Arch. Hydrobiol. 156 3 315–338 Stuttgart, February 2003

# Litter breakdown and invertebrate detritivores in a resource-depleted Appalachian stream

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With 6 figures and 4 tables

**Abstract:** We measured breakdown rates of leaves and small wood for the first three years in a stream in which detrital inputs were excluded for 7 years and in a reference stream located in the Appalachian Mountains of North Carolina, USA. Leaf and wood inputs were excluded using a gill-net canopy constructed over a 170-m section of stream. We hypothesized that red maple (*Acer rubrum*) and rhododendron (*Rhododendron maxima*) leaf breakdown rates would decline in the litter exclusion stream as shredder production decreased with each year of litter exclusion. In contrast, we expected faster wood breakdown rates in the litter exclusion stream as microbes and invertebrates shifted from leaves to wood as their primary organic matter resource. Consistent with our predictions, wood breakdown rates were significantly faster in the litter exclusion stream. We also found significantly slower processing rates of maple leaves in the litter exclusion stream compared to the reference stream during years 2 and 3. Slower breakdown rates for red maple leaves in the litter exclusion stream were associated with lower shredder production and estimated consumption rates in years 2 and 3. Shredder production and consumption rate estimates were also lower in the exclusion stream for rhododendron leaves, but leaf breakdown rates were not affected. We also found that shredder production in litterbags was 3–4× greater than in benthic substrates in the litter exclusion stream. In contrast, shredder production in litterbags was similar to that in benthic substrates in the reference stream. These differences were probably due to the relatively low availability of organic matter in benthic substrates in the litter exclusion stream. Our data show shredders track high quality organic matter resources (leaves) and contribute to their loss rate, illustrating the interdependence of stream organisms and terrestrial organic matter input.

**Key words:** organic matter, decomposition, litter exclusion, detritus, resource island, aquatic macroinvertebrates, wood, streams.

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DOI: 10.1127/0003-9136/2003/0156-0315 0003-9136/03/0156-0315 $ 6.00
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## Introduction

Allochthonous inputs form the basis of production in small streams draining forested watersheds (FISHER & LIKENS 1973, VANNOTTE et al. 1980, MINSHALL et al. 1983, WEBSTER & MEYER 1997). Microbes and invertebrates use leaf detritus as a carbon source (KAUSHIK & HYNES 1971, ANDERSON & SEDELL 1979, CUMMINS & KLUG 1979, FINDLAY & ARSUFFI 1989). Wood also serves as a food resource and habitat for stream organisms (e.g. DUDLEY & ANDERSON 1982, BENKE et al. 1985). Detritus, especially wood, stabilizes ecosystem functioning during disturbances (ODUM 1963, BILBY & LIKENS 1980, O'NEILL & REICHLE 1980).

Primary and secondary production, decomposition and nutrient dynamics have been used as measures of ecosystem functioning in response to biodiversity loss (e.g. SCHULZE & MOONEY 1993, MOONEY et al. 1996, LOREAU et al. 2001 and references within). GESSNER & CHAUVET (2002) made a case for using litter breakdown as a means of assessing stream ecosystem functioning. RUESINK & SRIVASTAVA (2001) demonstrated the effects of shredder species loss on leaf breakdown in artificial streams. In the natural environment, however, litter breakdown rates can be influenced by a variety of factors, including stream nutrient concentrations, pH, stream size, leaf or wood species, invertebrate density, physical abrasion, stream retention, or microbial colonization (see reviews by WEBSTER & BENFIELD 1986, SUBERKROPP 1998, GRAÇA 2001). These confounding factors must be considered when predicting changes in ecosystem functioning due to disturbance.

In August 1993, we began a litter exclusion manipulation at Coweeta Hydrologic Laboratory, North Carolina, USA, to examine the consequences of disturbing the stream-riparian zone linkage on ecosystem functioning. Leaf standing crops in the litter-excluded stream at Coweeta declined rapidly following litter exclusion (WALLACE et al. 1997, 1999). We measured the effects of litter exclusion on one measure of ecosystem function, leaf and wood breakdown, during the initial stages of the manipulation. We hypothesized that leaf breakdown would occur faster in the litter exclusion stream than in a nearby undisturbed stream because of increased nutrient availability and microbial activity (ELWOOD et al. 1981, MEYER & JOHNSON 1983, TANK et al. 1998, TANK & WEBSTER 1998), as well as the remaining leaves serving as resource "islands", for invertebrates that are not capable of using alternate organic matter resources such as wood (e.g. WEBSTER & WAIDE 1982, MEYER & JOHNSON 1983, BENFIELD et al. 1991, PAUL & MEYER 1996, SCHOFIELD et al. 2001). As standing crops of leaf detritus declined during the exclusion period, we expected to see a reduction in shredder production and thus, a decrease in leaf breakdown rates. This decrease in processing rates has previously been demonstrated in an insecticide-treated stream at Coweeta (WALLACE et al.

1982), as well as in experimental streams (PETERSEN & CUMMINS 1974, MULHOLLAND et al. 1985).

During year 1 of litter exclusion, wood breakdown rates measured using wood veneer strips were higher in the litter exclusion stream when compared to the reference stream (TANK & WEBSTER 1998, TANK et al. 1998). TANK & WEBSTER (1998) hypothesized that this was due to increased nutrient availability for microbes associated with wood in the litter exclusion stream. Enzyme activity, fungal biomass, and microbial respiration were all significantly greater on wood in the litter exclusion stream than in a reference stream (TANK & WEBSTER 1998). Breakdown rates of the thin strips of poplar and oak veneer used in this experiment (TANK & WEBSTER 1998) were 2–3 × higher than those reported by GOLLADAY & WEBSTER (1988) for small woody debris in Coweeta streams. We predicted that natural red maple stick processing rates in the exclusion stream would be faster than that of the reference stream due to increased microbial colonization, benthic invertebrate feeding, and physical abrasion, but at a slower rate than that reported by TANK & WEBSTER (1998) due to a decreased surface area to volume ratio of natural sticks.

We tested these hypotheses by measuring annual breakdown rates of red maple and rhododendron leaves and marked red maple sticks for three years in the litter exclusion and reference streams. The objectives of the study were: 1) to quantify leaf processing rates in a headwater stream decoupled from its riparian habitat compared to a reference stream, 2) to examine breakdown rates of small wood in the litter exclusion stream and reference stream, and 3) to calculate the abundance, biomass and production of litterbag invertebrate taxa for each stream. We compared our leaf breakdown rates to long-term data for these streams at Coweeta, which includes data encompassing extremes in annual precipitation (CUFFNEY et al. 1990, CHUNG 1992, CHUNG et al. 1993).

