Hydrobiologia **211**: 123–136, 1991.

Eucalypt leaf decomposition in an intermittent stream in south-eastern Australia

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Received 19 September 1989; accepted 20 April 1990

Key words: Leaf decomposition, intermittent stream, microbial conditioning, functional feeding groups, Australia

Abstract

Eucalypt leaf packs were placed at two sites in an intermittent stream during summer to examine the hypothesis that terrestrially-exposed leaf litter accumulates a richer microbial flora than submerged leaves – a phenomenon observed in Canadian temporary vernal pools. This did not occur; during the experiment, microbial biomass (as ATP) rose steadily on submerged leaves but remained low on terrestrially-exposed leaves. Densities of most functional feeding groups on the submerged leaves increased with time. Scrapers appeared to be more important than shredders in eucalypt leaf breakdown at both sites.

Introduction

Allochthonous detritus, as leaf-fall, is an important energy source for communities in forested upland streams in North America and Europe (review in Bird & Kaushik, 1981) and Australia (Blackburn & Petr, 1979; Towns, 1985). Australian forested catchments are dominated by *Eucalyptus* species whose litter-fall is mostly leaf material (Maggs & Pearson, 1977) and seasonal, occurring primarily over the summer months (Pressland, 1982). Thus, many Australian streams receive a pulse of litter-fall at a time of low discharges and high water temperatures, in contrast to the autumnal litter input into streams draining northern hemisphere deciduous forests (Lake, 1982; Bunn, 1986). In intermittent streams, the summer pulse of *Eucalyptus* leaf fall accumulates in large quantities on the dry stream bed or in receding stagnant pools where leaf leachates turn the water dark brown (Towns, 1985; Boulton & Suter, 1986).

Microbial enrichment of terrestrially-exposed (hereafter referred to as 'exposed') leaf material in a temporary vernal pool was first demonstrated by Barlocher *et al.* (1978) in western Ontario. When decaying detritus is exposed to air during the waterless period, its protein content (and hence, nutritional quality) becomes greater than that of detritus submerged in nearby permanent pools. This increase in protein content is attributed to microbial colonization that can proceed with little or no interference from invertebrate consumers for 4–5 months. Feeding trials in the laboratory demonstrated that such exposed litter was more palatable to three species of caddis-fly larvae than detritus that had been submerged. Barlocher *et al.* (1978) suggest that this phe-

nomenon is partly responsible for the rich animal communities of temporary vernal pools.

Given the large amounts of eucalypt leaf litter that accumulate on the dry stream beds of Australian temporary streams (e.g. Towns, 1985), there is potential for considerable microbial enrichment to occur over the waterless summer months. When flow resumes, an abundant (and possibly nutritionally superior) food resource may await the many detritivores that arrive early in the system (Boulton, 1988). This investigation tests this hypothesis by comparing the rates of microbial and macroinvertebrate colonization and decomposition of exposed and submerged Manna Gum (*Eucalyptus viminalis* Labill.) leaves at two sites on an intermittent stream in Victoria.

Materials and methods

Field methods

Newly-fallen, blemish-free, dead leaves of *E. viminalis* were collected in February, 1984 from exposed cobble-beds along the Lerderderg River, 5 km NNW of Blackwood, Victoria. Several weeks of dry weather prior to litter collection ensured that little pre-leaching by rainfall had occurred. The study areas are runs 2–3 m wide and 15–35 cm deep, with a pebble-gravel bed (phi = −5 to −1). Dominant riparian species are *E. viminalis* and Hazel Pomaderris (*Pomaderris aspera* Sieber. ex DC.). The area is fully described by Boulton & Smith (1985) and Boulton (1988, 1989).

During the study, conductivity declined from 92 μS cm^{-1} in mid-March to 68 μS cm^{-1} in early August at both sites. Dissolved oxygen saturation ranged from 93% to over 100% while minimum and maximum air and water temperatures fell gradually during the experiment (air: 21–0 °C, water: 15–3 °C). Water pH remained just below neutral (6.5–6.9). Current velocities ranged between 14 and 32 cm s^{-1} and average water depth over the leaf packs was 13 cm. During the experiment, current velocity and water depth did not differ significantly (Two-way ANOVA, $F = 0.529, p > 0.05$; $F = 0.009, p > 0.05$, respectively) between the sites. As spring, 1984 was unusually dry, the 'exposed' packs at both sites did not become submerged until a few days after day 71 of the experiment.

Experimental design

After air-drying the leaves for three days, they were grouped into packs of ten and weighed to the nearest milligram. Initial leaf surface areas (average of three determinations) were measured using a digital planimeter (Model Z110, Poland). Packs were constructed by tying leaves together with individual knots threaded around the central midrib of each leaf, close to the petiole. A numbered plastic tag was tied between the fifth and sixth leaf, and the packs were tethered in groups of three using monofilament fishing line (9.10 kg breaking strain) tied to steel pegs driven below the surface of the stream bed.

Ninety-six leaf packs (two sites × two treatments × three replicates × eight sampling dates) were emplaced in two shallow runs in early March, 1984 to coincide with the end of the summer period of peak leaf-fall. Two sites were chosen to avoid pseudo-replication (*sensu* Hurlbert, 1984) with the two treatments being 'submerged' packs tethered under water and 'exposed' packs arranged on the shore. As the river did not dry that summer, 'exposed' packs were anchored on pebble bars near the water's edge where they would be inundated when discharge increased in spring. Sampling dates were originally set at 0, 3, 10, 21, 41, 56, 71 and 90 days because the only other study on the decomposition of *E. viminalis* leaves (O'Keefe & Lake, 1987) indicated that 90% of the leaves would be processed in 45–56 days. However, by day 71, it was clear that decomposition rates for submerged leaves were much slower in the Lerderderg River so the final sampling date was set at day 143.

Packs were sampled by sliding a hand-net (300 μm mesh) under a randomly selected pack and cutting its tether. Water depth and current velocity were recorded at each submerged pack.

