Compliments
Jackie King

Leaf-pack dynamics in a southern African mountain stream

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SUMMARY. 1. The occurrence, composition and invertebrate fauna of naturally-occurring leaf packs were studied over 24 months in Langrivier, a second-order mountain stream in the south-western Cape, South Africa. Langrivier is shallow and fast-flowing and stores very low levels of allochthonous detritus, although natural leaf packs form an obvious part of the energy base in the stream throughout the year.

2. The occurrence and size of the packs were influenced mainly by stream discharge and by the timing and character of leaf fall from riparian trees. Packs were smallest (minimum dry mass 17 g, minimum volume 1.7×10^{-5} m^3) in winter when discharge was high, and largest (maximum dry mass 191 g, maximum volume 4.2×10^{-3} m^3) in spring when discharge decreased and leaf fall from the evergreen riparian trees began. Through the year the packs covered a mean 0.41% of the stream bed and had a mean abundance of 0.46 packs m^{-2} of stream bed. They were ephemeral, lasting on average <1.7 months and yet accounted for 29% of the stored detritus in the system. Wood was the dominant component of packs, and leaves at all stages of decomposition were present throughout the year.

3. The ratio of numbers of invertebrates in packs: numbers of individuals in the benthos was very low (0.002–0.030), presumably because of the rarity and small size of the packs. Nevertheless, the density of invertebrates per unit area covered by leaf packs was consistently much higher than the density in an equivalent area of the benthos, except during peak leaf fall (October to December).

4. Experiments were undertaken with artificial leaf packs in order to determine the extent to which these simulated natural packs. Although both natural and artificial leaf packs contained a high proportion of Plecoptera (46% and 29% respectively), the natural packs contained high numbers of simuliid larvae (33% of total), whereas artificial packs had a high percentage of chironomid larvae (62%). Several other taxa regularly occurred in both types of pack but in very low numbers. In addition,

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artificial packs contained more than twice as many invertebrates per unit mass of pack as did natural packs.

5. Natural packs are important refugia for stream invertebrates during the winter, when discharge is high and standing stocks of detritus are low. They also reflect the facility of the stream bed for retaining particulate organic matter. Artificial packs, while of use in carefully planned experiments, do not closely simulate natural packs.

Introduction

Over the last two decades a considerable body of knowledge has accumulated on the ecological functioning of small headwater streams in forested catchments. Such streams are often described as heterotrophic, since the bulk of the organic carbon stored in them is litter contributed by riparian trees (see Bird & Kaushik, 1981, for references).

Because of the unidirectional flow of water through stream systems there is a tendency for falling litter to be lost downstream instead of settling on the stream bed, where it would become available to the stream biota. The rate at which material is transported downstream can be reduced by physical storage, by biological uptake and storage, and/or by lower gradients and slower currents (Minshall *et al.*, 1983). In high-gradient, erosive mountain streams, current speeds are usually high enough for a considerable portion of each year to keep organic particles in suspension. The initial capture and subsequent retention of this transported material, which is critically important for the biota, is dependent on both the physical characteristics of the stream and the character of its riparian vegetation (Speaker, Moore & Gregory, 1984). Where the stream bed is uneven, buoyant particles such as leaves are likely to become trapped, while woody material falling into the stream from riparian trees may lodge between boulders and provide a framework upon which other transported material may accumulate. Such accumulations are usually known as debris dams if they are large (Bilby & Likens, 1980) or leaf packs if they are small, thereby distinguishing them from the uncompacted debris that lies scattered in varying amounts on most stream beds.

Recognized as an important component of carbon storage in streams, leaf packs have received considerable attention in the last decade, although most work has consisted of experimental manipulation of artificial leaf packs. Interest has centred both on the decomposition of leaves in the packs and on the fauna associated with them (Petersen & Cummins, 1974; Iversen, 1975; Short & Maslin, 1977; Blackburn & Petr, 1979; Winterbourn, 1978; Anderson & Sedell, 1979; Cummins *et al.*, 1980; Reice, 1980; Short, Canton & Ward, 1980; Mutch *et al.*, 1983; Rounick & Winterbourn, 1983).

We know of no work that deals with the year-round character and components of naturally-occurring leaf packs, while that dealing with similarities between natural and artificial packs is rare. In view of the amount of work done using artificial packs, it seemed timely to determine the extent to which they reflect conditions in natural packs at the same time as examining the distribution and content of natural packs on the stream bed through the year. We therefore studied various aspects of natural leaf packs over a 24-month period, and carried out experiments using artificial packs. In this paper we describe the dynamics of naturally occurring leaf packs in Langrivier, a southern African mountain stream, report on some of the experimental work with artificial packs, and outline the importance of the natural packs to the stream fauna.

The study area

The study area is described in detail by King *et al.* (1987). Briefly, the Jonkershoek Valley is located in the Hottentots-Holland mountain chain, 60 km east of Cape Town. The valley forms part of a State Mountain Catchment Area and is an important source of water for drinking and irrigation. The upper slopes of the valley support mountain fynbos, which typically consists of closed sclerophyllous shrubland on open slopes and moisture-loving trees in sheltered

kloofs (ravines) and riparian zones (Kruger, 1979a). Much of the lower part of the valley has been planted with the exotic pine *Pinus radiata* L. The Langrivier catchment is situated upstream of the pine plantations and, having been protected from fire since 1943, supports mature, undisturbed fynbos.

The catchment of Langrivier covers 246 ha on the north-eastern slope of the valley, and is surrounded by peaks approximately 1500 m high. Mean annual precipitation is 2242 mm (Bosch & Hewlett, 1982), less than 10% of which occurs in the dry austral summer (December–March: van der Zel, 1971). Mean annual streamflow is 1600 mm or 3.5×10^6 m^3 (Bosch & Hewlett, 1982).

Langrivier, the study stream, is 3 km long, 3–5 m wide, perennial, and has a flow pattern typical of the area, with high discharge in winter (mean 0.22 m^3 s^{-1}) and low discharge in summer (mean 0.03 m^3 s^{-1}). The stream bed at the study site has a mean gradient of 16.8% and consists almost entirely of bedrock, boulders and stones. The stream is shaded by a closed canopy of riparian trees, all of which are evergreen and endemic to the region; in appearance Langrivier is typical of second-order mountain streams in the region.

Langrivier is subject to violent spates and as a consequence it retains much less allochthonous detritus than most streams reported elsewhere (King *et al.*, 1987). Debris dams are rare, with an incidence of less than one per 100 m of stream length. For about half of each year the stream bed is almost free of organic debris, mid-winter levels of organic matter being as low as 23 g dry mass m^{-2} to a depth of 200 mm into the hyporheos. Through the year, scattered fragments of CPOM (coarse particulate organic matter: >950 μm) and FPOM (fine particulate organic matter: 80–950 μm) account for about 60% of the allochthonous detritus within the top 200 mm of the stream bed, UPOM (ultrafine particulate organic matter: 0.6–80 μm) accounts for about 19% and leaf packs comprise the rest (c. 21%).