## Study sites

The study was conducted in two headwater streams at Coweeta Hydrologic Laboratory (Macon Co.) in the southern Appalachian Mountains in North Carolina, USA. The reference stream (Catchment 53) is approximately 135 m in length and is located within one km of the litter exclusion stream (Catchment 55), which had all leaf litter and woody debris excluded from its 170-m length since August 1993. Direct-fall litter was excluded from the treatment stream using 1.2-cm mesh gill net canopy erected across the channel, while blow-in litter was trapped using 20-cm high bird netting along the stream sides (WALLACE et al. 1999). Small woody debris was manually removed from the exclusion stream in August 1996 after the leaf decomposition study. Large woody debris was removed from the stream in August 1998. Both catchments are forested primarily with tulip poplar (*Liriodendron tulipifera*), white oak (*Quercus alba*), red oak (*Quercus rubra*), and dogwood (*Cornus florida*). *Rhododendron maximum* forms a

**Table 1.** Physical characteristics of reference and litter exclusion streams at Coweeta Hydrologic Laboratory, NC. Elevations measured at the gauging flume.

| Variable | Reference | Litter Exclusion |
|---|---|---|
| Catchment | | |
| Area (ha) | 5.2 | 7.5 |
| Elevation (m a.s.l.) | 829 | 810 |
| Aspect | South | South |
| Channel length (m) | 135 | 170 |
| Wetted width (m) | 0.7–1.2 | 1.2–1.6 |
| Bankfull channel area ($m^2$) | 327 | 373 |
| Gradient (cm/m) | 27 | 20 |
| Canopy cover (%) | 88.9 | 91.7 |
| Substrate (% composition) | | |
| Mixed | 73 | 87 |
| Bedrock outcrop | 27 | 13 |
| Mean Annual Discharge (L/s) | | |
| 1985–1989 | 0.50 | 1.08 |
| 1993–1996 | 0.93 | 1.68 |
| Mean Annual Degree Days | | |
| 1985–1989 | 4486 | 4430 |
| 1993–1996 | 4427 | 4492 |
| Mean $NO_3$-N (μg/L) | | |
| 1985–1993 | 3 | 4 |
| 1993–1996 | 3 | 8 |
| Mean $NH_4$-N (μg/L) | | |
| 1985–1993 | 2 | 2 |
| 1993–1996 | 3 | 3 |
| Mean $PO_4$ (μg/L) | | |
| 1985–1993 | 3 | 2 |
| 1993–1996 | 2 | 2 |

dense understory, which reduces the sunlight reaching the stream bed year-round. The two streams are similar with respect to catchment area and substrate type (Table 1). The long-term leaf breakdown data set (1985–1995) for catchments 53 and 55 included the wettest and driest years on record at Coweeta. Differences in mean annual discharge, annual degree days, ammonium, and phosphate did not differ between streams before and after litter exclusion (Table 1, $p>0.05$, Before After Control Impact (BACI) analyses, Stewart-Oaten et al. 1986). Nitrate concentrations in the litter exclusion stream were significantly greater after the start of the litter exclusion (Table 1, $p<0.001$, BACI).

## Materials and methods

### Leaf breakdown

Leaf litter breakdown rates were measured for rhododendron and red maple leaves during 1993–1994, 1994–1995, and 1995–1996 (the first three years of litter exclu-

sion). Leaves were collected during October of each year from trees in each watershed and air dried until the beginning of the experiment. Approximately 15 g dry weight of each species was placed into 20×36-cm plastic 5-mm mesh bags. Litterbags (35 of each leaf species) were placed in the streams the first week of December each year of the 3-year study. Ten litterbags of each species were taken out to the field and immediately returned to the lab to correct for handling loss. Total dry weight of each leaf species added to each stream was 0.5 kg. Three to seven replicates were collected after ca. 7, 14, 28, 70, 96, 134, 170, 205 and 232 days for red maple bags, with later collection dates (298 and 350 days) for several sets of rhododendron bags due to slower breakdown rates. Collected litter bags were placed on ice and returned to the laboratory for processing.

Litterbag contents were washed to remove invertebrates and sediments, oven-dried (60 °C for 7 days), weighed, ashed (500 °C for 12 hours), and re-weighed to obtain ash-free dry mass (AFDM) remaining for each date. Processing rates were calculated using the exponential decay model by regressing the natural log of the percent AFDM remaining against incubation time in days (PETERSEN & CUMMINS 1974). We compared differences in breakdown rates between streams for each year of litter exclusion and leaf species using analysis of covariance (BENFIELD 1996) (JMP, version 4.0.4, SAS). Using long-term datasets from CUFFNEY et al. (1990), CHUNG (1992), and CHUNG et al. (1993), we examined relationships between red maple leaf breakdown rates and shredder production, mean annual discharge, annual degree days, and nitrate and phosphate concentrations in stream water using forward stepwise multiple regression analysis (Sigma Stat, version 2.0, SPSS). Differences in breakdown rates between streams before and after litter exclusion were compared using BACI analyses (STEWART-OATEN et al. 1986).

## Wood breakdown

Breakdown rates of small wood were assessed in each stream using individually marked red maple sticks (0.5–1.5 cm diameter, 12–30 cm length) cut from saplings in catchment 56 at Coweeta. Forty-five sticks were placed in each of two locations in each stream on 10 November 1993. Total wet weight of wood added to each stream was 1.26 kg and 1.20 kg for the litter exclusion and reference stream, respectively. Twenty sticks were collected from each stream in early December during 1994, 1995, and 1996. A final collection of 10 sticks from each stream was made in June 1998. Sticks removed from each stream were oven-dried (60 °C for 7 days), weighed, ashed (500 °C for 24 hours), and re-weighed to obtain AFDM estimates remaining for each date. Initial wet weights were converted to AFDM using a wet weight/AFDM regression developed from 40 additional sticks [g AFDM = 0.22625 + 0.66731 × g wet weight, $r^2$ = 0.99]. Breakdown rates were calculated using the exponential decay model (described above) and compared between streams using analysis of covariance (BENFIELD 1996) (JMP, version 4.0.4, SAS).

## Invertebrates colonizing litterbags

Invertebrates were separated from litterbags within 24 hours of collection using nested 1-mm and 250-μm mesh sieves and preserved in 7–8 % formalin with Phloxine B dye

to aid in sorting. All organisms were sorted under a dissecting microscope (15×). Invertebrates in the 250-μm fraction were subsampled if the total number of organisms in a sample exceeded 100 using a sample splitter (WATERS 1969) before being removed from the sample. All organisms were measured to the nearest mm (total body length) and identified to genus when possible. Chironomidae were identified as Tanypodinae or non-Tanypodinae. Non-insects were identified to order. Functional groups were assigned based on MERRITT & CUMMINS (1996) or gut content analyses. Length-weight regressions (BENKE et al. 1999) were used to convert body lengths to AFDM for biomass estimates presented as annual means. Secondary production estimates for shredder taxa were calculated using the size frequency method (HYNES & COLEMAN 1968, HAMILTON 1969) with a cohort production interval correction (BENKE 1979). 95 % confidence limits were calculated for shredder production data using methods of KRUEGER & MARTIN (1980) for size-frequency data.

Differences in invertebrate densities and biomass between streams and leaf species were compared using 2-way analysis of variance (ANOVA) of log (x+1) transformed data. In order to compare litterbag production to benthic production in mixed substrates, we converted annual litterbag production per bag to annual production per $m^2$ by dividing annual production per bag by litterbag area (0.055 $m^2$), and plotted litterbag production against mixed substrate (substratum of mixed silt, sand, pebble and cobble) production reported by WALLACE et al. (1999). We compared litterbag production to mixed substrate production because leaf detritus is more abundant in mixed substrates, compared to bedrock rockface habitat in these streams (WALLACE et al. 1997, 1999).

We calculated leaf consumption by shredders (BENKE & WALLACE 1980, CUFFNEY et al. 1990) in litterbags and mixed substrates of each stream for each year using the equation:

$$\text{Consumption (mg AFDM bag}^{-1}\text{ yr}^{-1}) = \text{Production (mg AFDM bag}^{-1}\text{ yr}^{-1})/(\text{AE} \times \text{NPE}),$$

where AE is assimilation efficiency and NPE is net production efficiency.