Dissolved oxygen, pH and conductivity were measured at both sites while air and water maximum and minimum temperatures were monitored between sampling dates. As soon as a pack was collected, eight discs (6 mm diam.) were punched out of the leaves for analysis of microbial adenosine tri-phosphate (ATP). The rest of the leaf pack and the contents of the hand-net were rinsed into a plastic bag which was sealed and stored on ice. In the laboratory, each pack was dismantled and all invertebrates were removed, identified, enumerated, and assigned to functional feeding groups. The leaves were dried at 60 °C for three days (to constant weight) before determining their surface area and dry weight. Corrections were made for the discs removed for ATP analysis.

ATP determination

ATP concentration is considered a reliable measure of microbial biomass (Holm-Hansen & Booth, 1966; Karl, 1980). Since dead leaves are unlikely to contain endogenous ATP, microbial biomass can be estimated directly, providing a useful indicator of the potential food quality of the leaf to macroinvertebrates (e.g. Ward & Cummins, 1979; Valett & Stanford, 1987). ATP was extracted from leaf discs using cold acid extraction (Karl & LaRock, 1975) and assayed using the bioluminescent reaction (Sharpe, 1973); light emission was detected using a Luminescence Biometer (Spectrofluo Model JY3, Jobin Yvin, France). Extracts often contained coloured substances that interfered with the reaction. To overcome this, the extract was analyzed, a known concentration of ATP was added to the sample and the extract was re-analyzed, enabling calculation of the 'quench' factor (St John, 1970). Efficiency of extraction ranged from 46.27% to 83.60% and showed little relationship with leaf age or experimental treatment. All values were corrected for this differential extraction efficiency.

Data analysis

Correlations between leaf surface area and dry weight were expressed as product-moment correlation coefficients (Zar, 1984). After transformation (arcsin $\sqrt{x}$, Zar, 1984) of the data, five models (linear, power, exponential, logarithmic and hyperbolic) were tested for goodness-of-fit to the curve of percentage weight loss with time for each site and treatment. Analysis of covariance (ANCOVA) (Zar, 1984) was used to compare the slopes and elevations of the regression lines.

Variations in densities of invertebrates over time and site were analyzed using two-way analysis of variance (ANOVA) (Zar, 1984). Three-way ANOVAs (Zar, 1984) were used to examine differences in leaf surface area, dry weight and ATP content among times, treatments, and sites. The significances of differences between total invertebrate densities and the densities of several functional feeding groups of the only treatment-time pair with an equivalent colonization period (i.e. comparing invertebrate densities on packs that had been 'submerged' for 71 days and those on 143-day old 'exposed' packs that were inundated approximately 70 days before sampling) were ascertained using a student *t*-test.

Results

Physical changes in the leaf packs

Initially, the leaf packs had an average surface area of 221.94 cm^2 (range, 158.55–280.96 cm^2) and an average dry weight of 4.517 g (3.525–5.790 g). Surface area and dry weight were highly significantly correlated ($r^2_{94} = 0.85$, $p < 0.001$), even after varying periods of submergence ($r^2_{52} = 0.79, p < 0.001$). 'Submerged' leaves decomposed faster than 'exposed' leaves (Fig. 1). After approximately 70 days submergence, leaf surface area at both sites had declined by only 10%, irrespective of previous exposure (cf. 'submerged' day 71 with 'exposed' day 143, Fig. 1a). Only 40% of the initial surface area remained after 143 days submergence (Fig. 1a). Changes in surface area differed significantly with time and treatment but not between sites (Table 1). The highly significant time by treatment two-way interaction (Table 1) was probably due to the

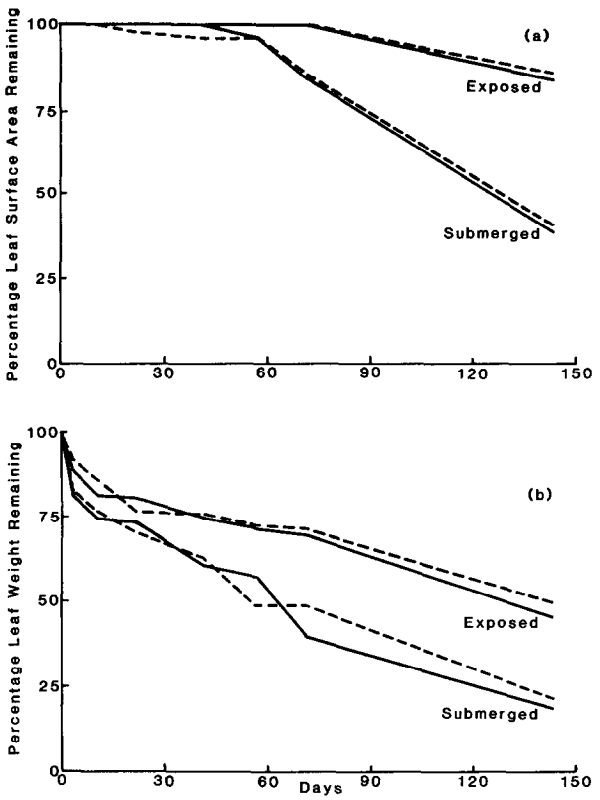

Fig. 1. Percent initial leaf surface area (a) and dry weight (b) remaining with time. Solid lines represent changes at the upstream site; broken lines represent changes at the downstream site.

inundation of the 'exposed' packs soon after day 71.

Submerged leaves at both sites lost approximately 20% of their initial dry weight by day 3 (Fig. 1b) due to leaching. Subsequent weight loss with time appeared linear (Table 2, Fig. 1b) although exponential and logarithmic models also significantly fit the curves (Table 2). Assuming a linear model, the slopes of the lines do not differ between sites (ANCOVA, $F_{3,20} = 0.206$, $p > 0.05$) for the 'submerged' leaves whose decomposition rates and processing half-lives (T_{50}) (Table 3) fall into the 'medium' processing category of Petersen & Cummins (1974). Since an exponential model also fits the data (Table 2), decay coefficients and processing half-lives directly comparable with those calculated by O'Keefe & Lake (1987) were determined

Table 1. Three-way ANOVAs of surface area remaining, weight remaining and leaf ATP content by day, site and treatment. Significance levels as follows: NS = not significant, $p > 0.05$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$.

i) Surface area remaining by day, site and treatment.

