scarce on *A. montana* leaves and did not show any significant

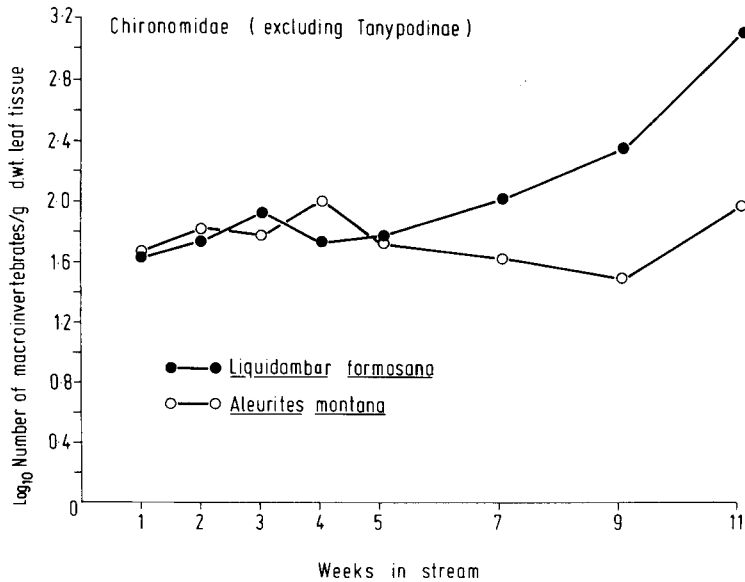


Fig. 9. The numbers of Chironomidae (excluding Tanypodinae) (Diptera) associated with *Liquidambar formosana* and *Aleurites montana* leaves with increasing length of exposure in Tai Po Kau Forest Stream.

temporal variation in abundance. A second plecopteran, *Amphinemura* T₁ (Nemouridae), displayed no obvious pattern of succession on either type of litter although there was a general tendency for numbers to increase over time.

Two trichopteran taxa were consistently associated with leaf litter. *Stenopsyche* cf. *angustata* MARTYNOV did not show any trend in abundance on either species of leaf. *Anisocentropus* T₁ (Calamoceratidae) showed a relatively constant pattern of abundance and was more numerous on *L. formosana* than on *A. montana* litter where larval numbers fluctuated more noticeably (Fig. 12).

Larval dipterans have been referred to above with regard to certain components of the Chironomidae. Tanypodinid chironomids were recovered from all leaf litter samples in Tai Po Kau Forest Stream. Their numbers remained fairly constant throughout the investigation, showing only a slight increase toward the end of the study. There were no significant differences in the numbers of Tanypodinae recorded from the different types of litter. Simuliid larvae (*Simulium* T₁) were also recorded on both species of leaf and increased in abundance toward the end of the study. They were more numerous on *L. formosana* litter but, in view of their filter-feeding habit, may not have used that leaf material as an energy source.

The relative palatability of *A. montana* and *L. formosana* litter to a stream detritivore, *Brotia hainanensis*, was studied in the laboratory. As Table 2