We used an average value of 13 % for AE and 38 % for NPE based on studies by MCDIFFETT (1970) and PERRY et al. (1987). We also calculated a range of consumption estimates using a high AE and NPE of 20 % and 40 %, respectively, and low AE and NPE of 10 % and 30 %. Shredder consumption was divided by initial mass of leaf material in litterbags to obtain the proportion consumed. To calculate proportion of leaves in the mixed substrates consumed by shredders, we divided shredder consumption by the maximum leaf standing crop measured in each stream for each year (WALLACE et al. 1999). The weight of leaf litter introduced into each stream in the litterbags (1 g AFDM/$m^2$) was added to the maximum leaf standing crop in the consumption calculations.

## Results

### Litter breakdown

The breakdown rate of red maple leaves was similar in the treatment stream (k = 0.0087 $day^{-1}$) and the reference stream (k = 0.0084 $d^{-1}$) during the first year of litter exclusion (Fig. 1). Breakdown rates in the litter exclusion stream increased to 0.0108 and 0.0102 $day^{-1}$ during years 2 and 3, respectively, but were significantly slower ($p < 0.001$, ANCOVA) than those measured in the reference stream (k = 0.0172 and 0.0177 $d^{-1}$, respectively). Breakdown rates of rhododendron leaves during the first two years were faster in the litter exclusion stream (k = 0.0066 and 0.0064 $day^{-1}$), than in the reference stream (k = 0.0041 and 0.0032 $d^{-1}$ for years 1 and 2, respectively) (Fig. 1). The difference in rhododendron breakdown rates differed significantly between streams during year 2 ($p < 0.001$, ANCOVA). During year 3, the rhododendron breakdown rate in the reference stream (k = 0.0058 $d^{-1}$) was similar to that in the litter exclusion stream (k = 0.0047 $d^{-1}$). When we compared differences in breakdown rates between streams before and after litter exclusion, we found no significant difference for either leaf species (red maple p = 0.14; rhododendron p = 0.69,

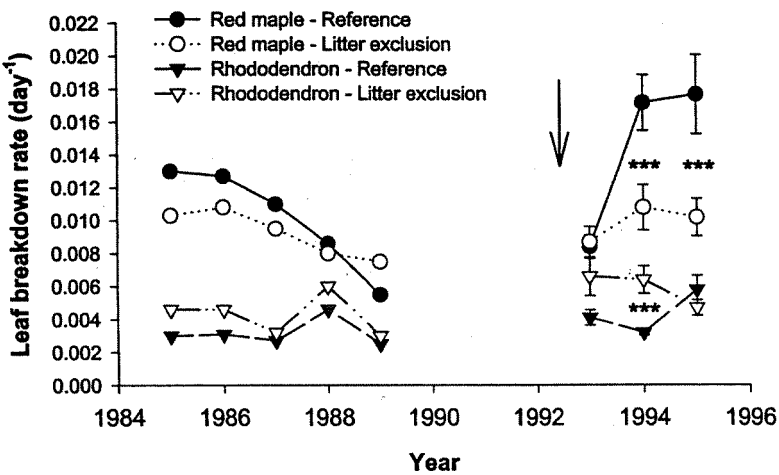


**Fig. 1.** Leaf breakdown rates ($d^{-1}$) ± 1 SE for red maple and rhododendron litterbags in reference and litter exclusion streams from 1993 to 1995. Arrow indicates start of litter exclusion. *** indicates $p < 0.001$, using ANCOVA. No data collected from 1990 to 1992. Data from 1985 to 1989 from CUFFNEY et al. (1990) and CHUNG (1992). $R^2$ for reference stream red maple regressions for 1993, 1994, 1995: 0.95, 0.95, 0.92. $R^2$ for reference stream rhododendron regressions for 1993, 1994, 1995: 0.91, 0.98, 0.86. $R^2$ for litter exclusion stream red maple regressions for 1993, 1994, 1995: 0.93, 0.93, 0.94. $R^2$ for litter exclusion stream rhododendron regressions for 1993, 1994, 1995: 0.82, 0.89, 0.94.

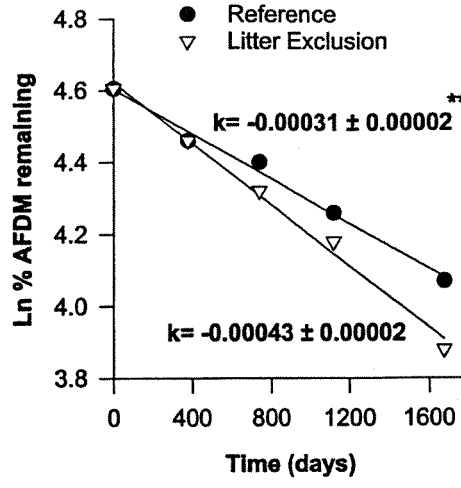


**Fig. 2.** Red maple stick breakdown rates ($day^{-1}$) ± 1 SE in reference and litter exclusion streams from November 1993 to June 1998. $R^2$ for reference stream regression = 0.99, $R^2$ for litter exclusion stream = 0.99. ** indicates $p<0.01$, using ANCOVA.

df = 6 for both tests, BACI analysis). However, the power of the BACI analyses was low (0.21 and 0.05) due to the low degrees of freedom.

Breakdown rates of red maple sticks were significantly faster in the litter exclusion stream than in the reference stream ($p<0.01$, ANCOVA) (Fig. 2). The percent AFDM remaining (87 %) was similar in each stream after the first year, but the difference between streams increased with each additional year. Sticks removed from the litter exclusion stream after 4.5 years were classified as decay class IV or V, based on ROBISON & BESCHTA's (1990) decay class system ranging from I (least decayed) to V (most decayed). The majority of the sticks had no bark remaining and wood texture ranged from slightly softened to deeply grooved. The cross-sectional shape of most sticks changed from round to oval-shaped by the end of the experiment. Sticks from the reference stream were classified as decay class III or IV, most with portions of intact bark and light-colored, firm wood.

## Invertebrate abundance, biomass and production

Invertebrate abundance per litterbag was greater for red maple (range: 1041–2709 individuals per bag), than for rhododendron (range: 669–1159 individuals per bag) in both streams during our study (Figs. 3 A & B). Species in the collector-gatherer and predator functional feeding groups (FFGs) dominated invertebrate abundance in both types of litterbags. Total invertebrate abundance, collector-gatherer, primary consumer (non-predators), and predator abundance in red maple litterbags did not differ significantly between streams