Source of variation	F-value	Significance
Main effects	258.61	***
Day	297.29	***
Site	0.00	NS
Treatment	246.42	***
Two-way interactions	51.42	***
Day × Site	0.47	NS
Day × Treatment	109.70	***
Site × Treatment	0.11	NS
Three-way interactions	0.13	NS
Day × Site × Treatment	0.13	NS

ii) Dry weight remaining by day, site and treatment.

Source of variation	F-value	Significance
Main effects	160.89	***
Day	180.97	***
Site	0.57	NS
Treatment	180.63	***
Two-way interactions	6.28	***
Day × Site	0.99	NS
Day × Treatment	12.47	***
Site × Treatment	0.03	NS
Three-way interactions	1.11	NS
Day × Site × Treatment	1.11	NS

iii) ATP content by day, site and treatment.

Source of variation	F-value	Significance
Main effects	27.80	***
Day	32.97	***
Site	0.03	NS
Treatment	19.36	***
Two-way interactions	1.86	**
Day × Site	0.26	NS
Day × Treatment	3.52	*
Site × Treatment	1.46	NS
Three-way interactions	0.53	NS
Day × Site × Treatment	0.53	NS

(Table 3). These indicated that *E. viminalis* litter decomposed at least three times slower in the Lerderderg River than recorded by O'Keefe & Lake (1987).

Rainfall and dew during the first three days of the experiment apparently leached over 10% of the initial dry weight of the 'exposed' leaves (Fig. 1b). After day 3, the rate of weight loss declined (Fig. 1b) increasing slightly after day 71 when the 'exposed' packs were inundated. Equivalent percentages of initial dry weight (approx.

Table 2. Coefficients of determination (r^2), F-ratios and their significance levels (as for Table 1) for the curves of best fit to five models describing leaf pack decomposition (as weight loss) for each site by treatment combination.

Model	'Exposed'		'Submerged'	
	Site 1	Site 2	Site 1	Site 2
Linear (r^2)	0.85	0.90	0.96	0.98
(F)	29.40 **	48.97 ***	121.18 ***	294.93 ***
Power (r^2)	0.41	0.48	0.54	0.55
(F)	3.48 NS	4.63 NS	6.10 NS	6.10 NS
Exponential (r^2)	0.83	0.88	0.94	0.94
(F)	24.58 **	37.03 **	81.07 ***	78.76 ***
Logarithmic (r^2)	0.44	0.53	0.71	0.74
(F)	4.06 NS	5.61 NS	12.56 *	14.14 **
Hyperbolic (r^2)	0.15	0.20	0.32	0.34
(F)	0.89 NS	1.28 NS	2.35 NS	2.53 NS

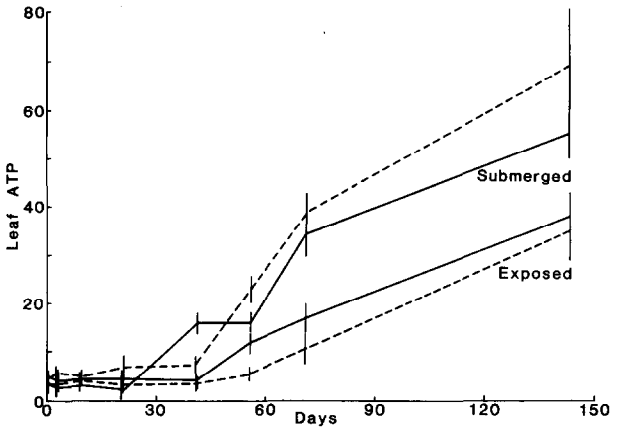

Fig. 2. Temporal changes in leaf ATP content (microbial biomass) expressed as relative units of ATP per unit surface area. Solid lines represent changes at the upstream site; broken lines represent changes at the downstream site.

50%) remained after 70 days submergence, regardless of treatment or site (Fig. 1b) paralleling temporal changes in surface area (Fig. 1a). Again, there were highly significant differences among times and treatments but not between sites (Table 1).

The decomposition curves of the 'exposed' litter after day 3 best fitted a linear model (Table 2) although there was also a significant fit to an exponential model (Table 2). Slopes did not differ between sites or treatments (ANCOVA, $F_{3,20} = 0.206$, $p > 0.05$). Elevations of the lines describing the decomposition of 'exposed' leaves were significantly higher ($p < 0.05$) than those of the 'submerged' leaves.

The ATP content of 'submerged' leaves did not begin to rise until after 20 to 40 days (Fig. 2). 'Exposed' leaves never accumulated a richer microbial flora (as ATP) than 'submerged' leaves at either site (Fig. 2). In fact, the opposite occurred and ATP levels became significantly greater on 'submerged' leaves (Table 1, Fig. 2). Leaf ATP content rose with time but did not differ between sites within treatments (Table 1).

Table 3. Processing rates and the times in days for 50 (T_{50}) and 90 (T_{90}) percent of *Eucalyptus viminalis* leaves to be broken down in the study by O'Keefe & Lake (1987) and this study.

Site	Decay coefficient (−k)	T_{50} (days)	T_{90} (days)
O'Keefe & Lake 1987)			
Site 1	0.041	17	56
Site 2	0.051	14	45
(This study-exponential model)			
Site 1	0.0152	46	151
Site 2	0.0138	50	169
(This study-linear model)			
Site 1	0.0064	62	171
Site 2	0.0061	55	169

Biotic changes on the leaf packs

Eighteen terrestrial taxa (mostly collembolans, spiders and mites) were collected from the 'exposed' leaf packs. These invertebrates comprised only 6% of the total and are not considered further. Of the 49 aquatic taxa collected from submerged packs, the abundances of only four exceeded 10% of the total (Table 4). Most of the taxa were predators and collector-gatherers (Table 5) whereas the numerically dominant functional feeding groups were collector-scrapers, collector-gatherers and scrapers (Table 5).