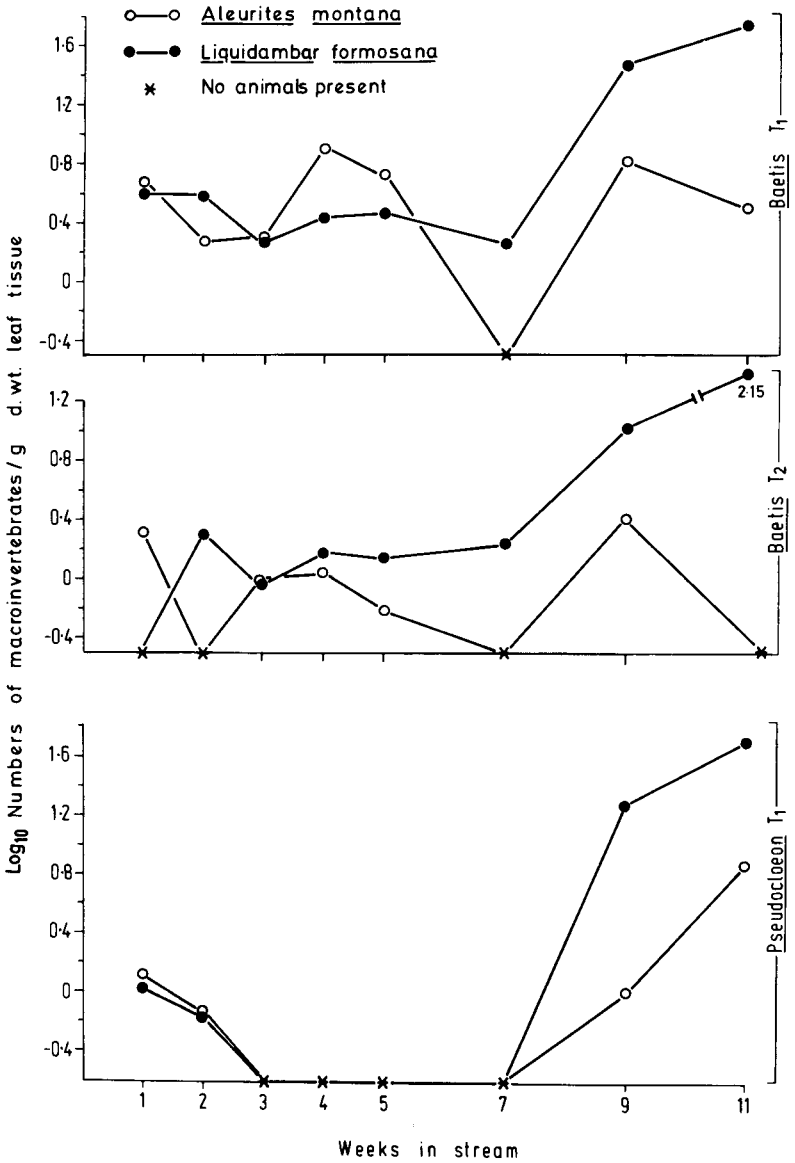


Fig. 10. The numbers of *Baetis* T₁, *Baetis* T₂ and *Pseudocloeon* T₁ (Ephemeroptera: Baetidae) associated with *Liquidambar formosana* and *Aleurites montana* leaves with increasing length of exposure in Tai Po Kau Forest Stream.

shows, it was apparent that in the absence of an alternative food source both types of litter were eaten in approximately equal amounts; the mean rate of consumption per g dry weight of snail per week for *A. montana* and *L. formosana* being very similar (0.24 ± 0.07 and 0.20 ± 0.04 g dry weight respectively).

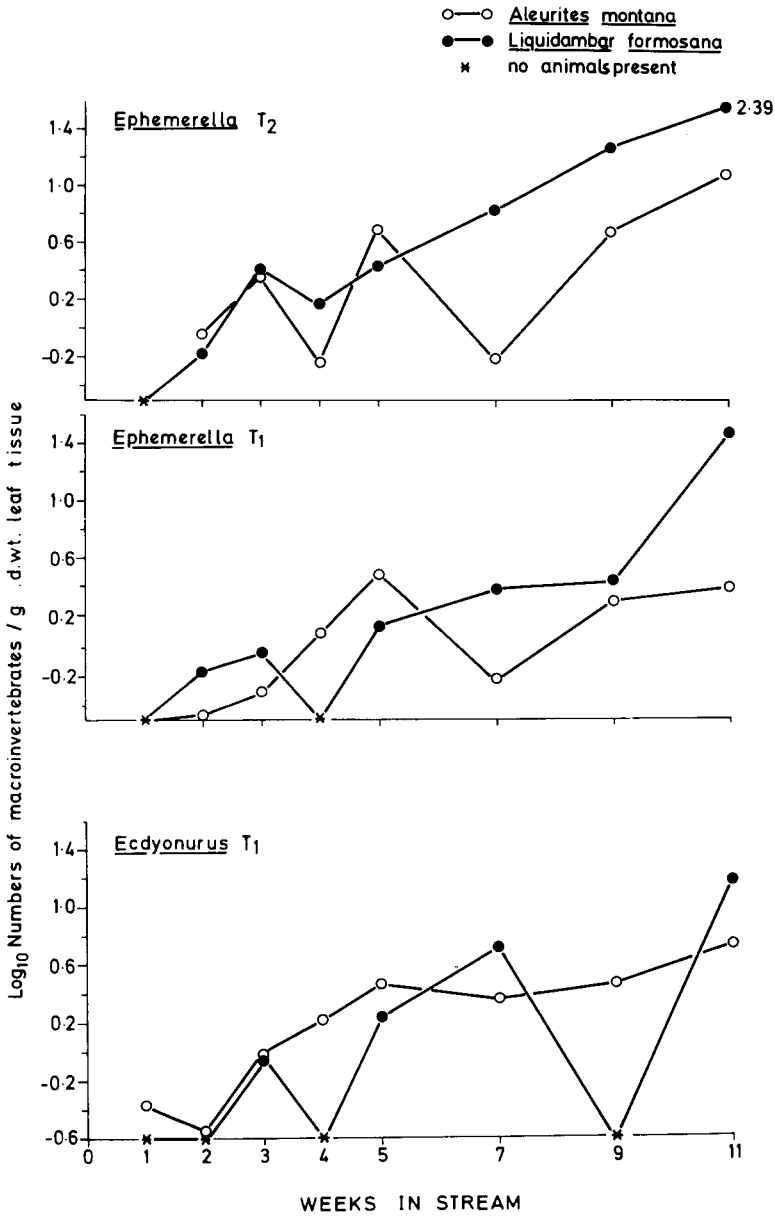


Fig. 11. The numbers of *Ephemera* T₁, *Ephemera* T₂ (Ephemeroptera: Ephemerellidae) and *Ecdyonurus* T₁ (Ephemeroptera: Heptageniidae) associated with *Liquidambar formosana* and *Aleurites montana* leaves with increasing length of exposure in Tai Po Kau Forest Stream.