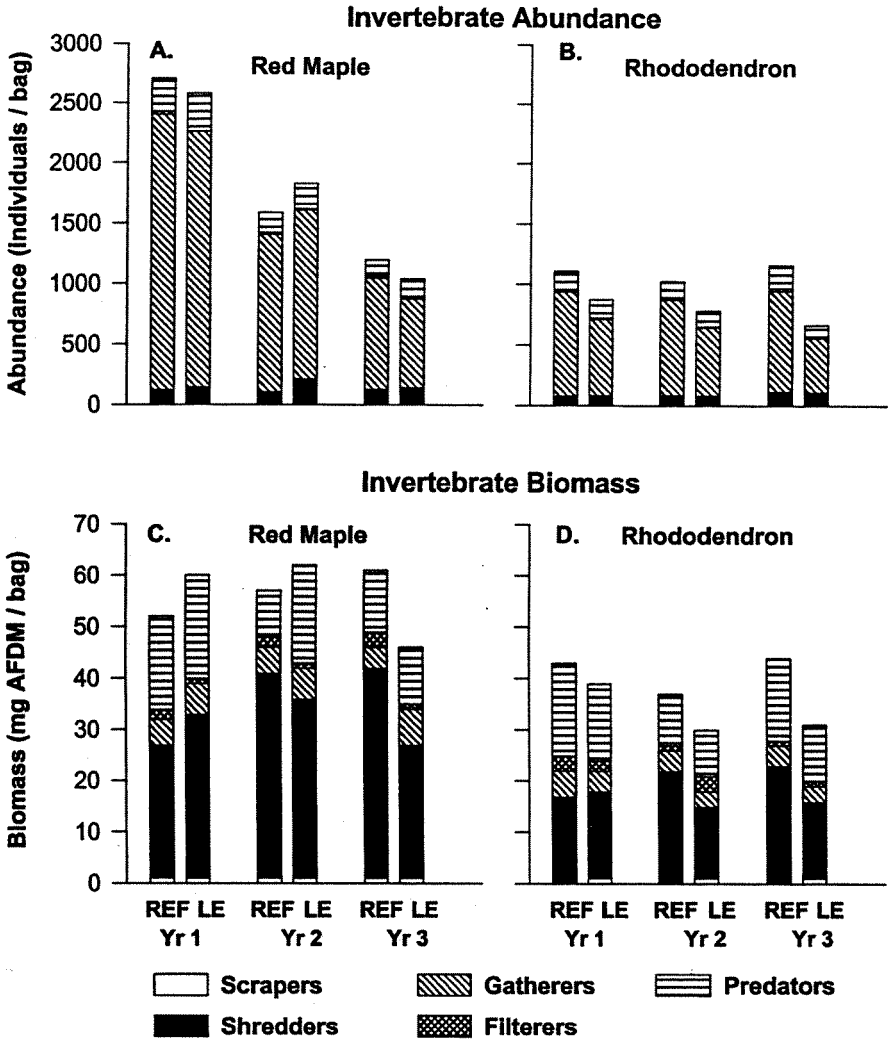


**Fig. 3.** Mean annual abundance (**A** and **B**) and biomass (**C** and **D**) of invertebrate functional groups in red maple and rhododendron litterbags in the reference (REF) and litter exclusion stream (LE) during Yr 1 (1993–1994), Yr 2 (1994–1995), and Yr 3 (1995–1996) of litter exclusion.

for any year ($p > 0.05$, ANOVA) (Table 2). Scrapers and shredders were significantly greater in red maple bags in the litter exclusion stream than in the reference stream for all three years (Fig. 3 A, Table 2). We found no difference in abundances of shredders, filterers, predators, or total invertebrates in rhododendron litterbags between streams for any year (Fig. 3 B, Table 2). Collector-gatherer and primary consumer abundances were significantly ($p < 0.05$,

**Table 2.** Results of 2-way ANOVA comparing abundance and biomass of invertebrates in red maple and rhododendron litter bags between streams [reference (Ref) and litter exclusion (LE)] and among years (1993 = yr 1, 1994 = yr 2, 1995 = yr 3). Data were log (x+1) transformed. Multiple comparisons testing significance of each invertebrate group separately were made using Tukey's test. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, NS = not significant.

| Invertebrate group | Red Maple | | | | Rhododendron | | | |
|---|---|---|---|---|---|---|---|---|
| | Stream | Year | Stream × Year | Multiple comparisons | Stream | Year | Stream × Year | Multiple comparisons |
| **Abundance** | | | | | | | | |
| Scrapers | *** | NS | NS | LE>Ref | *** | NS | NS | LE>Ref |
| Shredders | * | NS | NS | LE>Ref | NS | NS | NS | |
| *Leuctra* spp. | ** | NS | * | LE>Ref during yr 2 | NS | NS | NS | |
| Peltoperlidae | NS | ** | NS | yrs 1 & 3>yr 2 | NS | NS | NS | |
| *Lepidostoma* spp. | NS | NS | NS | | NS | NS | NS | |
| *Pycnopsyche* sp. | ** | ** | NS | Ref>LE, yr 3>yr 2 | ** | NS | NS | Ref>LE |
| *Molophilus* sp. | * | *** | NS | LE>Ref, yr 1>yrs 2 & 3 | NS | NS | NS | |
| *Tipula* spp. | NS | *** | NS | yr 2>yrs 1 & 3 | NS | NS | NS | |
| *Fattigia pele* | ** | NS | NS | LE>Ref | * | * | NS | LE>Ref, yr 3>yr 2 |
| Gatherers | NS | NS | NS | | * | NS | NS | Ref>LE |
| Filterers | ** | NS | NS | Ref>LE | NS | NS | NS | |
| Primary Consumers | NS | NS | NS | | * | NS | NS | Ref>LE |
| Predators | NS | NS | NS | | NS | NS | NS | |
| Total invertebrates | NS | NS | NS | | NS | NS | NS | |
| **Biomass** | | | | | | | | |
| Scrapers | ** | NS | NS | LE>Ref | *** | NS | NS | LE>Ref |
| Shredders | NS | NS | NS | | NS | NS | NS | |
| *Leuctra* spp. | ** | NS | NS | LE>Ref | NS | NS | NS | |
| Peltoperlidae | NS | NS | NS | | NS | NS | NS | |
| *Lepidostoma* spp. | NS | NS | NS | | NS | * | NS | yr 3>yr 1 |
| *Pycnopsyche* sp. | *** | ** | NS | Ref>LE, yr 3>yr 1 | *** | NS | NS | Ref>LE |
| *Molophilus* sp. | * | NS | NS | LE>Ref | NS | NS | NS | |
| *Tipula* spp. | NS | *** | NS | yr 2>yrs 1 & 3 | NS | NS | NS | |
| *Fattigia pele* | NS | NS | NS | | ** | * | NS | LE>Ref, yr 3>yr 2 |
| Gatherers | NS | NS | NS | | NS | NS | NS | |
| Filterers | ** | NS | NS | Ref>LE | NS | NS | NS | |
| Primary Consumers | NS | NS | NS | | NS | NS | NS | |
| Predators | NS | NS | NS | | NS | NS | NS | |
| Total invertebrates | NS | NS | NS | | NS | NS | NS | |

ANOVA) greater in rhododendron bags in the reference compared to the litter exclusion stream for all three years.

As with abundance, total invertebrate biomass was greater for red maple litter bags (range: 46–52 mg AFDM per bag), than for rhododendron litterbags (range: 30–45 mg AFDM per bag) in both streams (Figs. 3 C & D). Proportionally, shredder biomass dominated (39–73 %) both types of litterbags. Total invertebrate and shredder biomass in red maple and rhododendron bags did not differ significantly between streams for any year (Figs. 3 C & D, Table 2). Scraper biomass was significantly greater in the litter exclusion stream