As leaf surface area and dry weight were highly

Table 4. The relative abundances of common (>0.5%) aquatic taxa collected from submerged leaf packs at both sites. The functional feeding groups to which they were allocated are included; abbreviations as follows: Cg = Collector-gatherer, Cg-Scr = Collector-scraper, Cg-Shr = Collector-shredder, Pred = Predator, Scr = Scraper, Shr = Shredder. (NMV species numbers match voucher specimens in the National Museum of Victoria).

Taxon	Relative abundance	Feeding group
Illiesoperla australis (Tillyard)[1]	25.29	Cg
Angrobia sp.[2]	14.14	Scr
Riekoperla rugosa (Kimmins)[1]	11.52	Cg-Scr
Nousia spp.[3]	10.27	Cg-Scr
Physastra gibbosa (Gould)[2]	7.45	Scr
Dinotoperla thwaitesi Kimmins[1]	6.49	Cg-Scr
Triplectides similis Mosely[4]	3.38	Shr
Calopsectra sp.[5]	2.41	Cg
Triplectides ciuskus Mosely[4]	2.18	Shr
Calocidae sp.[4]	2.07	Shr
Podonomopsis sp. 1 (NMV sp. 71E)[5]	1.63	Cg-Scr
Riekoperla karki-reticulata group[1]	1.60	Cg-Scr
Hydra ?oligactis Pallas[6]	1.19	Pred
Acruroperla atra (Samal)[1]	1.11	Shr
Ptychobiosis nigrita (Banks)[4]	0.99	Pred
Paramerina spp. (nr NMV sp. 32E)[5]	0.93	Pred
Apsilochorema gisbum (Mosley)[4]	0.78	Pred
Stempellina sp.[5]	0.76	Cg
Riethia sp. (NMV sp. 5E)[5]	0.70	Cg
Brillia sp. 2[5]	0.52	Cg
Additional 29 taxa	4.59	

[1] Plecoptera, [2] Gastropoda, [3] Ephemeroptera, [4] Trichoptera, [5] Diptera, [6] Hydrozoa

correlated, for brevity most of the results presented below are in terms of numbers per unit dry weight (density). At both sites, the density of aquatic taxa rose steadily with time (Fig. 3a) and

Table 5. The proportions of seven functional feeding groups collected from submerged leaf packs at both sites.

Feeding group	Percentage by taxon	Percentage abundance
Predators	24.5	4.99
Collector-gatherers	22.5	30.41
Collector-scrapers	16.3	31.82
Shredders	14.3	9.35
Scrapers	12.2	22.61
Collector-shredders	8.2	0.53
Collector-filterers	2.0	0.29

was significantly correlated with leaf ATP content (Table 6). Similarly, there was a steady increase in the total density of individuals with time (Fig. 3b), also highly significantly correlated with ATP concentration (Table 6). The most rapid increases in densities of taxa and individuals (Fig. 3), however, did not coincide with the marked rise in ATP content between days 21 and 71 (Fig. 2).

Increases in densities of individuals and taxa with time were highly significant but did not differ between sites (Table 7). Decomposition rates of 'submerged' litter were correlated with the densities of taxa ($r^2_{52} = 0.45$, $p < 0.001$) and individuals ($r^2_{52} = 0.64, p < 0.001$), and ATP content ($r^2_{52} = 0.79, p < 0.001$). There were no significant differences between the densities of the six most common functional feeding groups at each site and only collector-shredder densities did not vary with time (Table 7). All two-way interactions of

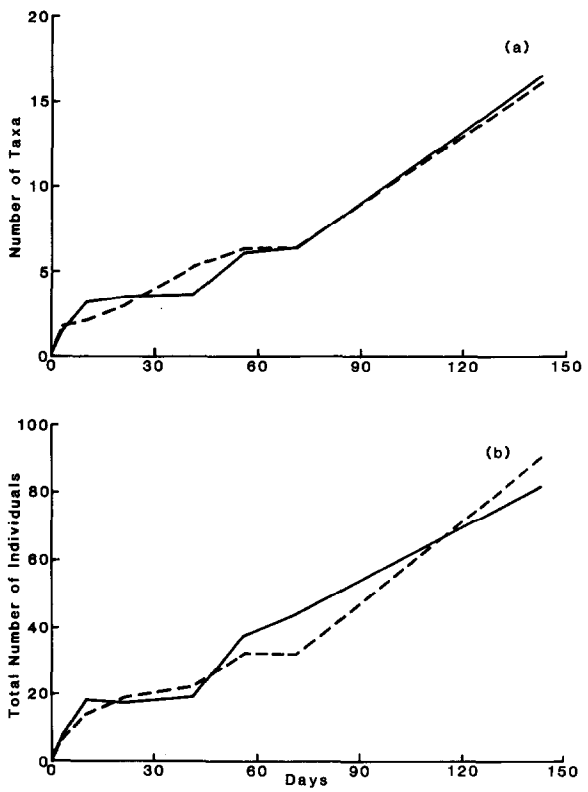

Fig. 3. Temporal changes in the number of taxa (a) and total number of individuals (b) per gram dry weight on leaf packs submerged at the upstream (solid lines) and downstream (broken lines) sites.

Table 6. Correlations of the densities of taxa, total densities of individuals and densities of six functional feeding groups with ATP content of submerged leaf packs at both sites. Significance levels as for Table 1.