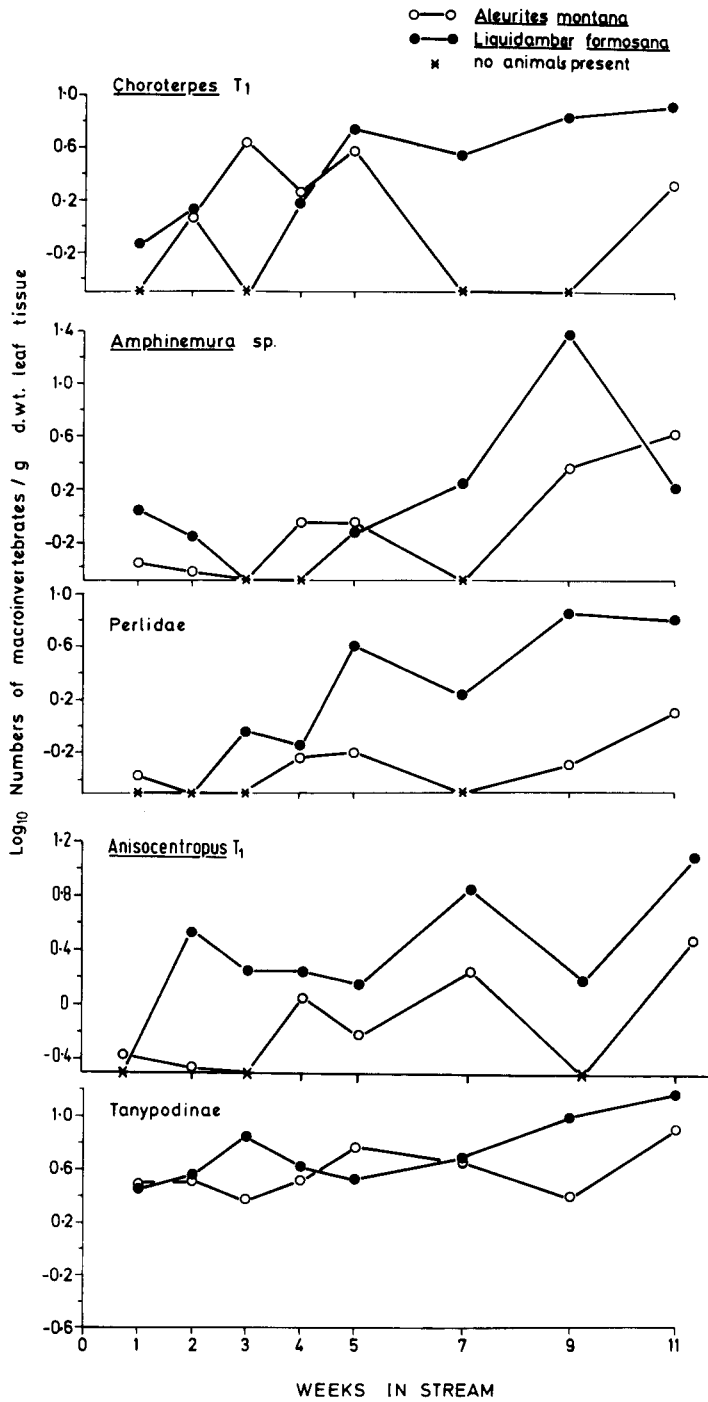


Fig. 12. The numbers of *Choroterpes T1* (Ephemeroptera: Leptophlebiidae), *Amphine-mura T1* (Plecoptera: Nemouridae), *Perlidae* (Plecoptera), *Anisocentropus T1* (Trichoptera: Calamoceratidae) and *Tanypodinae* (Diptera: Chironomidae) associated with *Liquidambar formosana* and *Aleurites montana* leaves with increasing length of exposure in Tai Po Kau Forest Stream.

Table 2. Consumption of dead leaves in laboratory tanks by *Brotia hainanensis* (1 leaf species/tank).

D. Wt. Leaves at Start	D. Wt. Leaves Consumed	D. Wt. Leaf Consumed per g D. Wt. Snail per Week	% of Leaves Available Consumed	% Organic Matter in Remaining Leaf Tissue
<i>Aleurites montana</i> : (Dry weight of snails in experimental tank = 6.55 g)				
5.57	1.60	0.24	28.73	85.45
4.00	2.26	0.35	56.50	87.25
4.96	1.14	0.17	22.98	90.57
4.24	1.12	0.17	26.42	92.16
5.26	1.67	0.25	31.74	91.41
\bar{x} - -	- -	0.24 ± 0.07	33.27 ± 13.37	89.37 ± 2.88
<i>Liquidambar formosana</i> : (dry weight of snails in experimental Tank = 4.56 g)				
4.18	1.18	0.26	28.23	75.89
3.11	1.25	0.27	40.19	91.61
2.23	0.67	0.15	30.04	85.52
2.12	0.54	0.12	25.47	85.79
2.38	0.81	0.18	34.03	85.81
\bar{x} - -	- -	0.20 ± 0.04	31.59 ± 5.72	84.88 ± 5.65

Additionally, the snails ingested similar proportions of both types of litter and the percentage organic matter in the remaining leaves after feeding was not significantly different from that recorded at the start. When the snails were presented with a mixed food source comprising 50% by weight of *A. montana* and *L. formosana*, the two types of litter were not consumed in equal amounts. In all replicates, the snails ate a greater percentage of the *L. formosana* leaves (Table 3). This trend was not altered by changing the duration of the feeding time from 7 to 14 days although the proportion of the original material that was consumed increased. The mean values for the rate of litter consumption in tanks where both types were present were 0.27 and 0.16 g dry weight litter/g dry weight snail/week for *L. formosana* and *A. montana* respectively, indicating that the former species was eaten by the snails at a faster rate. Student's 't' test carried out on these figures indicated that this difference was significant where $P < 0.05$ ('t' = 2.44 with 12 degrees of freedom).