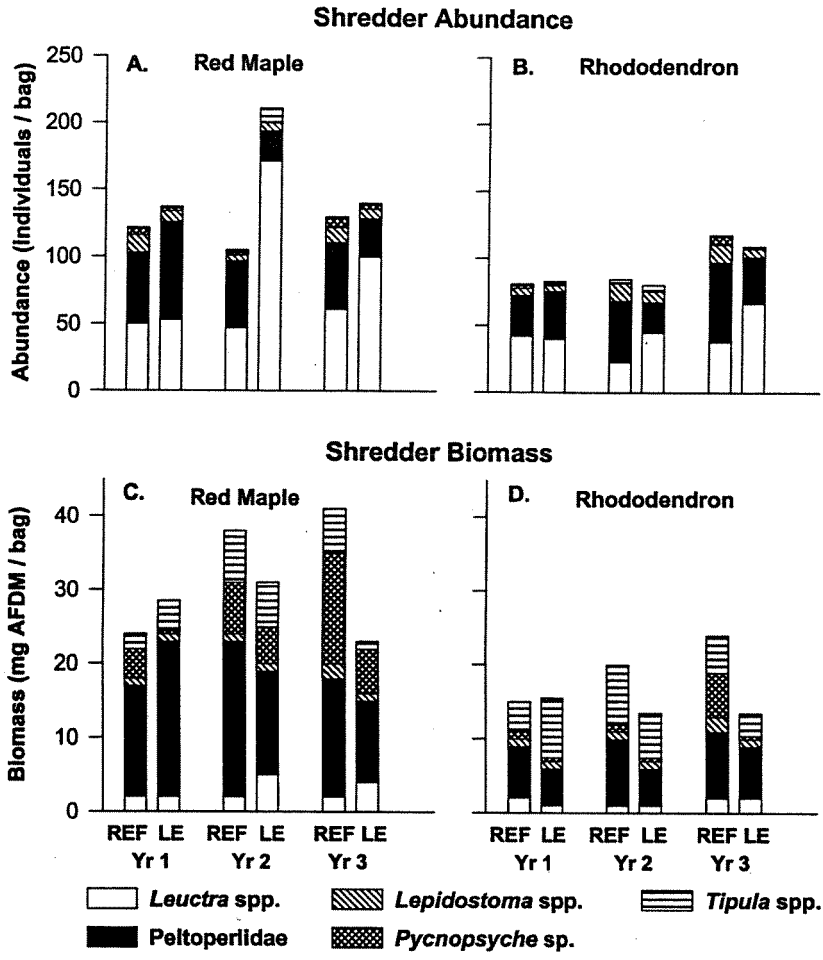


**Fig. 4.** Mean annual abundance (**A** and **B**) and biomass (**C** and **D**) of shredder taxa in red maple and rhododendron litterbags in the reference (REF) and litter exclusion stream (LE) during Yr 1 (1993–1994), Yr 2 (1994–1995), and Yr 3 (1995–1996) of litter exclusion.

($p < 0.01$, ANOVA) for both leaf species, while filterer biomass was significantly greater in the reference stream ($p < 0.01$, ANOVA) in red maple bags (Table 2).

*Leuctra* spp. and Peltoperlidae were the most abundant shredders in red maple and rhododendron litterbags, together making up 78–91 % of shredder abundance (Figs. 4 A & B). *Leuctra* spp., *Molophilus* sp. and *Fattigia pele* abundances were all significantly greater in red maple bags in the litter exclusion stream than in the reference stream (Table 2). Shredder biomass was more evenly split among the five dominant taxa than it was for abundance (Figs. 4 C

& D). Peltoperlidae and *Pycnopsyche* sp. biomass was dominant in red maple bags, whereas Peltoperlidae and *Tipula* spp. biomass dominated rhododendron bags. Overall, we found only a slight decline in shredder biomass over the three years of litter exclusion in the treatment stream for both red maple and rhododendron bags.

Total shredder production in red maple and rhododendron litterbags was greater in the treatment stream, than in the reference stream during year 1 (Table 3). This pattern reversed during years 2 and 3, when total shredder production in the litter exclusion stream declined to 84 and 44 % of that found in reference stream red maple bags. For rhododendron litterbags, shredder production in the exclusion stream dropped to 78 % of that estimated for the reference stream during years 2 and 3. Production of *Leuctra* spp., *Molophilus* sp., and *Fattigia pele* remained as high, or higher in the litter exclusion stream than in the reference stream regardless of leaf species (Table 3). Production of other taxa such as *Lepidostoma* spp. and *Tipula* spp. did not decline in the exclusion

**Table 3.** Annual secondary production (mg AFDM litterbag$^{-1}$ yr$^{-1}$) ± 95 % CL of shredders in reference and litter exclusion streams from 1993 to 1995.

| Taxon | 1993 | | 1994 | | 1995 | |
|---|---|---|---|---|---|---|
| | Reference | Litter Exclusion | Reference | Litter Exclusion | Reference | Litter Exclusion |
| **Red Maple** | | | | | | |
| *Leuctra* spp. | 20.3±7.3 | 25.2±8.9 | 15.3±5.5 | 31.1±6.8 | 18.0±10.8 | 19.7±3.9 |
| Peltoperlidae | 64.7±17.8 | 65.7±20.4 | 132.7±24.9 | 84.4±28.1 | 69.1±18.9 | 52.2±14.9 |
| *Lepidostoma* spp. | 10.8±4.7 | 12.7±5.5 | 9.0±2.9 | 9.3±1.9 | 23.3±7.4 | 7.3±3.1 |
| *Pycnopsyche* sp. | 34.6±23.0 | 4.6±7.7 | 46.4±22.8 | 12.3±8.3 | 117.0±38.4 | 24.5±19.6 |
| *Molophilus* sp. | 3.2±3.3 | 6.5±3.9 | 4.8±8.9 | 2.0±1.7 | 2.7±2.1 | 4.7±3.9 |
| *Tipula* spp. | 5.8±3.3 | 31.9±19.4 | 43.4±23.7 | 67.3±46.6 | 42.3±33.1 | 6.1±6.6 |
| *Fattigia pele* | 1.0±1.0 | 4.0±2.2 | 1.4±1.6 | 3.4±2.0 | 2.3±2.5 | 2.9±2.5 |
| *Psilotreta* sp. | 0.1±2.1 | 1.5±1.9 | 0.2±1.0 | 0.1±2.0 | 0.0±0.0 | 1.9±2.4 |
| *Limonia* sp. | 0.2±0.4 | 0.3±0.6 | 0.0±0.0 | 0.4±0.7 | 0.4±0.9 | 2.6±5.2 |
| *Anchytarsus* sp. | 0.1±0.1 | 0.0±0.0 | 0.2±0.3 | 0.0±0.0 | 0.0±0.0 | 0.4±0.8 |
| *Lipsothrix* sp. | 0.0 | 0.0 | 0.0 | 2.3 | 0.0 | 0.0 |
| Total shredders | 140.8 | 152.4 | 253.4 | 212.6 | 275.1 | 122.3 |
| **Rhododendron** | | | | | | |
| *Leuctra* spp. | 20.6±8.7 | 56.5±16.8 | 7.7±2.7 | 15.2±3.6 | 16.1±7.5 | 24.9±13.3 |
| Peltoperlidae | 33.8±7.5 | 36.6±9.9 | 56.5±12.0 | 24.9±6.1 | 61.5±11.1 | 53.1±28.5 |
| *Lepidostoma* spp. | 6.9±6.1 | 6.7±2.4 | 11.2±4.0 | 7.0±3.5 | 14.5±4.7 | 8.4±3.5 |
| *Pycnopsyche* sp. | 17.3±14.2 | 5.7±9.5 | 8.2±6.2 | 2.5±3.8 | 24.5±15.1 | 5.2±6.8 |
| *Molophilus* sp. | 3.0±3.3 | 1.0±1.7 | 5.1±6.7 | 3.4±2.1 | 1.7±1.3 | 1.6±1.4 |
| *Tipula* spp. | 31.1±19.7 | 63.7±33.6 | 62.8±27.1 | 65.1±36.2 | 37.1±21.5 | 24.7±18.4 |
| *Fattigia pele* | 0.2±0.3 | 3.8±1.9 | 0.6±0.6 | 0.6±0.6 | 1.1±0.7 | 3.0±1.3 |
| *Psilotreta* sp. | 0.4±0.8 | 4.1±5.7 | 0.0±0.0 | 0.4±0.7 | 0.1±0.1 | 0.7±0.8 |
| *Limonia* sp. | 0.0±0.0 | 0.1±0.2 | 0.2±0.2 | 1.0±0.9 | 0.5±0.5 | 0.4±0.5 |
| *Anchytarsus* sp. | 0.3±0.5 | 0.2±0.5 | 0.6±0.6 | 0.0±0.0 | 0.0±0.0 | 0.1±0.1 |
| *Lipsothrix* sp. | 0.0 | 0.1 | 0.0 | 0.2 | 0.0 | 0.0 |
| Total shredders | 113.6 | 178.5 | 152.9 | 120.3 | 157.1 | 122.1 |