Methods

Our study site is a stretch of stream, 100 m long, immediately above a gauging weir and approximately 50 m above the confluence of Langrivier

with the Eerste River, the main river draining the Jonkershoek Valley. Five leaf packs were collected randomly from the stream bed every month from August 1984 to June 1986. A hand-net with 80 μm mesh was held downstream of each pack as it was lifted and the pack, together with the contents of the net, was transferred to a plastic bag. From November 1985 onwards, the linear dimensions of each pack were recorded so that the proportion of stream bed covered by packs could be calculated. The packs were stored at -18°C until processed.

Each pack was sorted into wood and bark (hard fractions), fragments and various species of leaves (soft fractions), and animals. The animals were stored in 70% alcohol, sorted to the lowest taxonomic level possible and counted. Sorted leaves were rated on a scale of 1–5 with respect to fragmentation and skeletonization in order to determine the relative state of decomposition of different leaf species during the year. Leaves with a rating of 1 were whole, while those rated 5 were barely identifiable to species, being little more than mid-ribs and veins. Rating was done on a sub-sample of not less than twenty leaves for each species when the packs were large.

For the first 15 months, leaf-pack biomass was determined by drying the separated leaves, wood, bark and fragments to constant weight at 60°C and weighing. The samples of fragments were ashed at 450°C for 4 h to determine by weight loss the amount of organic material present. For the last 7 months packs were sorted into wood/bark, CPOM and FPOM in order to investigate the storage of fine particles within the packs.

Concurrent with the above work, a 10 m stretch of stream above the sampling site was delineated for studying the occurrence and longevity of packs. The stretch was mapped accurately so that individual packs could be recognized and measured from month to month.

Artificial leaf packs were placed in the stream in order to trace their decomposition and colonization by invertebrates in a natural system. Freshly abscissed leaves of three species of riparian trees (*Brabejum stellatifolium* L., *Ilex mitis* (L.) Radlk, and *Cunonia capensis* L.) were dried, divided into portions of approximately 2 g dry mass, weighed accurately and placed in coarse-meshed (aperture 3–4 mm) or fine-meshed (aperture 250 μm) bags. Two kinds of

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bags were used in order to determine the effects of large shredders on the litter and the rate of loss of fine leaf fragments. Three replicates of each species in each kind of bag (eighteen bags in all) were placed together in a large loose-meshed bag (probably akin to the 'onion bag' of Rounick & Winterbourn, 1983). Seven such large bags were placed in the stream in February 1985, at a time of high natural input of leaves. One large bag was removed after each of the following submersion periods: 2, 4, 6, 8, 12, 16 and 20 weeks. The last bag was removed in mid-winter (July 1985). The bags were submerged in water approximately 200 mm deep, immediately downstream of several large boulders to which they were secured with fishing line. Two smooth, heavy stones were placed inside each large bag as ballast. When removed from the stream the bags were individually placed in plastic bags and stored at $-18°C$. Later, the leaves were gently swilled in water, dried and weighed. The animals were sorted, using a dissecting microscope, and stored in 70% alcohol. Detailed results of the decomposition of the leaves will be dealt with elsewhere; in this paper we concentrate on the fauna colonizing the packs.

FIG. 1. (a) Mean discharge per month; (b) litter fall from riparian trees; (c) number of leaf packs m^{-2} of stream bed, during the study period in Langrivier. (a) and (b) from King *et al.* (1987).

Results

Abundance and size of natural packs

The presence and size of leaf packs were influenced by two main factors: stream discharge and the timing and magnitude of litter fall. The Jonkershoek Valley lies in a winter rainfall area, and the flow pattern of Langrivier is characteristic of streams in this region (Fig. 1a). Discharge peaks in winter (June–August) and is usually lowest in late summer (February). During the study period, mean discharge measured over 24 h reached 2.29 m³ s⁻¹ on a few isolated days each winter, while mid-summer minima measured over the same period were approximately 0.02 m³ s⁻¹.

Stream discharge decreased in spring each year at the same time that leaf fall of the evergreen riparian trees began (Figs. 1a, b). Peak intensity of leaf fall occurred in summer, when stream flow was minimal, so that much of the material falling into the stream was retained until about mid-autumn. The onset of winter rains brought spates that scoured most debris
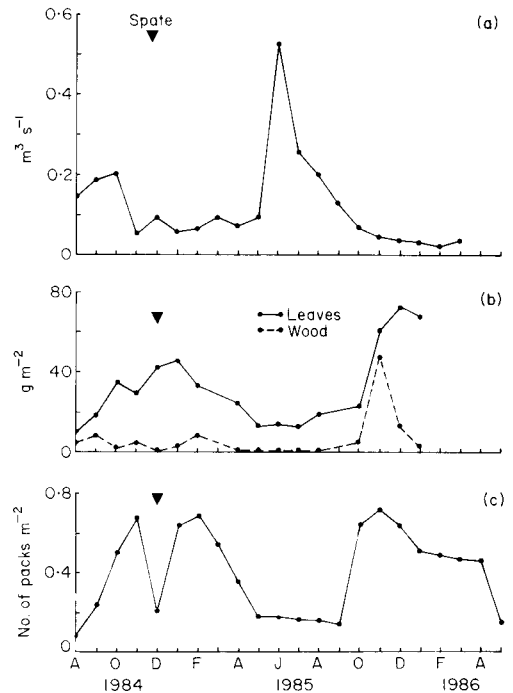
from the stream bed (Fig. 1c and King *et al.*, 1987).