Group	Site 1	Significance	Site 2	Significance
Total taxa	0.72	***	0.85	***
Total individuals	0.79	***	0.75	***
Predators	0.81	***	0.56	**
Shredders	0.18	NS	0.13	NS
Scrapers	0.15	NS	−0.00	NS
Collector-gatherers	0.83	***	0.87	***
Collector-shredders	−0.03	NS	0.38	NS
Collector-scrapers	0.72	***	0.66	***

Table 7. Two-way ANOVAs of the densities of taxa, total densities of individuals and densities of six functional feeding groups on submerged leaf packs in the Lerderderg River with site and time. Significance levels (Sig.) as for Table 1.

Group	Site	Sig.	Day	Sig.	Interaction	Sig.
Total taxa	0.01	NS	76.82	***	0.64	NS
Total individuals	0.06	NS	34.40	***	0.41	NS
Predators	1.90	NS	6.74	***	1.21	NS
Shredders	0.17	NS	4.12	***	2.79	*
Scrapers	1.84	NS	4.23	***	0.89	NS
Collector-gatherers	1.62	NS	23.53	***	0.55	NS
Collector-shredders	0.08	NS	0.86	NS	1.25	NS
Collector-scrapers	0.02	NS	19.35	***	0.77	NS

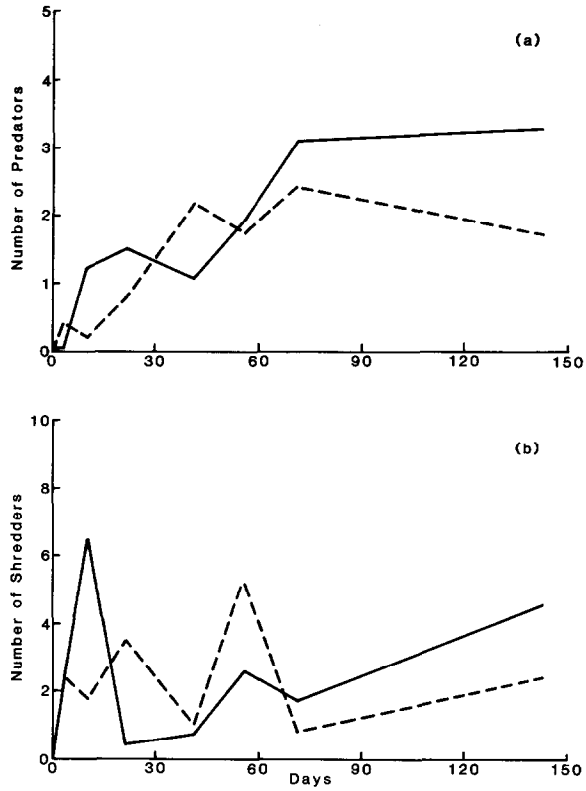

Fig. 4. Temporal changes in the number of predators (a) and shredders (b) per gram dry weight on leaf packs submerged at the upstream (solid lines) and downstream (broken lines) sites.

site by time were non-significant except for that of shredder density (Table 7). While the density of predators rose gradually with time (Fig. 4a), possibly in response to increased prey densities (Fig. 3b), shredder densities at both sites varied erratically (Fig. 4b). Predator densities were highly significantly (probably indirectly) correlated with leaf ATP content (Table 6). On the other hand, there was no significant correlation between the density of shredders and ATP levels (Table 6).

Scrapers were common, reaching maximum densities on the leaf packs at both sites by day 21 (Fig. 5a) but densities were not significantly correlated with ATP content (Table 6). There were steady increases in the densities of collector-gatherers with time at both sites (Fig. 5b), significantly correlated with leaf ATP levels (Table 6). Collector-shredder densities fluctuated erratically (Fig. 6a) and did not increase significantly with time (Table 7) or correlate significantly with ATP content (Table 6) unlike the densities of collector-scrapers (Fig. 6b, Tables 6 and 7).

Unfortunately, discharge in early spring 1984 was the lowest for 37 years and the 'exposed' packs did not become inundated until early June, shortly after day 71. Therefore, the only possible comparison of invertebrate densities on submerged packs with different terrestrial exposure times was between 'submerged day 71' and 'exposed day 143' packs. The single significant difference between the two treatments at both sites was a higher density of predators on the 'submerged day 71' packs at one site. Considering the similarities in leaf surface area, dry weight and ATP content between these two treatments (Figs 1 and 2, Table 1), these results are not sur-

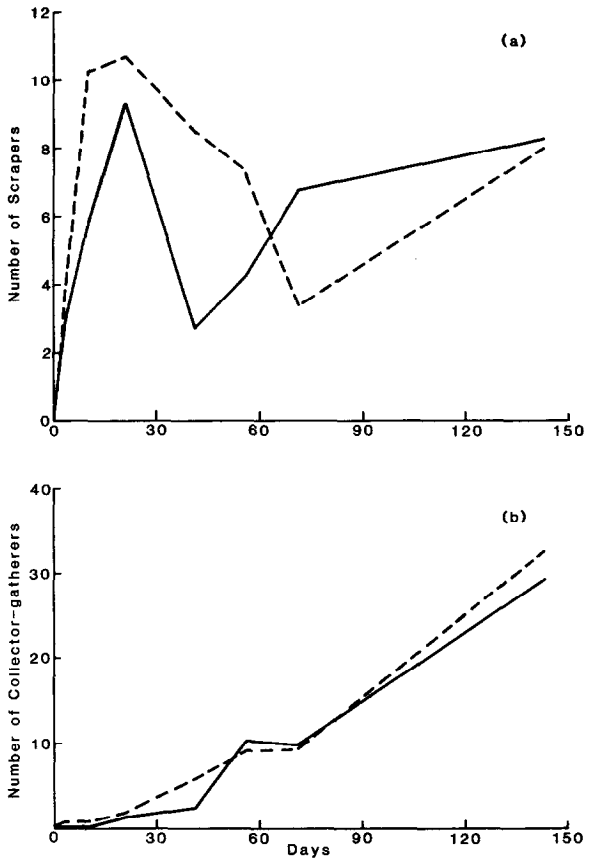

Fig. 5. Temporal changes in the number of scrapers (a) and collector-gatherers (b) per gram dry weight on leaf packs submerged at the upstream (solid lines) and downstream (broken lines) sites.