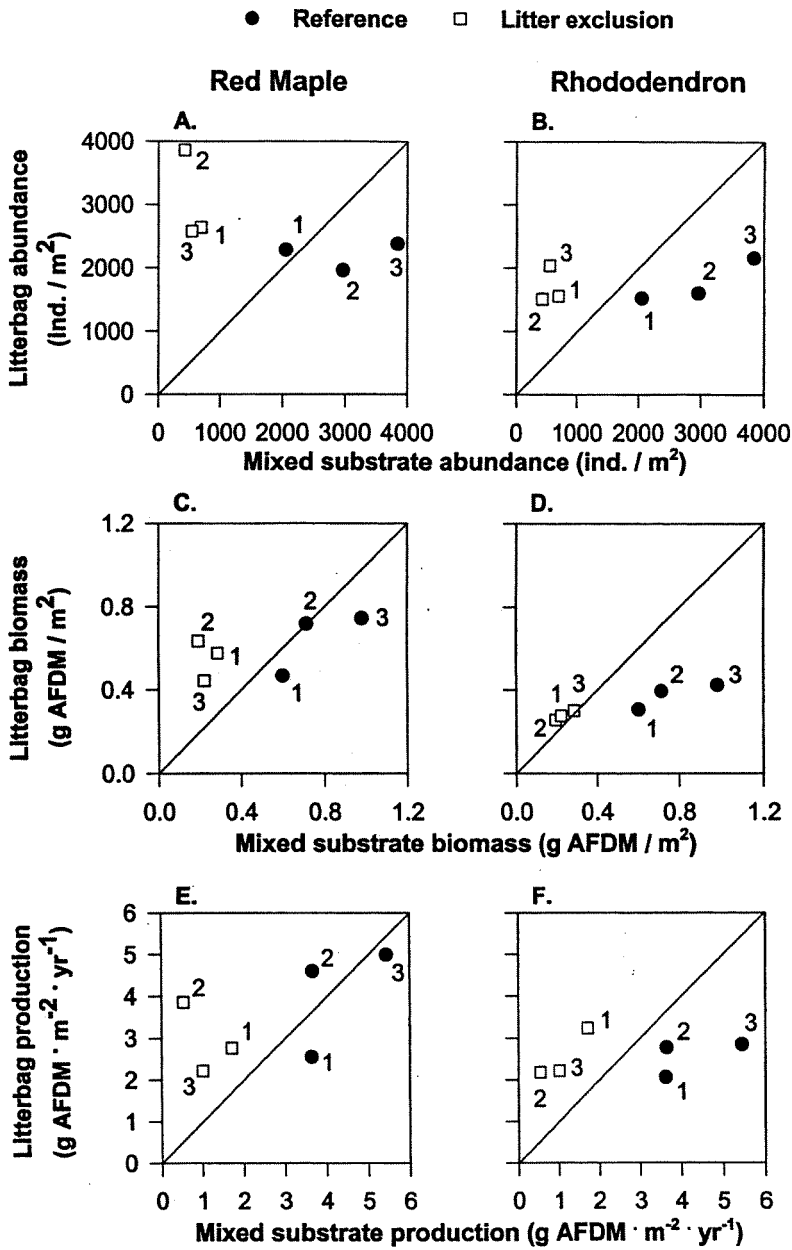


**Fig. 5.** Shredder abundance (**A** and **B**), biomass (**C** and **D**), and production (**E** and **F**) in litterbags and mixed substrates in reference and litter exclusion streams. Diagonal line = 1 : 1 line. Numbers refer to Yr 1, 2 or 3 of litter exclusion study.

stream until the third year of litter exclusion. *Pycnopsyche* sp. production declined immediately in the litter exclusion stream in both red maple and rhododendron litterbags, while Peltoperlidae declined in years 2 and 3.

We compared shredder abundance, biomass, and production in litterbags to that found naturally in benthic mixed substrates (WALLACE et al. 1999) by converting both production measures to the same units. We found greater shredder production in the litter exclusion litterbags than in the mixed substrates for each of the three years of the study (Fig. 5). Shredder production in litterbags in the litter exclusion stream was 4× greater for red maple leaves and 3× greater for rhododendron leaves than shredder production in mixed substrates of the litter exclusion stream. Shredder abundance, biomass and production in litterbags in the reference stream were similar or lower than that measured in the mixed substrates (Fig. 5).

## Consumption and processing rates

Using literature estimates of AE and NPE, we estimated that shredders consumed an average of 17–45 % of leaves in the litterbags annually in the reference stream (Table 4). Invertebrate consumption was higher for red maple leaves than rhododendron, and consumption increased slightly from years 1 through 3 in the reference stream. In the litter exclusion stream, however, the proportion of leaf litter consumed by shredders generally decreased with each year of exclusion. Shredder consumption of leaf litter in the mixed substrates of the reference stream from 1993 to 1996 paralleled that calculated for the litterbags. In the mixed substrates of the litter exclusion stream, however, the

**Table 4.** Estimated annual leaf consumption by shredders in red maple and rhododendron litterbags, and mixed substrates in reference and litter exclusion streams from 1993 to 1995. Average annual consumption based on annual shredder production, assimilation efficiency (AE) of 13 %, and net production efficiency (NPE) of 38 %. High (AE = 20 %, NPE = 40 %) and low (AE = 10 %, NPE = 30 %) bioenergetic efficiencies in parentheses.

| | Year | Reference % leaf litter consumed | Litter exclusion % leaf litter consumed |
|---|---|---|---|
| Red Maple | 1993 | 21.5 (13.2–35.3) | 23.2 (14.3–38.2) |
| | 1994 | 38.4 (23.7–63.3) | 32.3 (19.9–53.2) |
| | 1995 | 45.4 (28.0–74.7) | 20.1 (12.4–33.2) |
| Rhododendron | 1993 | 17.3 (10.7–28.4) | 27.2 (16.8–44.7) |
| | 1994 | 23.7 (14.6–39.0) | 18.1 (11.2–29.8) |
| | 1995 | 24.2 (14.9–39.8) | 18.7 (11.6–30.9) |
| Mixed Substrates | 1993 | 12.9 (8.0–21.2) | 35.0 (21.6–57.6) |
| | 1994 | 14.9 (9.2–24.5) | >100.0 |
| | 1995 | 24.4 (15.0–40.1) | >100.0 |