The number, mass and volume of packs fluctuated during the year in response to changes in discharge and litter fall. Though leaf fall was much heavier in the second than in the first year of the study, the number of packs in the mapped zone peaked at the same summer level of 0.70 packs m^{-2} of stream bed (Fig. 1c). In winter the stream-bed area increased due to flooding of stony bankside areas, while the number of packs dropped to 0.15 m^{-2} of streambed. The only deviation from this pattern was in December 1984 when high discharge on the day before the sampling trip washed most packs away. Numbers therefore were low that month, but had returned to the level of the preceding month by January 1985, as leaf-fall intensity was still high. The mean abundance of packs through the year (January–December 1985) was 0.46 packs m^{-2}, and their mean longevity (August 1984 to January 1986) was 1.7 months (SE±0.12).
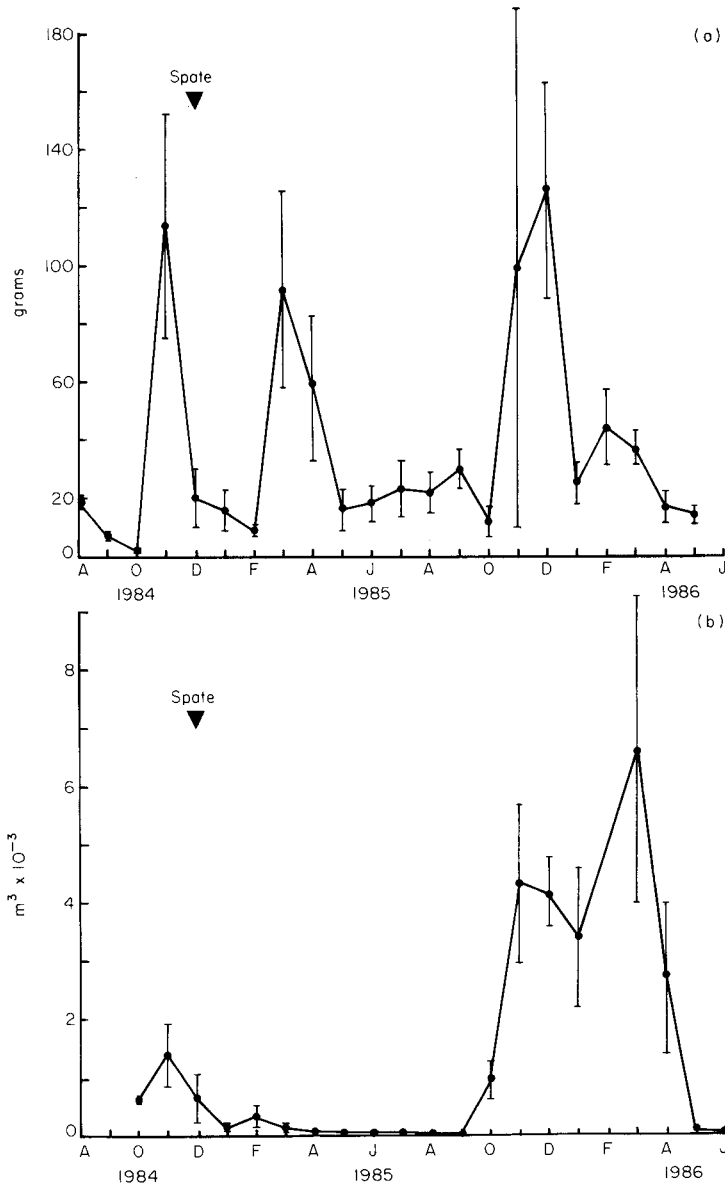
Changes in the mass and volume of packs

FIG. 2. Monthly changes in (a) mean dry mass of leaf packs and (b) mean volume of leaf packs in Langrivier. Error bars are ±1 SE.

showed the same general trends (Figs. 2a, b), with high values recorded from late spring to early autumn and very low values for the rest of the year. While the average mass of packs was similar in both summers, volumes were much smaller during the first summer. This appeared to be due at least partly to the spate in December 1984, which washed away most of the packs and decreased the number, mass and volume of

those remaining. Though more packs formed in the ensuing weeks, these remained considerably smaller than those present before the spate, until a slight increase in discharge in March brought bankside material into the system. The mean mass of the packs then increased but their mean volume did not, possibly because of an increased woody content and/or because discharges were already sufficiently high to cause them to com-

pact (see below). In the following summer (December 1985 to February 1986) discharges were much lower (Fig. 1a), although a brief increase in discharge 8 days prior to the sampling in January 1986 was probably responsible for the temporary reduction in the bulk of the packs at the time (Fig. 2). Other than that, summer and autumn volumes of packs were relatively high, probably because the stream lacked the force to compact them. Mean values for both mass and volume of packs dropped to the winter low by May 1986.

Mean dry mass of packs during 1985 was 51.6 g (SE±16.4) and mean volume between August 1985 and July 1986 was 3.4×10^{-3} m^3 (SE±0.0021). Mean standing stock levels were 27.2 g m^{-2}, with seasonal values ranging from 3.0 g m^{-2} (winter) to 130.0 g m^{-2} (spring). The longer-lasting packs accumulated and lost debris through the months before their final disappearance (Table 1), although no common trend was apparent.

A close correlation was shown between total dry mass and volume of packs (Fig. 3), and between soft litter and volume, with a slightly weaker correlation between hard litter and volume ($P<0.001$ in all three cases, $N=30$). Compacting of the packs occurred when discharge was high and resulted in packs differing in density through the year. Pack density (mass/volume) was always very low in the drier months (monthly means 0.02–0.06 g cm^{-3}), with a sharp increase after the advent of winter rains (0.55–1.58 g cm^{-3}).

Composition of natural leaf packs

During summer and early autumn, leaf packs occurred as large, low-density accumulations of freshly-fallen leaves, but in winter most comprised one or two twigs with a few trapped leaves. This predominance of wood, as well as the compaction caused by high discharges, contributed to the higher densities of winter packs. Only occasionally, and then only in the months of peak leaf fall, did leaves account for more than half of the dry mass of a pack (Table 2). In winter they contributed as little as 10% to a pack's weight, the remainder being twigs.

The proportions of different leaf species in

TABLE 1. Fluctuations in volume (m$^3 \times 10^{-6}$) of individual, long-lasting leaf packs from appearance to disappearance

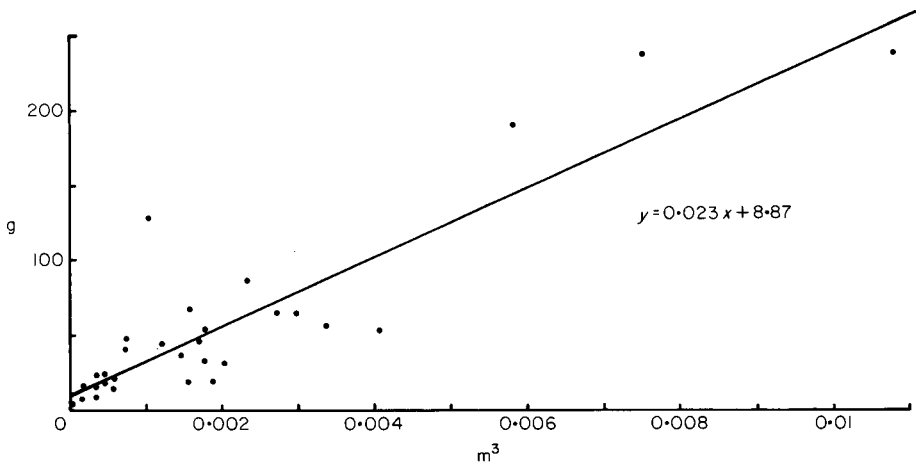| Leaf pack	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.
1	48	80	48	207	17					
2	375	20	360	48						
3					8	9	60	360	7104	

FIG 3. The relationship between dry mass and volume of leaf packs. Data from August 1985 to June 1986.