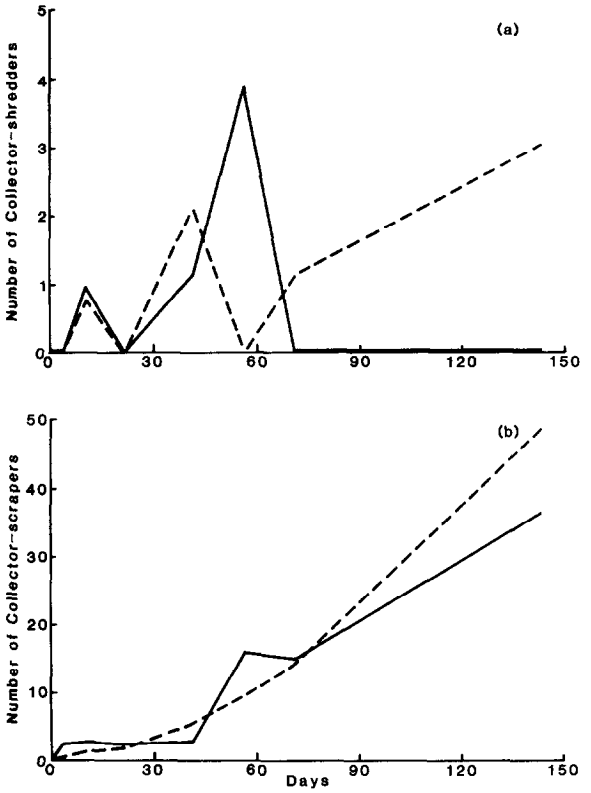

Fig. 6. Temporal changes in the number of collector-shredders (a) and collector-scrapers (b) per gram dry weight on leaf packs submerged at the upstream (solid lines) and downstream (broken lines) sites.

prising, although some seasonal variation was expected.

Discussion

Physical changes

The initial dry weight losses due to leaching of *E. viminalis* leaves in the Lerderderg River resembled those observed for other eucalypt species (22–25% *E. globulus* F. Muell., Hart & Howmiller, 1975; Wenner & Busath, 1977; 22–24% *E. obliqua* L. Her., Barmuta, 1978; 22% *E. camaldulensis* Dehnh., Briggs & Maher, 1983; 25–30% *E. marginata* Sm., Bunn, 1988a) and for *E. viminalis* (20%. O'Keefe & Lake, 1987). Lower leaching losses (6–8%) recorded for *E. regnans* F. Muell. (Blackburn & Petr, 1979) probably reflect different characteristics of the leaves and differing experimental conditions.

In this study, the pattern of leaf weight loss after leaching is best described by a simple linear regression, although an exponential model also showed a significant fit to the data. Pidgeon & Cairns (1981) also attributed a linear model to weight loss from *E. blakelyi* Maiden leaves but there are few other reports of this kind (e.g. Suberkropp *et al.*, 1976; Davis & Winterbourn, 1977; Mutch *et al.*, 1983); most curves best fit exponential decay models (e.g. Petersen & Cummins, 1974; Sedell *et al.*, 1975; Triska & Sedell, 1976; Short *et al.*, 1980; O'Keefe & Lake, 1987). Other studies found both linear and

exponential models were applicable (e.g. McCammon, 1980; Herbst & Reice, 1982; Cuffney & Wallace, 1987; Bunn, 1988a), possibly reflecting the ease with which different rate models significantly fit data that become increasingly variable with time (Boulton, 1988).

T_{50} values (the time in days for 50% of the litter to be processed) of *E. viminalis* leaves in the Lerderderg River were comparable to those of other *Eucalyptus* species in eastern Australia (*E. obliqua* T_{50} = 54, Barmuta, 1978; *E. regnans* T_{50} = 83–86, Blackburn & Petr, 1979; *E. blakelyi* T_{50} = 68–82, Pidgeon & Cairns, 1981); all fall into the 'medium' processing category of Petersen & Cummins (1974). However, T_{50} values and rates of weight loss from *E. viminalis* leaves in the Lerderderg River were almost three times lower than those observed by O'Keefe & Lake (1987) for the same species in a small creek north-east of Melbourne. In their study, leaves were enclosed in mesh bags and stream temperatures were lower than in the Lerderderg River so that breakdown rates should have been slower. However, macroinvertebrate densities on the mesh bags were almost twice those on leaf packs in the Lerderderg River and current velocity (potentially responsible for physical abrasion and fragmentation) was much higher around the bags (Dr P. S. Lake, Monash University, pers. com.) probably accelerating leaf breakdown. Such differences in decomposition rate partly reflect exposure technique, local spatial variation and the timing of the study and poignantly illustrate the great variability in rates of breakdown of the same leaf species that can be obtained in different streams (e.g. Rounick & Winterbourn, 1983; Cuffney & Wallace, 1987).

Leaves decompose more slowly in intermittent streams than permanent ones because of the duration of the dry period (Tate & Gurtz, 1986) that catastrophically reduces aquatic invertebrate populations (Herbst & Reice, 1982; Kirby *et al.*, 1983). Lower densities of invertebrates on the leaf packs probably reflect the harsh physicochemical conditions prevailing during summer when leaves accumulate in the remaining pools, turning the water dark and lowering pH and oxygen saturation while water temperatures rise. Microbial activity is also retarded severely at low pH (Allard & Moreau, 1986; Chamier, 1987). During this experiment, the river did not dry up and physicochemical conditions were relatively mild (Boulton, 1988). Consequently, breakdown rates of submerged litter in the Lerderderg River are probably even slower when flow ceases.