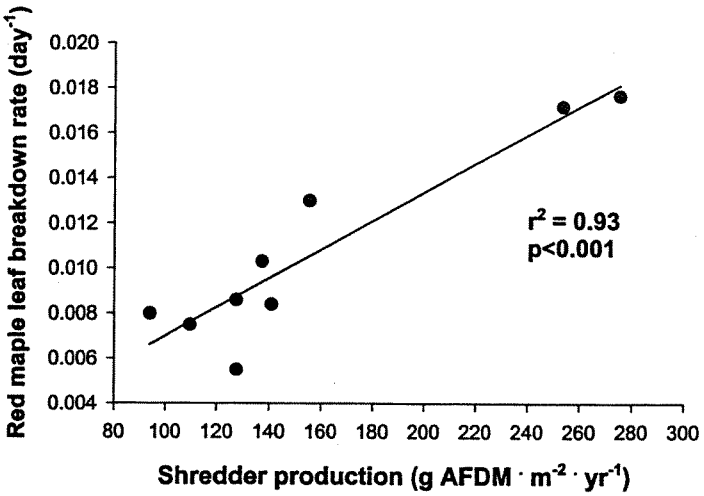


**Fig. 6.** Long-term relationship between shredder production (g AFDM $m^{-2}\,yr^{-1}$) and red maple leaf breakdown rates ($d^{-1}$) in the reference stream (C 53) and litter exclusion stream (C 55) during non-treatment years of 1985, 1988, 1989, 1993, 1994, and 1995. Regression equation line: $-k = 0.000628 + (0.0000638 \times \text{shredder production})$.

proportion of maximum leaf standing crop consumed by shredders increased to more than 100 % during years 2 and 3 (Table 4), indicating that shredders were consuming resources other than leaf detritus.

Multiple regression analyses showed that red maple breakdown rates were strongly and significantly correlated with annual litterbag shredder production ($r^2 = 0.93$, $p < 0.001$, $n = 9$, Fig. 6). When we added mean annual discharge and annual degree days to the model, each independent variable explained only an additional 1 % of the variance in breakdown rates. Mean annual nitrate and phosphate concentrations did not explain any additional variance in processing rates when added to the model.

## Discussion

### Leaf breakdown

The strength of the relationship between shredders and red maple breakdown rates in the long-term data set, and the lack of significant relationships between breakdown rates and nutrients, water temperature and discharge demonstrate the importance of shredders in these streams. Many studies have found that leaf processing rates are related to shredder abundance and biomass (e.g. Rounick & Winterbourn 1983, Benfield & Webster 1985, Cuffney et al. 1990, Stewart 1992, Fazi & Rossi 2000, Hieber & Gessner 2002). Without

litter inputs to the litter exclusion stream, we expected to see much faster breakdown rates for both leaf species during year 1, when compared to the reference stream. Contrary to our predictions, processing rates for red maple and rhododendron were similar between streams during the first year. This result can be partially explained by the timing of the start of the litter manipulation. The canopy was installed in August 1993, before autumn litter fall. A small standing crop of slowly decaying leaf species such as rhododendron and oak remained in the stream, offering a poor quality, but available carbon source for the microbial and invertebrate communities. Microbial respiration and fungal biomass were significantly greater on wood surfaces in the exclusion stream (TANK et al. 1998, TANK & WEBSTER 1998). Total shredder production in mixed substrates declined by 5 % (year 1), 70 % (year 2), and 44 % (year 3) compared to pretreatment levels during the first three years of litter exclusion (WALLACE et al. 1999). Shredders were disproportionately more abundant in the litterbags than in the mixed substrates of the exclusion stream compared to the reference stream (Fig. 5). Following the start of litter exclusion, the litterbags served as 'resource islands' in a resource-depleted environment. We did not observe this pattern in the reference stream, nor did we find any significant differences between streams for total shredder biomass in red maple and rhododendron litterbags (Table 2).

The concept that leaf packs serve as resource islands in streams has been previously described by WEBSTER & WAIDE (1982), MEYER & JOHNSON (1983), BENFIELD & WEBSTER (1985), BENFIELD et al. (1991), and BENFIELD et al. (2001). Rhododendron leaves in larger Coweeta streams are thought to serve as patches of food resources when other leaf species are flushed out during floods (PAUL & MEYER 1996), or during summer months when other species have already disappeared (SCHOFIELD et al. 2001). PALMER et al. (2000) offered direct evidence that detritus accumulations serve as resource patches in a Virginia stream, where they found higher chironomid and copepod densities in leaf patches than in sand. These organisms also preferentially colonized leaf patches containing fast decaying leaf species with high microbial abundances, over slow decaying leaf species with low microbial abundances. Long-term analyses of drift rates from the litter exclusion stream showed a greater proportion of shredder biomass drifting within the exclusion stream than in the reference stream at baseflow conditions (SILER et al. 2001). Presumably, these organisms were more actively searching for food in the litter-depleted stream. Higher invertebrate emigration from channels with reduced leaf litter was also observed in a 9-day microcosm experiment simulating litter exclusion (ROWE & RICHARDSON 2001).

We expected leaf breakdown rates would decline in the exclusion stream as shredder production declined during later stages of litter exclusion, yet breakdown rates for red maple increased from year 1 during the last 2 years of the

study for both streams. Shredder production in the red maple litterbags also increased compared to year 1 in both streams during year 2, and during year 3 in the reference stream (Table 3). Our comparison of shredder production in litterbags versus mixed substrates showed that shredders continued to be attracted to the litterbags in the exclusion stream (Fig. 5). TANK & WEBSTER (1998) suggested that microbes colonizing leaves and wood in low-nutrient forested headwater streams compete for a limited supply of water column nutrients. We suspect that by year 3, newly available dissolved nutrients due to the reduced leaf standing crop had stimulated microbial activity on litterbag leaves in the exclusion stream, maintaining average breakdown rates despite the decrease in shredder production. Although TANK & WEBSTER (1998) provided evidence of increased microbial activity on wood during year 3, we do not have measurements of microbial activity on leaves. Similar patterns of litter breakdown have been observed in cave streams isolated from allochthonous inputs (GALAS et al. 1996, SIMON & BENFIELD 2001).

It is unclear as to why rhododendron breakdown rates did not differ between streams after litter exclusion. Rhododendron breakdown rates declined in the treatment stream from years 2 to 3, but were still similar to pretreatment data from CUFFNEY et al. (1990) and CHUNG (1992) (Fig. 1). Although we do not have long-term data regarding the relationship between shredder production and rhododendron breakdown rates in these streams, shredder biomass and production were lower in rhododendron bags than in red maple bags. Previous work in a Coweeta stream treated with insecticide showed that rhododendron breakdown rates decreased by 62 % when shredder biomass was reduced (CUFFNEY et al. 1990). Rhododendron processing rates did not differ from red maple processing rates in the insecticide-treated stream until most of the red maple leaves had been processed. SCHOFIELD et al. (2001) found that insect shredder biomass was positively related to rhododendron leaf breakdown in a fourth-order Coweeta stream during summer months when only rhododendron leaves remained. Rhododendron leaves are a less preferred food resource compared to other leaf species such as red maple (WEBSTER & WAIDE 1982) and were probably consumed by shredders in the litter exclusion stream after the availability of more palatable leaf species (e.g. red maple) declined.