TABLE 2. Monthly values (mean±standard error) for hard and soft litter of natural leaf packs

Month	Soft litter (g dry mass)	Hard litter (g dry mass)	% Hard
Aug. 1984	7.96±0.36	11.02±2.78	58
Sept.	2.48±0.66	5.30±1.07	68
Oct.	2.05±0.20	0.58±0.52	22
Nov.	55.78±18.35	59.58±25.82	52
Dec.	10.06±5.65	9.73±7.71	49
Jan. 1985	7.95±4.97	8.69±3.90	52
Feb.	3.75±1.33	4.50±1.47	55
March	13.98±3.72	78.07±36.77	85
April	27.36±12.68	31.42±16.18	53
May	3.44±1.94	13.50±7.93	80
June	4.69±2.22	14.17±5.76	75
July	2.62±0.98	21.29±9.98	89

packs closely reflected their proportions in litter fall (Fig. 4), with four species of tree contributing the bulk (74–99%) of the soft litter.

Decomposition of natural packs

Data on fragmentation and skeletonization of leaves in the packs revealed no clear differences between species (Fig. 5). Whole leaves dominated the packs during leaf fall (October–January), while a somewhat higher proportion of partly decomposed leaves was evident from late summer onwards. Heavily decomposed leaves never dominated the packs and throughout the year unbroken leaves were prominent, if not the

most abundant, constituents of packs. As leaves disintegrated, most fragments must have been washed away or eaten, since the dry mass of FPOM was always less than 1 g pack^{-1}. Nor was there any obvious seasonal trend in the ratio of FPOM:CPOM in packs, FPOM comprising <1% of the total dry mass of each pack in all months except March (2.1%) and April (1.0%) 1986.

The fauna

(a) *The fauna of natural leaf packs*. The numbers of invertebrates in individual natural leaf packs was strongly correlated with the dry mass
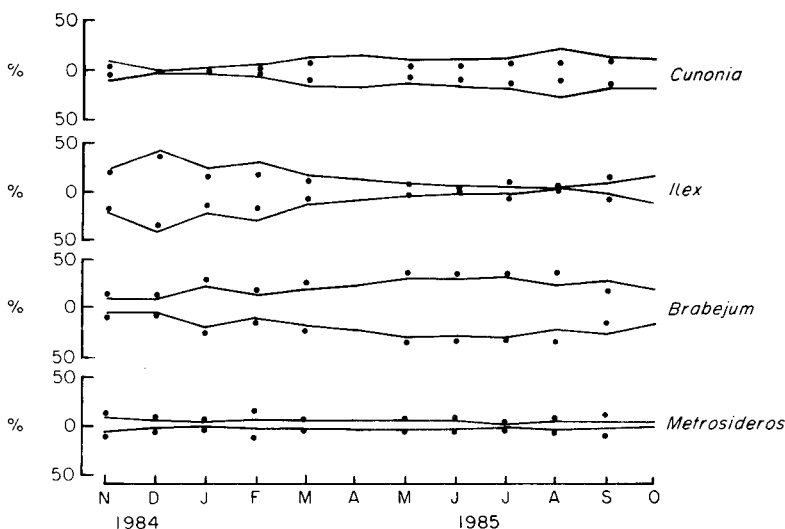

FIG. 4. The percentage occurrence of leaves of the dominant species of riparian trees in litter fall (dots) and in natural leaf packs (kites).
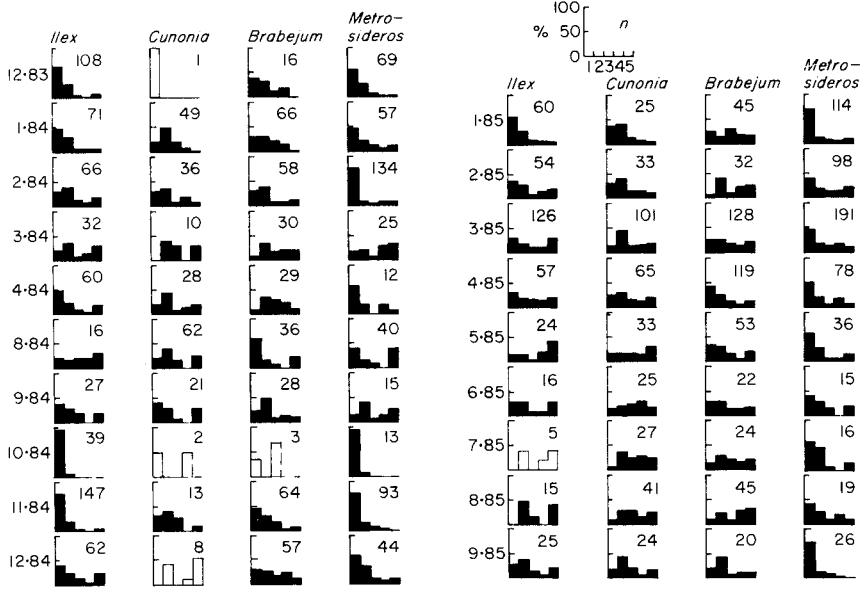
FIG. 5. The degree of fragmentation/skeletonization of leaves of the dominant species of riparian trees in natural packs through 19 months of the study in Langrivier. Histograms show the percentage of leaves at each level of decomposition (1=no damage; 5=little more than midrib and veins remaining). *n*=total number of leaves counted; blank histograms=<10 leaves in sample.

of the packs ($P<0.001$, $N=64$), with the smallest packs having fewest animals. Knowing monthly values for the wetted area of the mapped zone, the number of leaf packs occurring in the zone, the mean number of invertebrates per pack and the density of invertebrates in the benthos (unpublished data) it was possible to calculate the proportion of the fauna that occurred in packs. Numbers of animals in packs, expressed as the number per square metre of stream bed, ranged from four in winter to 105 in summer, giving ratios of leaf-pack animals : benthic animals between 0.0018 and 0.0296 (Fig. 6). The
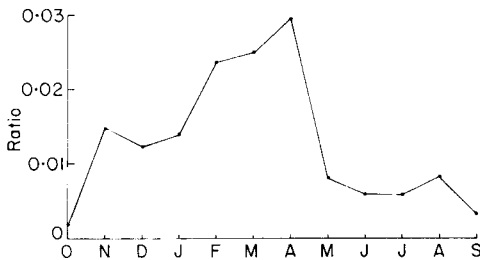

FIG. 6. Ratio of invertebrates in natural leaf packs: invertebrates in benthos based on numbers m^{-2} of stream bed. Data for leaf packs collected in 1984/85; data for benthos collected in 1983/84.

ratios, although always low, were lowest in winter and highest in summer to autumn, suggesting that packs were of least importance to the fauna in winter. Data on the number of animals per pack supported this suggestion, for numbers were lowest in winter (21–38 pack^{-1}) and highest in summer/autumn (154–173 pack^{-1}) (Table 3). When the abundance and size of the packs was taken into account, however, the reverse appeared to be true, as packs were much smaller in winter than in summer, so that the number of invertebrates per unit area of pack actually increased sharply in winter. If the numbers of invertebrates were related to the surface area covered by leaf packs, then as many as 43,700 animals could have occurred per square metre of leaf pack in mid-winter. In contrast, considerably smaller numbers would have been present in spring and early summer (1700 and 4900 animals m^{-2} of pack in October and November 1984, respectively).