Microbial colonization

Microbial enrichment of 'exposed' leaf litter demonstrated by Barlocher *et al.* (1978) and postulated to occur on *Eucalyptus camaldulensis* litter (Herbst & Reice, 1982) was not evident on *E. viminalis* litter on the banks of the Lerderderg River. Merritt *et al.* (1984) found that pignut hickory (*Carya glabra* (Mill.) Sweet) leaves conditioned in a stream for 5 weeks decomposed faster than leaves exposed on a floodplain for 17 weeks. These authors attributed this to greater microbial conditioning in the stream. Similarly, in an intermittent prairie stream in Kansas, Gurtz and Tate (1988) showed that leaves of bur oak (*Quercus macrocarpa* Michx.) and hackberry (*Celtis occidentalis* L.) decomposed more rapidly in the channel than on the adjacent bank. Environmental conditions in the Lerderderg River appear more similar to those in the intermittent prairie stream than those in a Canadian temporary vernal pool; this may explain why the results reported here are opposite to those obtained by Barlocher *et al.* (1978).

Leaching appears to be necessary before microbial conditioning can occur. Bunn (1986, 1988b) suggested that microbial colonization of jarrah (*E. marginata)* leaf litter was delayed until most of the soluble polyphenols were leached. Polyphenols, found in high concentrations in eucalypt leaves (Cork & Pahl, 1984; Bunn, 1986; 1988a), reduce detritus palatability to invertebrates (Feeny, 1970; Alongi, 1987) and inhibit microbial colonization and enzyme activity (Rosset *et al.*, 1982). For example, tannins, particularly common in eucalypt leaves (Fox & Macauley, 1977) can immobilize microbial enzymes (Chamier,

1987) or form indigestible complexes with dietary proteins, lowering the nutritional value of the material (Feeny, 1970). Tannins leached from Chinese tallow leaves inhibited the feeding rates of two peracarids in several Texan ephemeral ponds (Cameron & La Point, 1978). Other factors probably retarding eucalypt litter decomposition include the thick waxy cuticle of the leaf (Bunn, 1986) and the high lignin content (15–30% dry weight, Cork & Pahl, 1984). Lignin content exerts a major control over decomposition rates of woody detritus (Melillo *et al.*, 1982) and terrestrial leaf litter (review in Webster & Benfield, 1986).

High concentrations of secondary compounds in *E. viminalis* leaf litter interfered with ATP determination of the extracts. Dark-coloured substances were common (especially in extracts of 'exposed' leaves) and low efficiencies of ATP extraction and determination (~45–60%) were usual. Such interferences from secondary compounds in leaf detritus have been previously noted (e.g. Suberkropp & Klug, 1976; Rosset *et al.*, 1982) and organic acids appear to be especially problematic (Cunningham & Wetzel, 1978). Nonetheless, ATP seems a better indirect measure of microbial biomass than nitrogen and protein which is seldom entirely due to microorganisms (Iversen, 1975) and may not be in a form readily available to detritivores (Odum *et al.*, 1979; Peters *et al.*, 1987).

Future studies of the decay of *Eucalyptus* leaves should include direct methods such as scanning electron microscopy (SEM) to provide information about the taxonomic composition of the micro-organisms (e.g. Bunn, 1986) and the importance of the cuticle and palisade cell layers in protecting the mesophyll from microbial attack. Attention should also be given to elucidating the interspecific interactions among the microbial species colonizing dead leaves in streams (Rossi, 1985). For example, Arsuffi & Suberkropp (1984) observed that larval caddisfly preferences for conditioned leaves reflected the interactions among various fungal species rather than conditioning time or the species of fungus alone; clearly microbial conditioning of detritus is more complex than simply the accumulation of micro-organisms on the leaf.

Faunal dynamics

There were significant correlations between the densities of taxa and individuals on the leaves and the decomposition rates of *E. viminalis* litter in the Lerderderg River. Hart & Howmiller (1975) claimed that differences in breakdown rates of several eucalypt leaf species in two Californian streams were due to macroinvertebrate feeding. While further studies report similar results for different leaf species (e.g. Iversen, 1975; Short *et al.*, 1980; Mutch & Davies, 1984), other authors (e.g. Kaushik & Hynes, 1971; Gurtz *et al.*, 1982; Allard & Moreau, 1986) suggest invertebrates are unimportant in leaf decomposition in streams. This apparent anomaly simply reflects the varying importance of physical abrasion and macroinvertebrate feeding in the breakdown of various leaf species in different streams.

Traditionally, shredder activity has been considered to be a major pathway by which CPOM is comminuted to FPOM (Cummins, 1974; Cummins & Klug, 1979) and there is much experimental and field evidence to support this (reviewed by Bird & Kaushik, 1981 and Webster & Benfield, 1986). Low densities of shredders in two Virginian temporary streams were held responsible for the slower rates of breakdown of red maple leaves compared with rates in nearby permanent streams (Kirby *et al.*, 1983). However, Dance *et al.* (1979) suggested that periods of low flow and stagnation promoted shredding activity in a temporary stream in Ontario, resulting in greater proportions of coarse organic matter being processed into smaller particles (< 253 μm) than in a nearby permanent stream. Gurtz & Tate (1988) reported that increased decomposition of hackberry leaves in an intermittent prairie stream coincided with higher shredder densities.

O'Keefe & Lake (1987) found that shredders were the most abundant functional feeding group present on bags of *E. viminalis* leaves. This was not the case on submerged leaf packs of *E. viminalis* in the Lerderderg River where shredders comprised less than 10% of the total abundance. Instead, collector-gatherers and collector-scra-

pers were most abundant (62% of total abundance), resembling the pattern considered typical of northern hemisphere streams by Bird & Kaushik (1981) where collectors are the most numerous feeding group but shredders generally account for most of the leaf weight loss. The most abundant collector-gatherers on leaf packs in the Lerderderg River were small nymphs of the stonefly *Illiesoperla australis* (Tillyard) which occurred in especially high densities on recently inundated leaves. Other stonefly (*Dinotoperla thwaitesi* Kimmins, *Riekoperla rugosa* (Kimmins)) and mayfly (*Nousia* spp.) nymphs were also common, possibly feeding on FPOM accumulating in the pack (cf. Short *et al.*, 1980).