Discussion

The present investigation was designed to provide information on the community processing of leaf litter in a tropical forest stream and to supply

Table 3. Comparative palatability of dead leaves in laboratory tanks to *Brotia hainanensis* (2 leaf species/tank).

Dry Weight of snails (g)	Feeding Period (days)	D. Wt. Leaves at Start (g)	D. Wt. Leaves Consumed (g)	D. Wt. Consumed/g Snail	D. Wt. Leaves Consumed/g Snail/Week	% of Available Leaves Consumed	Leaf Type
6.55	7	3.68	1.59	0.24	0.24	43.21	<i>Liquidambar</i>
6.55	7	4.10	1.18	0.18	0.18	28.78	<i>Aleurites</i>
4.56	7	4.76	2.02	0.44	0.44	42.44	<i>Liquidambar</i>
4.56	7	4.67	1.03	0.23	0.23	22.06	<i>Aleurites</i>
6.55	9	4.00	2.15	0.33	0.26	53.75	<i>Liquidambar</i>
6.55	9	4.33	1.45	0.22	0.17	33.49	<i>Aleurites</i>
4.56	9	3.83	2.26	0.50	0.39	59.01	<i>Liquidambar</i>
4.56	9	3.57	1.14	0.25	0.19	31.93	<i>Aleurites</i>
4.56	14	2.89	2.09	0.46	0.23	73.32	<i>Liquidambar</i>
4.56	14	3.19	1.43	0.31	0.16	44.83	<i>Aleurites</i>
6.55	12	2.38	1.29	0.20	0.12	54.20	<i>Liquidambar</i>
6.55	12	2.60	0.94	0.14	0.08	36.15	<i>Aleurites</i>
4.56	12	2.25	1.71	0.38	0.22	76.00	<i>Liquidambar</i>
4.56	12	2.68	0.93	0.20	0.12	34.70	<i>Aleurites</i>

data for comparison with what is known of leaf breakdown in temperate environments. A further aim was to determine whether contrasting types of litter would break down at different rates in a tropical stream and, if so, to monitor physical and biotic changes associated with such variations.

In common with what is known of allochthonous leaf litter in temperate aquatic habitats, laboratory investigations indicated that a significant percentage of soluble material is leached from litter during the first 24 hours of inundation (KAUSHIK & HYNES, 1971; HYNES et al. 1974; PETERSON & CUMMINS, 1974; MCDOWELL & FISHER, 1976; BLACKBURN & PETR, 1979). The immediate weight loss in *Liquidambar formosana* was substantial (14.5%) and although that of *Aleurites montana* was much smaller (6.3%) it still represented a considerable loss of soluble material. Some investigations into the significance of dissolved material in lotic habitats have been undertaken (LUSH & HYNES, 1973, 1978; LOCK & HYNES, 1975, 1976) but MCDOWELL & FISHER (1976) are the only workers to have considered its importance in the stream energy budget. They concluded that the utilization of dissolved organic matter (largely leaf leachates) accounted for 7–11% of ecosystem respiration in Roaring Brook, New Hampshire. The large amounts of *L. formosana* litter entering parts of Tai Po Kau Forest Stream (DUDGEON, 1982a) indicate that leaf leachate may be an important substrate for consumer respiration, particularly after it has flocculated into fine particles (LUSH & HYNES, 1973) and become

available to filter-feeders (WOTTON, 1976). Downstream increases in B.O.D.₅ have been recorded in a shaded riffle reach in Tai Po Kau Forest Stream (DUDGEON, 1982b) indicating that such localities may be in a predominately exporting mode with respect to leaf leachates.

Over both short and long term there are obvious differences in the magnitude of weight loss due to leaching from *L. formosana* and *A. montana* litter. BLACKBURN & PETR (1979) have also recorded magnitudes of loss varying according to leaf species; the patterns of loss from Australian litter were, however almost identical, which was not the case in the present study. While the mechanisms accounting for the variations in weight loss due to leaching in *A. montana* and *L. formosana* are not known, the cuticle is thick and well developed in the former species but rather thin and flimsy in *L. formosana*. BLACKBURN & PETR (1979) have attributed differences in leaching from various species to the properties of the waxy leaf cuticle. Interestingly the rate of leaching from *L. formosana* in the first 24 hours after immersion is comparable to the values recorded for *Acer* spp. (KAUSHIK & HYNES, 1971; LUSH & HYNES, 1973), leaves which generally decay relatively quickly in temperate streams (PETERSON & CUMMINS, 1974; TRISKA & SEDELL, 1976).

Litter breakdown in Tai Po Kau Forest Stream took place rapidly. All introduced leaves in the study area had disappeared by the 13th week, 10% of the original *L. formosana* biomass remaining after 11 weeks as compared to 17% of the *A. montana* at that time. Surprisingly, the weight loss during the first week in the stream was the same for both types of litter indicating that a greater proportion of the loss of *A. montana* was due to fragmentation or biotic processing rather than leaching.