Comparison of the numbers of animals per unit area of pack and benthos revealed that these were similar from spring until mid summer (Fig. 7). The numbers per unit area of pack then increased steadily for 3 months before decreasing sharply to a low of 5400 animals m^{-2} of pack

TABLE 3. Summary of the numbers and standing stocks of natural leaf packs and accompanying invertebrates

|	1984			1985									
	O	N	D	J	F	M	A	M	J	J	A	S	O
Mean no. of animals pack^{-1}	36	154	173	17	154	155	83	21	38	35	34	27	54
No. of packs 10 m^{-1} of stream	14	19	6	18	19	15	10	9	9	8	8	7	18
No. of animals in packs 10 m^{-1} of stream	504	2926	1038	306	2926	2325	830	189	342	280	272	189	972
Area of stream bed covered by leaf packs (m^2)	0.30	0.60	0.41	0.10	0.17	0.06	0.02	0.04	0.04	0.02	0.02	0.01	0.30
No. of animals m^{-2} of leaf pack	1658	4877	2532	3155	17626	36905	43684	5400	9243	14737	18133	21000	3197
Percentage of stream bed covered by packs	0.6	2.1	1.5	0.4	0.6	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.6
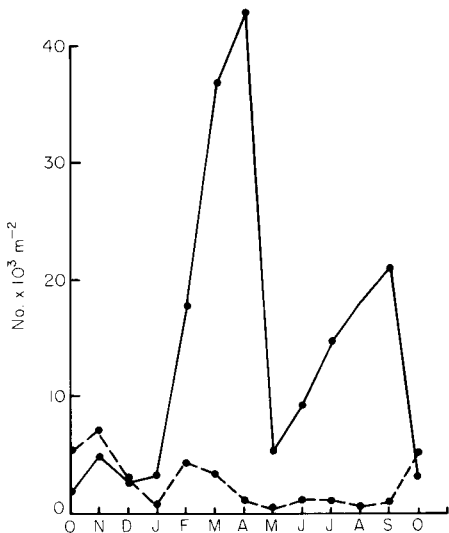
FIG. 7. Numbers of invertebrates m^{-2} of natural leaf pack (—) and m^{-2} of benthos (---). Data for leaf-packs collected in 1984/85; data for benthos collected 1983/84.

in late autumn (May), while those in the benthos remained fairly steady. Numbers on the stream bed then remained low through the winter, but numbers per unit area of pack rose steadily, reflecting the growing scarcity of organic material on the stream bed (King *et al.*, 1987). As discharge decreased and the seasonal leaf fall began in October, the number of animals in packs decreased to about the same density as for the benthos.

The relationship between the number of animals present in packs and benthos can be described using the power curve $y=ax^b$ (Fig. 8). As the proportion of stream bed covered by packs decreased, so the density of animals in packs increased relative to densities on the stream bed. The ratio of animal numbers in packs to numbers in the benthos was high in autumn and winter, when leaves were lost in spates, and low in mid-spring, when heavy leaf fall commenced. The ratio was lowest in November, when leaf fall began and benthic detritus was thus abundant, and highest in April, when the winter rains began.

The fauna was dominated by nymphal Plecoptera (46% overall) and larval Simuliidae (33%), which together accounted for 60–92% of the individuals present in packs each month (Table 4). Other animals that were present regularly, but in much lower numbers, were Chironomidae (monthly means <1–9%, 21% in one month), baetid Ephemeroptera (<1–9%), the leptophlebiid ephemeropteran *Castanophlebia calida* Barnard (<1–11%) and an helodid beetle larva (1–7%). Occasional individuals of about twenty other taxa were found in the packs.

A comparison of the faunal composition of leaf packs, benthos and drift (unpublished data) showed that Plecoptera, Simuliidae and/or Chironomidae were numerically dominant in all three, and that Ephemeroptera, Coleoptera and Trichoptera were represented consistently in one or more of the sets (Table 5). Other taxa each comprised <1% of the total numbers of invertebrates in any one set. The numerical pro-
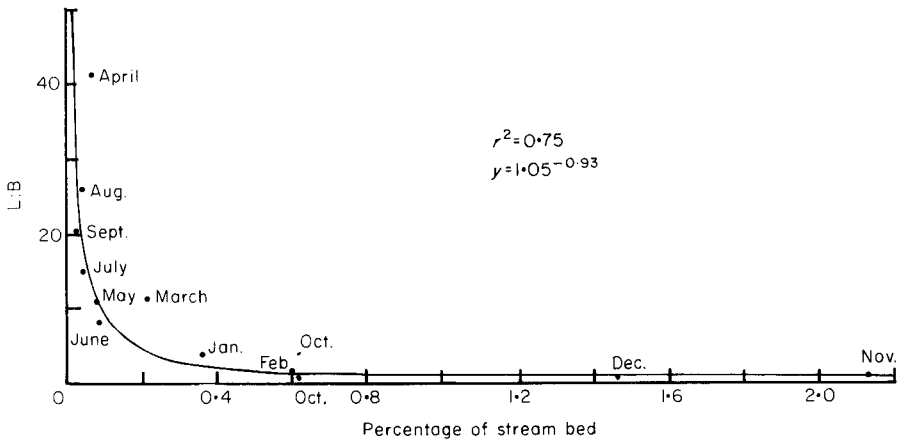
FIG. 8. The relationship between the numerical proportion of invertebrates m^{-2} of leaf pack and m^{-2} of benthos (L:B), and the percentage of stream bed covered by leaf packs.