The proportion of leaves consumed by shredders in the litterbags declined from 23–32 % during years 1 and 2 of exclusion to 19–20 % during year 3 (Table 4). At the same time, consumption of red maple and rhododendron leaves in reference stream litterbags increased from 17–38 % to 24–45 %. Annual leaf consumption estimates from litterbags during 1988 and 1989 ranged from 14–19 % for the litter exclusion stream, which was undisturbed during 1988 and 1989, and 20–24 % for the reference stream (CHUNG 1992). In benthic mixed substrates, we estimated the proportion of annual leaf consumption in the exclusion stream to be well over 100 % during the second and third

years of exclusion, which indicates that some shredders consumed resources other than leaves. HALL et al. (2000) examined organic matter flows in food webs during the second year of litter exclusion and found a greater proportion of total invertebrate production derived from wood rather than leaf detritus. They also reported an overall decline in detrital flows in the exclusion stream and the loss of taxa from the food web. Some taxa such as *Pycnopsyche* sp. did not switch to alternate food resources, and did not survive in the exclusion stream (EGGERT et al., unpubl. data). Taxa (e.g. *Tipula* spp., *Leuctra* spp., Peltoperlidae, and *Molophilus* sp.) capable of using alternate food resources such as small wood or fine particulate organic matter, switched to other resources as leaf standing crops declined (EGGERT et al., unpubl. data).

Physical abrasion may have also played a role in the leaf breakdown rates measured in this study. Coarse and fine inorganic particle transport increased significantly during the first year of litter exclusion as particles were flushed from the stream associated with reduced organic matter retention (WALLACE et al., unpubl. data). Current velocities also increased significantly in the treatment stream following the start of litter exclusion (MEYER et al., unpubl. data). Litterbags in the litter exclusion stream became buried in sediments more often than those in the reference stream. The movement of sediments resulting in bag burial (WEBSTER & WAIDE 1982, MAYACK et al. 1989) and increased current velocities (DOBSON et al. 1992, PAUL & MEYER 1996) may have affected breakdown rates of leaves in the exclusion stream, but we have insufficient data to address this hypothesis.

## Wood breakdown

As predicted, we found that small wood (<15 mm diameter) breakdown rates in the litter exclusion stream were significantly faster (1.4×) than in the undisturbed stream. Processing rates for small wood in this study are similar to those reported in Coweeta headwater streams by GOLLADAY & WEBSTER (1988) for small red oak sticks ($k = 0.00033-0.00077\,d^{-1}$) and WEBSTER et al. (1999) for <20 mm diameter yellow poplar and white pine sticks ($k = 0.00024-0.00062\,d^{-1}$). TANK & WEBSTER (1998) found that decomposition rates of poplar wood veneers in spring 1995 were 1.8× faster in the litter exclusion stream compared to the reference stream. Their rates ($k = 0.0048-0.0085\,d^{-1}$) were extremely fast due to the high surface area to volume ratio of the 1-mm thick veneers used for breakdown measurements. MELILLO et al. (1983) found very fast breakdown rates ($k = 0.00329-0.00110\,d^{-1}$) for alder and aspen in Canadian headwater streams. However, they used 1-cm diameter wood chips with high surface area to volume ratios. Alder is also a nitrogen-rich species (MELILLO et al. 1983).

We did not examine the mechanisms behind the increased wood breakdown rates. Experiments conducted by TANK & WEBSTER (1998) and TANK et al. (1998) showed greater microbial respiration, extracellular enzyme activity and fungal biomass on wood in the litter exclusion stream. They concluded that higher microbial colonization on wood substrates was related to the higher availability of dissolved nutrients due to the absence of leaves. In a study conducted during the third year of litter exclusion, TANK et al. (1998) found that relative phosphorus availability was two times greater and relative nitrogen availability was five times greater in the litter exclusion stream due to the absence of leaves. Our water chemistry data showed that phosphorus concentrations from 1993 to 1996 remained similar in the exclusion stream, while nitrate concentrations doubled (Table 1).

Macroinvertebrates can play an important role in the mineralization and nutrient cycling of woody debris in small streams (ANDERSON et al. 1984). Xylophages such as *Lara avara* (Coleoptera), *Heteroplectron californicum* (Trichoptera), and *Lipsothrix fenderi* (Diptera) have been reported to consume wood at a rate of 13 to 223 % of their body weight per day (ANDERSON et al. 1984, STEEDMAN & ANDERSON 1985). Small wood supporting xylophagous invertebrates typically decays faster than wood that does not. GOLLADAY & WEBSTER (1988) compared invertebrate taxa richness and abundance on tethered sticks in a stream subjected to clear-cutting and in a reference stream. Taxa richness was 2× greater and abundance 2.5× greater on sticks in the clear-cut stream, which also had the fastest breakdown rates. Some wood gougers depend on fungal communities to soften the wood and make it more palatable for invertebrate consumption (DUDLEY & ANDERSON 1982). Evidence from TANK & WEBSTER (1998) and TANK et al. (1998), along with our observations of heavily grooved sticks found in the litter exclusion stream suggest that the significantly greater fungal biomass found on wood in the litter exclusion stream made the remaining wood material and associated microbial biofilms a good alternate food resource for some invertebrates.

Another possible explanation for the higher breakdown rates of sticks in the exclusion stream is increased movement of sediments. GOLLADAY & WEBSTER (1988) reported greater breakdown rates for sticks subjected to periodic burial and rewetting as sediment moved in a stream draining a clear-cut watershed. In our study, the lack of organic matter inputs and rapid breakdown of the leaf biomass in the exclusion stream greatly decreased the retention of fine and coarse inorganic particles. Some of these sediments were alternately deposited on and flushed from marked sticks in this study and may have played a role in the higher breakdown rates.

## Effects of litter exclusion on ecosystem functioning

The exclusion of leaf litter and woody debris for three years resulted in significantly lower benthic organic matter standing crops in the manipulated stream (WALLACE et al. 1999). In-stream generation of dissolved organic carbon was reduced by 30 % (MEYER et al. 1998), and invertebrate production declined to 42 % of pre-treatment levels (WALLACE et al. 1999). The data presented here demonstrate additional impacts of disrupting the riparian zone-stream linkage on litter breakdown and invertebrate colonization. The higher shredder production in litterbags compared to benthic mixed substrates shows the importance of leaf litter as a food resource for invertebrates in the exclusion stream. For shredders, the litterbags represented resource patches in a resource-depleted environment. Long-term data also clearly related red maple leaf breakdown rates to shredder production.

Even though the litterbags served as resource islands, breakdown rates of red maple leaves in the exclusion stream were still slower than those in the reference stream. Studies by TANK & WEBSTER (1998) and TANK et al. (1998) showed that microbial activity increased in the litter exclusion stream, but even the enhanced colonization of litter by microbes could not replace the function of the shredder populations. Leaf burial may have also played a role in the reduced breakdown rates. The faster breakdown rates of small woody debris in the exclusion stream also impacted ecosystem function by reducing the supply of an alternate food resource for some animals (HALL et al. 2000), and decreasing the retention of organic matter (WALLACE et al., unpubl. data) and nutrients (WEBSTER et al. 2000). Based on results of this study and previous work in these streams, it is apparent that maintaining riparian connections with small streams is critical to the normal functioning of these ecosystems.

## Acknowledgements

We thank DERRICK CARTER, LAUREL CHAFIN, GRETA CHRISTENSEN, BRIAN KEELEY, ERICH LINNEMAN, DEBBIE ROWE, SCOTT STROUD, and SARA BLANKENSHIP for technical assistance. Drs. DAROLD BATZER, STEPHEN GOLLADAY, JOHN HUTCHENS, JUDY MEYER, AMY ROSEMOND, ROBERT WETZEL, and two anonymous reviewers provided valuable comments to improve this manuscript. Drs. WAYNE SWANK, BRIAN KLOEPPEL and the staff at Coweeta Hydrologic Laboratory assisted with site support. This research was funded by The National Science Foundation (Grants DEB-9207498 and DEB-9629268).

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Submitted: 14 May 2002; accepted: 15 October 2002.