As Table 4 shows, the rate of disappearance of litter in Tai Po Kau Forest Stream was more rapid than that recorded in any other study of this type, the values of TRISKA & SEDELL (1976) being most similar to the present investigation. The reasons for this marked difference may reflect unusual conditions in the study area, or characteristics of the species of leaves selected for study. Alternatively, the exposure technique used in this investigation may have speeded litter breakdown. Considering the latter point, the rationale for the exposure technique used has been discussed above and will not be repeated here. BENFIELD et al. (1979) state that breakdown rates vary according to the exposure technique employed. As the present technique has not been used previously, there are difficulties in making comparisons with published investigations. However, the reduction of certain mechanical and biotic effects as a result of the use of mesh bag or leaf pack exposure techniques (PETERSON & CUMMINS, 1974; REICE, 1974, 1977; BENFIELD et al. 1979; MEYER, 1980) suggests that the rate of processing in this study may have been a more accurate measure of the in situ value than those recorded in previous investigations.

Table 4. A list of rates of leaf breakdown in a variety of aquatic habitats, as drawn from recent literature.

	Length of study (weeks)*	% original weight remaining	Water tem- perature (°C)	Leaf species used
IVERSON 1973	52	10	1.8–12.8	<i>Fagus sylvatica</i>
DE LA CRUZ & GABRIEL 1974	52	60	–	<i>Juncus roemerianus</i>
PETERSON & CUMMINS 1974	32–60	10	0–11	<i>Carya glabra</i> <i>Quercus alba</i> <i>Acer</i> spp. <i>Tilia americana</i> <i>Populus</i> spp. <i>Fraxinus</i> sp. <i>Cornus amomum</i> <i>Decodon verticillatus</i>
PADGETT 1976	32	0	–	<i>Buchenavia capitata</i> <i>Manilkara bidentata</i> <i>Dacryodes excelsa</i> <i>Sloanea berteriana</i> <i>Corida borinquensis</i>
TRISKA & SEDELL 1976	6–10	50	6±0.5	<i>Acer</i> spp. <i>Alnus rubra</i> <i>Pseudotsuga menziesii</i>
BRINSON 1977	56	25	–	<i>Nyssa aquatica</i>
BLACKBURN & PETR 1979	13–15	20–39	4.0–8.5	<i>Eucalyptus regnans</i> <i>Nothofagus cunninghami</i> <i>Quercus</i> sp.
BENFIELD et al. 1979	14	32–91	–	<i>Platanus occidentalis</i>

* As calculated to the nearest week from published units of time (days, weeks, months).

Species specific differences in leaf breakdown rate are well known (HYNES et al. 1974; PETERSON & CUMMINS, 1974; PADGETT, 1976; TRISKA & SEDELL, 1976; DE LA CRUZ & POST, 1977; POST & DE LA CRUZ, 1977; BLACKBURN & PETR, 1979; MEYER, 1980). Consequently, it is possible that the rapid rate of decomposition in Hong Kong simply reflects the species composition of the litter. However, it is surprising to find that two species of leaves of dissimilar form and structure break down more rapidly than any of the wide variety of types recorded in the literature. Possibly such swift breakdown reflects differences operating at a higher level than regional variations in the species composition of litter. Temperature of the stream water during processing was 11.3–20.8 °C (\bar{x} 16.21 ± 3.56 °C) and may have affected breakdown rates which are known to be enhanced by warm conditions (KAUSHIK & HYNES, 1968, 1971; SUBERKROPP et al. 1975). REICE (1974) has noted seasonal differences in breakdown rates of allochthonous litter and attributes this phenomenon to

a form of temperature dependence. Significantly, SUBERKROPP et al. (1975) have found that oak leaf packs lose 50% of their original weight in 40 days at 20 °C whilst at 10 °C only 10% of the original weight was lost. The rate of weight loss at 20 °C is similar to that recorded during the present investigation, indicating that observed water temperatures may account for the relatively rapid rate of litter breakdown in Tai Po Kau Forest Stream. PADGETT (1976) has studied leaf decomposition in a neotropical stream the mesh bag exposure technique employed rules out direct comparison with the findings of the present study.

Water temperature, in association with exposure technique, may account for the speed of litter breakdown in Tai Po Kau Forest Stream. However, a number of authors have emphasized the role of microflora (KAUSHIK & HYNES, 1968, 1971; HOWARTH & FISHER, 1976; PADGETT, 1976; SUBERKROPP & KLUG, 1976; TRISKA & SEDELL, 1976) and macroinvertebrates (CUMMINS, 1973; CUMMINS et al. 1973; PETERSON & CUMMINS, 1974; WINTERBOURN & DAVIS, 1976; McDIFFET & JORDAN, 1978), as well as interactions between such organisms (BÄRLOCHER & KENDRICK, 1973 a, 1973 b; CUMMINS et al., 1973; IVERSON, 1973; HYNES et al. 1974), in leaf decomposition. There is also evidence that a succession of consumers occurs on leaf litter (KAUSHIK & HYNES, 1968, 1971; PETERSON & CUMMINS, 1974; SUBERKROPP & KLUG, 1976). Consequently, attention was paid to changes in the abundance of fungi, bacteria and macroinvertebrates associated with litter in the study area in an attempt to delineate patterns of succession and to compare them with those known from temperate regions.