TABLE 4. Percentage by numbers of each animal taxon in natural leaf packs during each month of the year

	1984			1985								
Taxon	O	N	D	J	F	M	A	M	J	J	A	S
Plecoptera	14	52	30	70	21	69	58	62	58	60	59	56
Diptera												
Simuliid larvae	77	26	52	12	71	11	2	14	24	17	29	22
Simuliid pupae	1	<1	2	—	—	<1	1	2	—	—	—	—
Chironomid larvae	—	<1	6	3	2	9	21	2	3	2	<1	2
Blepharicerid larva	1	—	1	—	<1	—	—	—	—	—	<1	1
Other Diptera	—	1	—	3	<1	1	1	—	—	—	—	—
Ephemeroptera												
Baetidae	3	2	1	—	1	5	1	5	3	6	<1	4
Castanophlebia calida	1	9	4	3	<1	<1	2	2	2	3	3	2
Other Ephemeroptera	—	—	—	—	—	—	—	2	—	—	—	—
Coleoptera												
Helodid larva	1	4	2	3	1	1	7	5	5	6	6	7
Other Coleoptera	—	1	—	3	<1	1	—	—	—	2	—	4
Amphipoda												
Paramelita nigroculus	—	1	<1	—	—	—	—	—	—	—	—	—
Trichoptera												
Chimarrha sp.	—	—	<1	—	—	<1	3	2	2	—	—	—
Cheumatopsyche sp.	1	<1	<1	—	1	<1	1	2	2	2	1	1
Other Trichoptera	—	1	—	—	—	—	—	—	—	2	<1	1
Megaloptera												
Chloroniella sp.	—	<1	1	3	—	<1	—	—	—	—	—	—
Taeniochauliodes sp.	—	—	—	—	<1	<1	—	—	—	—	<1	—
All others	1	1	<1	—	1	<1	1	—	1	—	—	—

portions of the major faunal groups varied between the three sets of samples, however. Thus, the proportion of Plecoptera in packs (46%) and in drift (50%) was almost the same, while this group comprised only 26% of the benthos. Simuliidae were most abundant in packs (33%) and least abundant in drift (4%), while 35% of the Chironomidae occurred in the drift and only 5% in packs. Ephemeroptera consistently occurred in higher proportions on the stream bed than in packs and were very rare in drift, while Coleoptera and Trichoptera were common in drift and benthos, but rare in packs.

(b) *The fauna of artificial leaf packs.* Weight

TABLE 5. Percentage composition of the fauna in natural and artificial leaf packs, benthos and drift. Values for natural leaf packs and benthos are means of monthly averages over 1 year. Values for artificial leaf packs are from the 20-week experiment. Values for drift are from 2-hourly sampling over 24 h in February 1984.

Species	Natural packs	Artificial packs	Benthos*	Drift*
Plecoptera	46	29	26	50
Diptera				
Simuliid larvae	33	<1	14	4
Simuliid pupae	<1	0	0	0
Chironomid larvae	5	62	16	35
Blepharicerid larva	<1	0	2	0
Other Diptera	<1	<1	1	0
Ephemeroptera				
Baetidae	3	<1	7 ⎫	
Castanophlebia calida	4	<1	12 ⎬	1
Other Ephemeroptera	4	<1	5 ⎭	
Coleoptera				
Helodid larva	<1	<1	7 ⎫	
Elmid larva	<1	<1	<1 ⎬	5
Other Coleoptera	<1	<1	2 ⎭	
Trichoptera				
Dipseudopsis sp.	<1	<1	<1 ⎫	
Chimarrha sp.	<1	<1	<1 ⎬	5
Cheumatopsyche sp.	<1	<1	<1 ⎬	
Other Trichoptera	<1	<1	3 ⎭	
Megaloptera	<1	<1	<1	0
Oligochaeta	<1	<1	<1	0
All others	<1	<1	<1	0

*Unpublished data

losses of submerged leaves in the bags increased from 16–22% after 2 weeks to 75–99% after 20 weeks (detailed results will be reported upon elsewhere). The 20-week bags were washed from the stream by a severe spate and contained no animals.

The composition of the fauna was similar in both coarse- and fine-meshed bags (hereafter called coarse and fine) and notably different from that of the fauna of natural packs (Fig. 9). The trend in both kinds of bags, and for all three species of leaves, was towards an increase in both taxa and numbers of animals per unit mass of pack until 6–8 weeks after submersion, followed by a decline in both values until the end of the experiment (16 weeks). Numbers peaked at 93 individuals g^{-1} of leaf remaining in coarse bags and at 113 individuals g^{-1} in fine bags. The highest number of taxa recorded was nine but, since only a few groups have been identified to species, the total number of taxa is probably higher than this.

Both coarse and fine bags were dominated by Plecoptera and larval Chironomidae; Simuliidae, which were common in natural packs (Fig. 9), were very rare in artificial packs, accounting for <1% of the total numbers. Other taxa became more common in artificial packs from 6 weeks onwards, with an helodid larva being the most prominent of these. Baetids and the leptophlebiid *C. calida* also were consistently present in the older bags but in very low numbers.

Plecoptera comprised about 90% of animal numbers in coarse bags after 2 weeks, the proportion subsequently decreasing until 16 weeks, when a slight increase occurred (Fig. 9). The same pattern was recorded in the fine bags, but densities were lower. The proportion of Chironomidae steadily increased until 12 weeks and then declined as the leaves neared total disintegration. The trend was more apparent in fine bags, where these larvae were more abundant, than in coarse bags. Their higher numbers in fine bags may have been due to the accumulation there of what appeared to be flocculated organic
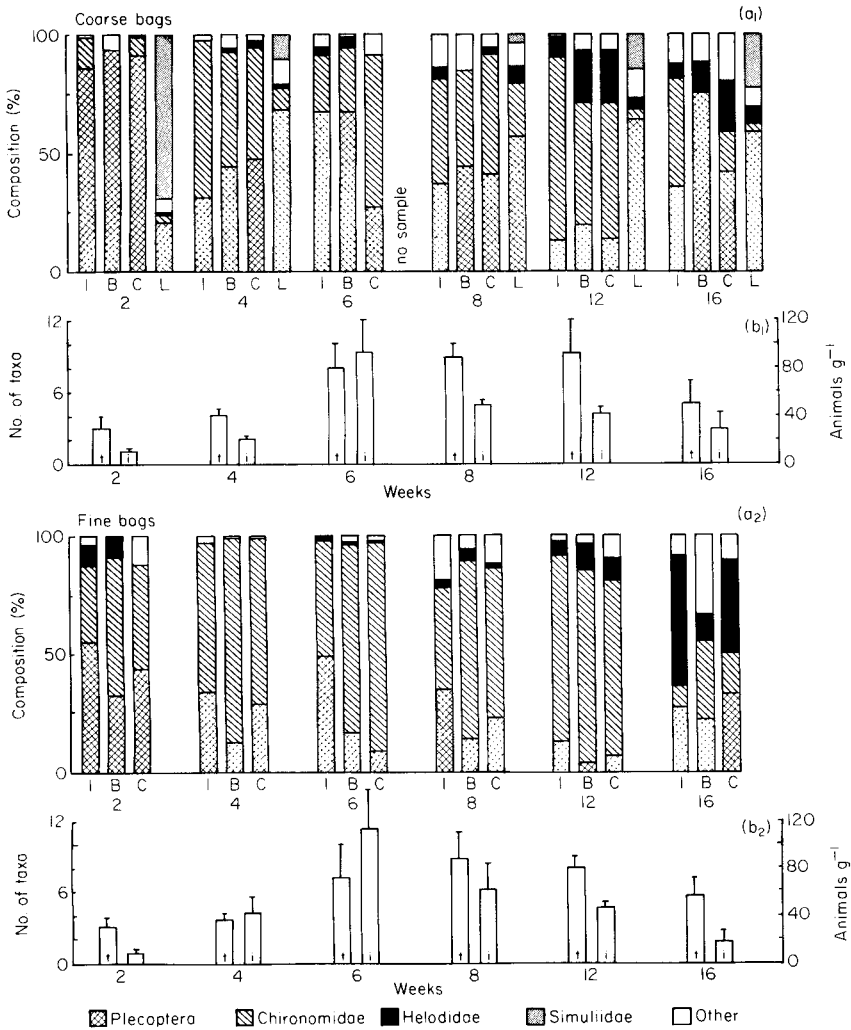
FIG. 9. (a_1 and a_2) Percentage composition of the fauna by numbers in natural (L) and artificial (I, B, C) leaf packs in coarse (a_1) and fine (a_2) bags over time. I=bags containing leaves of *Ilex mitis*; B=bags containing leaves of *Brabejum stellatifolium*; C=bags containing leaves of *Cunonia capensis*; (b_1 and b_2) numbers of taxa per sample (*t*) and numbers of invertebrates per gram of leaf (i) in coarse (b_1) and fine (b_2) bags over time; error bars above histograms are ±1 SD.