Surprisingly, shredder (and collector-shredder) densities were not significantly correlated with leaf ATP content. Experimental studies have demonstrated that shredders prefer to feed on microbially conditioned leaf material (Barlocher *et al.*, 1978; Barmuta, 1978) although other factors (e.g. lipids, Cargill *et al.*, 1985) may attract shredders and thus provide stronger correlations with shredder density. The significant correlation between predator density and ATP content is probably indirect, reflecting a relationship with prey density instead. Predators may influence decomposition rates by preying on detritivores (Oberndorfer *et al.*, 1984); this probably occurs in receding pools in late summer where the numbers of predators rise sharply as the streams dry up (Boulton, 1988).

Scrapers, represented mainly by the gastropods *Angrobia* sp. and *Physastra gibbosa* (Gould), were also common (23% of total abundance). Whereas physical abrasion probably removes much of the thick waxy cuticle of submerged eucalypt leaves, the feeding activities of scrapers may also be important (cf. Rogers & Breen, 1983; Collier & Winterbourn, 1986). Scrapers were common on the leaves after only three weeks submergence and before ATP levels began to rise. Their feeding activity may have opened up new areas for microbial attack by removing cuticle and palisade cells, resulting in a rise in leaf ATP content. However, the reason for the early colonization of the leaves by scrapers is unclear, reiterating the need for SEM studies of leaf decomposition. Reice & Herbst (1982) found a positive but nonsignificant correlation between snail densities and decomposition rates of *Phragmites australis* (Cav.) Trin. ex Steudel in three Israeli saline desert streams. They suggested that snails may control *Phragmites* decomposition but did not discuss likely mechanisms.

In coniferous litter, microbial leaching is retarded for 4–5 months by the thick cuticle and epidermal layers (Michaelides & Kendrick 1978) which prevent anti-fungal chemicals from leaching out of the needles (Barlocher *et al.*, 1979). Similarly, removal of the thick waxy cuticle of *Eucalyptus* leaves by scrapers or physical abrasion may hasten leaching of polyphenols that inhibit microbial colonization. Buttimore *et al.* (1984) demonstrated leaf cuticle dissolution by bacteria and fungi, and this may also be an important means by which waxy cuticle is removed from eucalypt leaves.

Actinomycete bacteria seem more important than hyphomycete fungi in conditioning eucalypt leaves in Australian streams (Barmuta, 1978; Bunn, 1986, 1988b). Consequently, the digestive physiology of Australian aquatic macroinvertebrates may differ from that of taxa in northern hemisphere streams where aquatic hyphomycetes primarily colonize leaves (Cummins, 1974; Bird & Kaushik, 1981). Numbers of microbial cells on leaves are often too low to account fully for the enhanced nutritional value of ingested detritus (Findlay *et al.*, 1984; Lawson *et al.*, 1984) and microbial catalysis of refractory leaf compounds into more easily digested particles (Barlocher & Kendrick, 1975; Chamier, 1985) may be more important. There is evidence that enzymes (fungal carbohydrases) ingested with the food remain active in the invertebrates' guts (Sinsabaugh *et al.*, 1985; Barlocher & Porter, 1986). Aquatic macroinvertebrates feeding on *Eucalyptus* detritus may acquire not only enzymes but develop a gut fauna (possibly bacterial) capable of dealing with such refractory detritus before it is fully conditioned. Other adaptations may include a basic gut PH and the use of surfactants to prevent precipitation of proteins by tannins (e.g. Martin & Martin, 1984).

Conclusions

The rate of decomposition of *Eucalyptus* litter on the dry stream bed is slow. Microbial enrichment of 'exposed' leaf litter like that observed by Barlocher *et al.* (1978) in temporary vernal pools in Canada was not observed, probably because the environments are so dissimilar. Leaching of polyphenols via rainfall and dew may be necessary before eucalypt litter can be broken down. When Australian intermittent streams resume flow, a pulse of detritus is carried down the stream (Boulton & Suter 1986). Although food is abundant, it is low in quality, and aquatic detritivores arriving early in the system probably rely heavily on less refractory leaf species (e.g. hazel pomaderris), stone-surface layers, invertebrate faeces and conditioned material (eucalypt leaves, wood, FBOM) from previous years. Unlike streams in the northern hemisphere where autumn-shed leaves enter the food chain within a year (Bird & Kaushik, 1981), eucalypt litter may require several years before it becomes incorporated into secondary production, highlighting the importance of retentive debris dams (Bilby, 1981) in Australian streams.

In the many Australian intermittent streams, extensive beds of aquatic macrophytes die back during summer and large quantities of plant detritus are stranded by the receding water. Although aquatic macrophytes are seldom fed upon while actively growing (Rodgers *et al.*, 1983), stored energy and nutrients are available when they die back. Decomposition rates of senescent macrophytes are much faster than those of *Eucalyptus* species (Pidgeon & Cairns, 1981; Herbst & Reice, 1982) and macrophyte detritus appears to be very palatable to macroinvertebrates (Gregory, 1983). The importance of this food resource in 'bridging the gap' while eucalypt leaves become sufficiently conditioned has yet to be established.

Acknowledgments

This work owes much to the enthusiastic supervision of Dr Sam Lake and was undertaken at the Centre for Stream Ecology, Monash University while I received a Commonwealth Postgraduate Research Award. Determination of ATP levels in *Eucalyptus* leaves would have been impossible without the help and equipment provided by Dr Sally Keleman, Biochemistry Department, Monash University.

I thank Gaye Spangaro, Bruce Weir and Steve Clively for help in the field, Daffyd Morton for supplying equipment and Drs Stuart Bunn, Sam Lake and Keith Walker for constructive comments on earlier drafts of this paper. Sandra Lawson prepared the manuscript for final submission.

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