The microorganisms associated with both types of litter showed marked temporal changes in abundance and considerable within-sample variation. This variation was a reflection of the serial dilution plating technique used to estimate microbial numbers. Problems of accuracy were also associated with preparation of the microfloral suspension from which dilutions were made. Although homogenizing of leaf discs has been employed by SUBERKROPP & KLUG (1976) (among others) it is far from satisfactory owing to the fragmentation of hyphae, rupturing of bacterial cells, and the possibility of contamination introduced by prolonged handling of the samples. To date, there is no single universally applicable method for obtaining accurate quantitative estimates of aquatic hypomycete populations (PADGETT, 1976; LINDSEY & GLOVER, 1976). The dilution plate method was used here due to its ease of application, the small amount of time needed for analysis (compared to direct counting), and its widespread use by microbiologists. The method was of particular value in this study as direct examination of fungi in *A. montana* litter was not possible by conventional clearing and staining techniques with lactophenol cotton-blue (IVERSON, 1973; PADGETT, 1976; SUBERKROPP & KLUG, 1976) due to the thickness of the cuticle.

There were generally more microorganisms on *L. formosana* litter. Successions of fungi were fairly well defined with an early peak in this species and a less obvious peak in the 5th week on *A. montana*. Poorly defined periods of maximum bacterial abundance were confined to the early stages of breakdown in both types of litter although this phase was more prolonged in *L. formosana*. *A. montana* showed a second, smaller, peak on the 11th week, possibly reflecting sample variability. KAUSHIK & HYNES (1968) have suggested that a competition mechanism may operate between the bacteria and fungi developing on fallen leaves. There is some evidence for this in the case of *A. montana* where peak densities of these populations do not overlap, but both bacteria and fungi were abundant in the early stages of *L. formosana* breakdown. HYNES et al. (1974) and PADGETT (1976) consider that fungi are significant agents in leaf decay, the former stating that they are more important than bacteria. It is surprising, therefore, that large numbers of fungi are not found throughout the breakdown, of both types of litter. Possibly the grazing effects of macroinvertebrates, which are known to feed on microorganisms (MACKAY & KALFF, 1973; BÄRLOCHER et al. 1978), may be of significance in this respect.

SUBERKROPP & KLUG (1976) record increased numbers of bacteria over time during leaf decomposition and report that mycoflora dominates the initial stages of processing of oak and hickory leaves with bacterial biomass peaking during the terminal stages. Hypomycetes (perhaps the dominant group of freshwater fungi) are able to degrade cellulose (PADGETT, 1976; SUBERKROPP & KLUG, 1976) but bacteria rarely have the ability to attack structural polymers. Possibly increased bacterial colonization must await fungal 'conditioning' of the leaf matrix resulting in an increased surface area and the availability of labile compounds (SUBERKROPP & KLUG, 1976). Observed succession of microorganisms on *L. formosana* leaves do not support this hypothesis as both bacteria and fungi are abundant in the initial stages of processing although the former are more numerous in the terminal stages. In contrast, fungi did not appear in large numbers on *A. montana* leaves until the 5th week of breakdown, a peak in bacterial abundance occurring during the first two weeks. As noted above, *A. montana* showed a weight loss comparable to that of *L. formosana*, and much greater than that expected on the basis of leaching, in the early stages of decomposition. It is possible that the abundant bacteria at this time utilize non-structural labile compounds in *A. montana* leaves thus speeding weight loss. Competition between microorganisms (KAUSHIK & HYNES, 1968) may have prevented fungal build-up until the 5th week of processing, by which time the bacteria would have exhausted the supply of labile compounds. Significantly, the decrease in fungi on the 7th week was followed by bacterial increase, a further indication of competition or fungal 'conditioning' of the leaf substrate making it more suitable for bacterial growth, as suggested by SUBERKROPP & KLUG (1976). Fungal 'conditioning' explains the persistence of

substantial bacterial populations after the reduction in fungi, but it is unclear why fungi and bacteria should coexist on one type of litter (*L. formosana*) but be mutually exclusive on another (*A. montana*). This observation may reflect varying interspecific interactions of different species of microorganisms which, as PADGETT (1976) has shown, may not be the same on all types of litter. Variations in microbial populations may reflect leaf biochemistry. Phenolic compounds may deactivate fungal extracellular enzymes and an effect of this type may account for the greater abundance of microflora on *L. formosana* litter. Reasons for fungal decline in the latter stages of processing are unknown but may be related to an increased surface area of the leaf matrix with an associated decline in planar surfaces for fungal colonization (SUBERKROPP & KLUG, 1976). Increased proportions of lignin as decomposition proceeds may be important in this respect, and respiration rates of leaf packs decrease when the litter is reduced to refractory lignin (TRISKA & SEDELL, 1976).

While KAUSHIK & HYNES (1968) and SUBERKROPP & KLUG (1976) state that fungi dominate the litter associated microflora during the initial phase of decomposition, SUBERKROPP & KLUG (1976) have demonstrated a succession of different hyphomycetes on leaves as decomposition proceeds. Conceivably, generalizations about the succession of fungi and bacteria on litter during decomposition mask what may be more significant changes in the species composition of certain elements of the microflora. As patterns of succession varied markedly between the two species of leaves examined here, it is doubtful whether, given the present state of knowledge, any useful and widely applicable generalizations can yet be made on this matter.