material, which was most abundant between 6 and 12 weeks, but was never present in the coarse bags.

Discussion

Reports on natural accumulations of debris in streams are rare. The most detailed report we have found is that of Bilby & Likens (1980), who reported on a North American stream with 'stair-step' stream-bed morphology caused by

debris dams, and a very high standing stock of 3.52 kg of organic matter m^{-2} of stream bed. In Langrivier, the fall of wood <100 mm diameter is comparable to that recorded for warm-temperate, angiosperm forests worldwide (King *et al.*, 1987), but fallen bole wood is rare. This is probably because the trees are small, tough and, because of frequent fires, either natural or anthropogenic, rarely reach more than 40 years of age (Kruger, 1979b). Debris dams, which form on foundations of large woody material, are thus very rare.

Langrivier consists of shallow, fast, free-flowing stretches through most of the year; quiet areas are rare and are confined to stream margins in the drier months. Its poor storage of coarse organic material results in standing stocks of this material being orders of magnitude lower than in the North American system: the mean value for Langrivier, excluding that in debris dams, was about 80 g dry mass m^{-2} in benthos and leaf packs combined. Nevertheless, the proportional dimensions of debris dams and leaf packs are of interest. Bilby & Likens (1980) reported that, in a second-order stream, debris dams covered 4.9% of the stream bed and contained slightly more than half (58.4%) of the stored organic matter (apparently only CPOM was measured). By comparison, leaf packs in Langrivier, although insignificant in size relative to debris dams, covered about one-tenth of the area of stream bed covered by debris dams (mean 0.41% as opposed to 4.9%) but accounted for more than one-third (36%) of the stored CPOM in the system (King *et al.*, 1987).

In our experience, a considerable portion of each debris dam is above the water line except during floods; if this situation holds in the North American system, then the proportional contribution of the wetted parts of debris dams to total standing stock of detritus in that stream will be less than the quoted 58% and may well be close to the 36% reported for Langrivier leaf packs. While whole debris dams do indeed retain much organic material that would otherwise be lost from the system, the portion that is not submerged is unavailable for colonization by the stream biota. That part of a debris dam above the water line may serve as a 'dry store', releasing material slowly into the stream, but presumably at some future time it may be washed away by flood waters. In either case it seems possible that only a small fraction of the material in the 'dry store' will become available to the biota of that reach. Leaf packs in Langrivier, on the other hand, occur at, or just below, the water surface and, because they are usually totally submerged, are wholly available for colonization by the biota of that reach. Though of modest proportions, the packs appear to account for a similar proportion of the available standing stock of wetted organic material as do the debris dams of Bilby & Likens (1980).

A critical ingredient for the development and maintenance of leaf packs is woody material from riparian trees. Speaker *et al.* (1984) found that the efficiency of sticks as traps for floating organic material was one to two orders of magnitude greater than that of inorganic substrata such as boulders, and concluded that the riparian vegetation is a major determinant of the retentive properties of streams. Wood accounted for 29% by weight of the allochthonous POM entering Langrivier but 45% of benthic POM and 65% of that retained in leaf packs. This suggests that the packs tend to occur at points in the stream where sticks are swept into a constricted area by the current, snag and accumulate.

Leaf packs in Langrivier are short-lived, the calculated mean longevity of 1.7 months probably being an over-estimate, as many packs must have formed and disintegrated between our monthly visits to the stream. Longevity of the packs bears no relation to the decomposition time of wood (Anderson & Sedell, 1979) and so the disappearance of a pack must be related to other features of the stream system. Changes in mass and volume of packs in Langrivier during the year indicate that stream discharge is the over-riding determinant of pack longevity. From our experiences of installed equipment being lost or buried during spates, we suggest that powerful upwelling of ground water through the stream bed at that time, together with the shifting of even very large boulders, must contribute to the loss of packs.

Such fragile and ephemeral habitats might be expected to have limited appeal to stream invertebrates, and yet the packs always contained animals and the number of animals per unit area of pack was highest when the packs were smallest (Table 3). Feminella & Stewart (1986) also commented upon the rapid colonization of unstable leaf packs by a variety of stream invertebrates. On the other hand, Reice (1980) stated that the 'presence of a leaf covering [of the sediment] is generally an insignificant factor in the choice of a patch by lotic invertebrates', a conclusion which may have been influenced by his use of artificial packs. Whether acting as a food source, as shelter or simply as sieves for drifting organisms, natural packs in Langrivier contained animals that, between mid-summer (January) and the beginning of leaf fall (September), were consistently present in densities more than 4, and up to 40 times, those in the benthos

(Figs. 7 and 8). Only during peak leaf fall (October–December), when benthic detritus was most abundant on the stream bed (King *et al.*, 1987) and stream discharge was low, were densities of animals in packs and in the benthos roughly equal; it appears that these are the months when packs are of least importance to the fauna.

Comparison of the invertebrate composition of natural and artificial leaf packs, benthos and drift (Table 5 and Fig. 9) suggests that natural packs are not treated by the fauna merely as extensions of the benthos (a point also made by Reice, 1980) or as sieves for drifting material. Proportions of the main taxa present differed markedly in the four sets of samples. Although detailed explanations of these differences await further research on the autecology and taxonomy of the invertebrates in the system, some generalizations can be made on the three dominant taxa.