The numbers of macroinvertebrates associated with decomposing litter increased during the decomposition of *L. formosana*. Diversity also showed a slight tendency to increase but numbers of associated taxa did not. These variables followed no observable trend over time in the case of *A. montana* litter. The association of macroinvertebrates with litter suggests that a trophic interaction is involved as no algae was present on the leaf surfaces and only a small proportion of the taxa commonly collected were filter-feeders (Simuliidae, Stenopsychidae and possibly some Chironomidae). Additionally, the associated taxa were not representative of the composition of the benthos as a whole and, as a number of taxa were consistently occurring, it is apparent that the presence of these animals was not simply fortuitous. This can be inferred from the observations of EGGLESHAW (1964, 1969) and ULFSTRAND (1968) on the distributional relationship between stream macroinvertebrates and detritus, as well as from studies of the diets of such animals (MINSHALL, 1967; FAHY, 1972; MECOM, 1972; CUMMINS, 1973). The utilization of leaf litter by stream detritivores has been reviewed by CUMMINS et al. (1973) and, on the basis of the feeding categories of CUMMINS (1973) and CUMMINS & PETERSON (1974), all of the taxa commonly found associated with litter in Tai Po Kau Forest Stream,

apart from the Plecoptera, the trichopteran *Anisocentropus* T₁ and the carnivorous Tanypodinae, were fine particle feeders. The plecopterans and *Anisocentropus* T₁ were probably not abundant enough to generate sufficient fine particles to sustain the collector or grazer taxa, indicating that microorganisms growing on the litter were an important food source for these fine particle feeders. PETERSON & CUMMINS (1974) hypothesized that time taken for microbial conditioning accounted for the delay in invertebrate colonization of decaying leaves in a North American stream. Indeed, it has been shown that some aquatic invertebrates feed preferentially on leaves which have a rich microflora (MACKAY & KALFF, 1973; HYNES et al. 1974; BÄRLOCHER et al. 1978). While there was little time lag between initial exposure of leaves and macroinvertebrate colonization most taxa on *L. formosana* showed a marked tendency to increase in numbers as breakdown proceeded. There was no evidence of a positive correlation between macroinvertebrate and microfloral abundance, and fungi and bacteria were least numerous on *L. formosana* litter when the greatest number of invertebrates were recorded. Possibly grazing pressure reduced microbial abundance at this time.

There is evidence that animals can select the most energetically 'desirable' foodstuff and macroinvertebrates preferentially consume leaves which decay rapidly (IVERSON, 1974; HYNES et al. 1974). Rapidly decomposing leaves would tend to have the highest populations of microflora and, as invertebrates feed preferentially on such leaves, it is not surprising to find a correlation between the number of animals and litter decay rate. In the present study, *L. formosana* supported greater microfloral and, as would be expected from the above, macroinvertebrate populations than *A. montana*. Significantly, the former species had a slightly faster breakdown rate. BLACKBURN & PETR (1979) have also presented data showing that macroinvertebrate numbers were highest on rapidly decomposing litter although they do not discuss this point.

There is evidence that macroinvertebrates can be significant in hastening leaf breakdown (PETERSON & CUMMINS, 1975; WINTERBOURN & DAVIS, 1976). However MEYER (1980) recorded no correlation between invertebrate abundance and decay rate in a North American Forest Stream. HOWARTH & FISHER (1976) state that the role of macroinvertebrates in leaf breakdown may depend upon the availability of nutrients and the chemical characteristics of the stream water. This theory has yet to be tested. REICE (1974; 1977) states that litter decomposition on sediments with high faunal diversity would be rapid as greater diversity would increase processing efficiency. However, the relationship between species diversity in leaf packs and rapid processing has yet to be convincingly demonstrated and was not immediately apparent in the present study.

If macroinvertebrates can influence the rate of decay of allochthonous detritus in streams, it is of interest to test whether detritivores consume more

of the litter which, in the present study, has the faster breakdown rate. Laboratory feeding experiments with the detritivorous snail *Brotia hainanensis* showed that *A. montana* and *L. formosana* were consumed at equal rates when presented separately. When the snails were given both types of leaves together, a marked increase in the consumption of *L. formosana* was noted with a concomitant decrease in the consumption of *A. montana*. The difference in the rate of feeding on these two species was statistically significant indicating that, under certain circumstances, particular species of macroinvertebrates may affect the rate of litter breakdown on the basis of food preferences. It is not known whether the larger amounts of microorganisms on *L. formosana* influences the palatability of these leaves. The experimental feeding period was never more than two weeks thereby maintaining the microfloral communities on the litter at a level which field studies indicate the differences between their microbial populations was greater than at any other time during the decay period. Since macroinvertebrates can select substrates rich in microorganisms (e.g. CUMMINS & KLUG, 1979) it is possible that this variable alone could result in the preference of *B. hainanensis* for *L. formosana* leaves. Alternatively, the snail may be responding to the same (unknown) factor which determines why more microorganisms grow on this species of leaf than on *A. montana*. Regardless of the reasons for selection, differences in the palatability of the leaves tested may help to explain differences in populations of microorganisms and macroinvertebrates that they support, as well as observed variations in breakdown rate in Tai Po Kau Forest Stream.

When terrestrial leaves fall into a stream they come under the influence of physical and biotic processes. While leaching and fragmentation, in association with water movement, makes the litter available to consumers elsewhere in the stream, the remainder is colonized by fungi and bacteria using the leaf as a substrate and energy source. Macroinvertebrates feed on the leaf and associated microbes. Through processes of pitting and fragmentation these animals create additional surfaces for microfloral growth and thereby increase their food source and enhance the rate of leaf breakdown. A complex set of interactions develop with coarse and fine particle detritivores interacting with each other as well as the microflora, the latter group growing on leaf fragments and faecal particles thus enhancing their food value. Such interactions can be maintained as long as the flow of terrestrial litter into the stream continues. Evidence from temporal changes in the standing stock of allochthonous detritus in Tai Po Kau Forest Stream (DUDGEON, 1982 a), and the findings of the present study, indicate that such trophic interactions dominate habitat metabolism. Differences in the rates of breakdown and the populations of organisms associated with different types of litter will affect the utilization of the variety of allochthonous inputs, with limiting stages occurring at the level of interactions between microflora and macroinvertebrates and their interactions with the

particular species of leaf substrate. The nature and significance of such interactions represents an important field for future research.

Summary

An investigation of the breakdown of two species of leaves in Tai Po Kau Forest Stream, Hong Kong, was undertaken during the winter and early spring of 1978. The work was carried out so as to coincide with the period following abscission of the test species, *Aleurites montana* and *Liquidambar formosana*. This is the first account of the physical and biotic changes associated with litter breakdown in an Asian tropical forest stream. Particular attention was paid to changes in the numbers of fungi and bacteria during decay as well as to the temporal succession of macroinvertebrate taxa.

Complete breakdown occurred by the 13th week of the investigation, the decomposition of *L. formosana* proceeding slightly faster than that of *A. montana*. The pattern of weight loss due to leaching was markedly different in these species as were the patterns of succession shown by bacteria and fungi on the leaf tissue. Microorganisms were generally more abundant on decaying *L. formosana* leaves and there was a general trend for the numbers and diversity (d) of the associated macroinvertebrates to increase as breakdown progressed. No such trends were evident for macroinvertebrates associated with *A. montana*.

The breakdown rates of litter in Tai Po Kau Forest Stream were among the most rapid recorded in any freshwater habitat. This was attributed to the temperature of the stream and the exposure technique used in this study, which avoided many of the disadvantages inherent in the use of mesh bags and leaf packs. The differences between the breakdown rates of the two types of litter were discussed. *A. montana* was not favoured as a substrate for microbial growth and may be avoided by macroinvertebrates. Feeding experiments using the detritivorous snail *Brotia hainanensis* indicated a statistically significant preference for *L. formosana* leaves over those of *A. montana*. It was not clear whether this preference reflected the greater number of microorganisms associated with *L. formosana* litter, but other factors may be important as both the macro- and micro-consumers involved in leaf breakdown were more numerous on this substrate.

The findings of this investigation were considered to support indications that Tai Po Kau Forest Stream is a predominantly heterotrophic system dependent on the surrounding terrestrial environment for a large proportion of its metabolic requirements.

Zusammenfassung

Der Abbau von 2 Fallaubarten, *Liquidambar formosana* und *Aleurites montana*, im Tai Po Kau Forest Stream, New Territories, Hong Kong, wurde untersucht. Beide Arten wurden sehr schnell abgebaut und waren nach der 13. Untersuchungswoche verschwunden. *A. montana* wurde langsamer zersetzt als *L. formosana*, die durch Auslaugung beträchtlich mehr an Gewicht verlor. Obwohl die Anwendung einer neuen Expositionstechnik die Abbaugeschwindigkeit erhöht haben mag, ist zu vermuten, daß die im Vergleich zu Fließgewässern der gemäßigten Zone höhere Wassertemperatur ein wichtiger Ursachenfaktor war. Die Häufigkeitskurven der Pilze und Bakterien waren bei den beiden Fallaubarten verschieden. *L. formosana* wies größere Mikroflora-Populationen auf und zeigte Maxima beider Typen von Mikrokonsumenten in den frühen Stadien der Zersetzung. Dagegen waren an *A. montana*-Blättern anfangs Bakterien vorherrschend, während Pilze an Bedeutung in der 5. Woche zunahmten und danach wieder abnahmen.

L. formosana wies eine reichere Makroinvertebraten-Gesellschaft auf als *A. montana*, und diese Konsumenten-Assoziation zeigte eine Zunahme an Häufigkeit und Diversität (d) mit fortschreitender Zersetzung. Solche Trends waren dagegen bei den mit *A. montana* assoziierten Invertebraten-Populationen nicht ersichtlich. Laborexperimente zeigten, daß die detritusfressende Fließwasserschnecke *Brotia hainanensis* im Wahlversuch signifikant größere Mengen von *L. formosana* verzehrte, was durch die reichere Mikroflora oder die bessere Schmackhaftigkeit der Blätter verursacht sein dürfte. Die Ergebnisse werden diskutiert im Hinblick auf den Laub-Abbau in den Gewässern der gemäßigten Zone. Es wurde geschlossen, daß das untersuchte tropische Wald-Fließgewässer wahrscheinlich zur Aufrechterhaltung seines vorhandenen Gemeinschafts-Stoffwechsels von Zufuhren aus seiner terrestrischen Umgebung abhängig ist.

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