Nymphs of the family Nemouridae are the only Plecoptera in south-western Cape streams, and are indistinguishable below the level of genus. In Langrivier the nymphs were abundant in all four kinds of samples and, in the absence of larger shredders (Amphipoda of the genus *Paramelita* occur in Langrivier but are mostly confined to higher, less strongly-flowing headwaters), appear to be the principal shredders of the system. They colonize a leaf soon after its submersion and for up to 16 weeks afterwards (Fig. 9) and feed by wearing away successive layers of the leaf until it is skeletonized (personal observations). As natural packs always contained a mixture of new and disintegrating leaves (Fig. 5), and as Plecoptera occurred in high proportions in both newly submerged and long-established artificial packs (Fig. 9), it is not surprising that the nymphs are a major component of leaf-pack fauna (Table 4); this was found also by Mutch *et al.* (1983) in a Canadian stream.

Simuliid larvae were rare in drift samples and patchily distributed in the benthos but accounted for a high proportion (33%) of the fauna of natural packs. Leaf packs form between obstructions, where drift is concentrated, so that drifting larvae may simply be sifted out of the water to accumulate in the packs, while attached ones may be attracted to the area by the concentration of drifting material. Their presence in such high proportions in packs suggests, however, that there is a 'deliberate' accumulation, possibly because of increased food availability within, or associated with, the packs. It was not possible to determine where the larvae were situated within the packs, but presumably fine particles of suspended organic material (from leaf disintegration and from feeding activities of other invertebrates) would be more concentrated within the pack and immediately downstream of it than in the water column as a whole. FPOM levels in the packs were very low (usually <1% of dry mass), but the larvae apparently feed on smaller particles in the range 0.45–100 μm (Chance, 1970; Merritt, Ross & Larson, 1982; Hart & Latta, 1986). Unfortunately, a good deal of this very fine material must have been lost when packs were removed from the stream, so its proportion in the packs is unknown.

The co-dominance of Simuliidae with Plecoptera in natural packs (Table 4) is of interest. Short & Maslin (1977) reported that the amount of leaf material available to Simuliidae (collectors) was increased by the feeding activities of nearby Plecoptera (shredders), thus providing benefits to the Simuliidae. They concluded that in stream ecosystems shredders such as the Plecoptera play an important role in making nutrients available to collector species.

Chironomid larvae accounted for a high proportion of drifting animals (35%) but for only 16% of the benthic fauna and 4% of the fauna of natural leaf packs. The susceptibility of many Chironomidae to catastrophic drift is well documented (see Davies, 1976, for references) and appears to be due to their inability to return rapidly to the substratum once dislodged. Our results suggest that leaf packs may well act as sieves for drifting Chironomidae, the larvae migrating back to the stream bed after becoming lodged in a pack.

Chironomidae consistently formed a greater proportion of the fauna in artificial packs (62%) than in natural packs (4%) (Table 5), suggesting that the artificial packs did not adequately simulate natural packs. Winterbourn (1978) and Mutch *et al.* (1983) also reported that, next to Plecoptera, Chironomidae formed one of the most abundant groups in artificial packs, the others being Baetidae, Trichoptera and (in the case of Winterbourn) Helodidae; all of these taxa were present in low numbers in our packs also. Reice (1980) reported that Chironomidae accounted for 87% of the individuals in his artificial packs and concluded that, in detritus-based

systems, leaves will support higher densities of animals than inorganic substrata. The greatest numbers of Chironomidae in our packs seemed to correlate with the presence of a fine organic flocculent, a particular feature of the fine bags during the middle stages of leaf decomposition, which might well have acted as a food source for the larvae. Winterbourn (1978) also found higher densities of Chironomidae in fine bags than in coarse bags, but attributed this to lower levels of predation and/or competition from larger animals. Although this is possible it is not supported by the findings of Mutch *et al.* (1983), who reported exceedingly high numbers of small invertebrates in bags that adequately allowed the entry of large invertebrates. We found very few predatory invertebrates in both fine and coarse bags (Table 5), and Feminella & Stewart (1986) found that predators other than Plecoptera were rare in natural leaf packs.

We attributed the differences that we noted between natural and artificial packs at least partly to the positioning of the packs in the stream, a conclusion that was also drawn by Mutch *et al.* (1983). Artificial packs are usually deliberately placed in areas where they will be completely submerged, which in most shallow streams would put them into direct contact with the stream bed, and perhaps in pools instead of riffles. Natural packs, on the other hand, usually occur in riffles, at or near the air/water interface, and have an obvious three-dimensional structure with only limited contact with the stream bed. This could well limit their colonization by invertebrates from the benthos and instead create conditions for a discrete community to form in them. In our case this was manifested mainly in the lower numbers of Simuliidae and higher numbers of Chironomidae relative to numbers in natural leaf packs. Additionally, we found that the numbers of invertebrates per unit mass of leaf pack were more than twice as high in artificial packs ($168 \, g^{-1}$) as in natural packs ($69 \, g^{-1}$) (means for February–July 1985), the former being close to the numbers recorded by Winterbourn (1978) in bags of similar mesh size. The higher numbers in artificial packs were mainly due to the presence of the Chironomidae.

We conclude that artificial packs, whilst providing much useful information on the decomposition of leaves in streams, do not simulate natural packs. Natural packs contained leaves at all stages of decomposition throughout the year, whereas in the artificial packs the level of decomposition was inevitably much more uniform. Thus, at any time, natural packs should be attractive to a greater variety of detritivores than should artificial packs. On the other hand, artificial packs provided conditions probably not replicated in natural packs, particularly with respect to storage of flocculated organic material; the nets used for collecting natural packs were of finer mesh size than those used for retaining artificial packs and yet did not retain obvious amounts of flocculated material. For this, and possibly for other, reasons, artificial packs supported a different fauna and higher numbers of invertebrates per unit mass than did natural leaf packs.

We also conclude that, while stream morphology is one of the prime factors influencing the retentive ability of different sections of a river system (Rounick & Winterbourn, 1983), within any one reach other factors such as stream discharge are also of great importance. In Langrivier, the same stretch of stream stored widely differing amounts of CPOM at different times of the year, mainly because of seasonal changes in discharge. In addition, input of wood from riparian trees was vital for the formation of leaf packs, which stored 36% of the CPOM in the system. The packs appeared to be refugia for stream invertebrates, particularly during the winter months of heavy discharge and low standing stocks of organic debris, for at this time the densities of animals in packs escalated. Nevertheless they harboured a relatively small proportion of the total insect fauna. Thus it would seem that the greatest significance of leaf packs lies not in their provision of a habitat for invertebrates but in their being one of the major stores for allochthonous POM entering the stream. While it is retained, this POM provides a source of food for the animals in the packs themselves and, presumably, biotic and abiotic processing of this material also provides finer POM to the downstream reaches.

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