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Leaf litter decomposition and macroinvertebrate communities in headwater streams draining pine and hardwood catchments

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Abstract

Benthic invertebrates, litter decomposition, and litterbag invertebrates were examined in streams draining pine monoculture and undisturbed hardwood catchments at the Coweeta Hydrologic Laboratory in the southern Appalachian Mountains, USA. Bimonthly benthic samples were collected from a stream draining a pine catchment at Coweeta during 1992, and compared to previously collected (1989–1990) benthic data from a stream draining an adjacent hardwood catchment. Litter decomposition and litterbag invertebrates were examined by placing litterbags filled with pine or maple litter in streams draining pine catchments and hardwood catchments during 1992–1993 and 1993–1994. Total benthic invertebrate abundance and biomass in the pine stream was ca. 57% and 74% that of the hardwood stream, respectively. Shredder biomass was also lower in the pine stream but, as a result of higher *Leuctra* spp. abundance, shredder abundance was higher in the pine stream than the hardwood stream. Decomposition rates of both pine and red maple litter were significantly faster in pine streams than adjacent hardwood streams ($p<0.05$). Total shredder abundance, biomass, and production were similar in maple bags from pine and hardwood streams. However, trichopteran shredder abundance and biomass, and production of some trichopteran taxa such as *Lepidostoma* spp., were significantly higher in maple litterbags from pine streams than hardwood streams ($p<0.05$). In contrast, plecopteran shredders (mainly *Tallaperla* sp.) were more important in maple litterbags from hardwood streams. Shredders were well represented in pine litterbags from pine streams, but low shredder values were obtained from pine litterbags in hardwood streams. Results suggest conversion of hardwood forest to pine monoculture influences taxonomic composition of stream invertebrates and litter decomposition dynamics. Although the impact of this landscape-level disturbance on invertebrate shredder communities appeared somewhat subtle, significant differences in decomposition dynamics indicate vital ecosystem-level processes are altered in streams draining pine catchments.

Introduction

The major energy source of headwater streams in the eastern United States is allochthonous detritus inputs (Fisher & Likens, 1973; Cummins, 1974; Cummins et al., 1983). This coarse particulate organic matter (CPOM) is generally retained within low- order reaches of the stream until it is converted to fine particulate organic matter (FPOM) (Naiman & Sedell, 1979; Wallace et al., 1982, Cummins et al., 1983), which is more amenable to transport. Conversion of CPOM to FPOM occurs through both physical abrasion and biological activity. Leaf shredding macroinvertebrates in low order streams feed directly on CPOM, and their feeding activities are an important mechanism for conversion of CPOM to FPOM (e.g., Cummins, 1973; Anderson & Sedell, 1979; Grafius & Anderson, 1980; Cuffney et al., 1990). In turn, shredder generated FPOM serves as the primary food for other invertebrate groups, such as collector-filterers and gatherers (Short & Maslin,

1977; Grafius & Anderson, 1980; Mulholland et al., 1985). This detritus cycle in stream systems of forested regions is ultimately dependent upon the riparian forest community for inputs of leaf litter and other CPOM.

Hynes (1975) suggested that both biological and physical linkages exist between stream systems and the surrounding terrestrial environment, and numerous investigators have recently demonstrated important aspects of this relationship. Altering riparian forests has been shown to affect physical components of stream habitats such as substrate composition and availability (Gurtz & Wallace, 1984), light and temperature regimes (Gurtz & Wallace, 1984; Sweeney, 1993), hydrologic regimes (Webster & Waide, 1982; Tuchman & King, 1993), and nutrient regimes and water chemistry (Webster & Waide, 1982, Cooper & Thomsen, 1988; Sweeney, 1993; Ormerod et al., 1993; Tuchman & King, 1993). Changes in riparian forests can also greatly influence the timing, quantity, and quality of allochthonous CPOM inputs to streams (Sweeney, 1993; Tuchman & King, 1993; Delong & Brusven, 1994). These alterations in riparian forests are often associated with agricultural practices, and can range from subtle changes in forest community structure to complete removal of the riparian forest. Although the influence of many such changes on physical characteristics of streams are well documented, effects on animal communities and biotic processes are less understood. However, biological changes should accompany alterations in the physical template, and Sweeney (1993) recently suggested that the presence or absence of riparian forests may be the single most important human altered factor affecting stream communities.

In the southeastern United States, conversion of native mixed hardwood forest to pine monoculture is a common practice. As of 1985, pine plantations accounted for 20 884 acres of forested land in the southern US, and ca. 50 000 acres of pine plantation are predicted in this region by the year 2030 (Barrett 1994). Some investigators have examined invertebrate communities inhabiting pine plantations in the eastern United States (e.g. Blair et al., 1994) and streams draining them (e.g. Woodall & Wallace, 1972), but the potential influence of this conversion on biotic communities and processes in stream ecosystems is poorly understood. Although not as striking as complete removal of all riparian vegetation, replacement of native riparian vegetation with pine monoculture can potentially influence a variety of physical characteristics and processes in streams. Additionally, pine litter has been shown to be nutritionally inferior to many deciduous litter types (Taylor et al., 1989; Klemmedson, 1992; Friberg & Jacobsen, 1994), and biological communities and processes associated with allochthonous energy inputs in streams draining pine forests may be negatively affected.

Table 1. Physical characteristics of the study streams. Catchments P1 and P17 are white pine catchments, and H18 and H55 are mixed hardwoods. Elevations were measured at gauging flumes. na = not measured during this study.

	P1	P17	H18	H55
Catchment				
Area (ha)	16	13	13	7.5
Elevation (m asl)	705	760	726	810
Channel				
Length (m)	335	265	305	170
Substrate (%)				
Bedrock outcrop	17.5	12.5	7.5	13.1
Boulder & cobble	15.5	64.2	51.9	31.8
Pebble & sand	29.5	14.5	36.6	49.0
Silt	37.5	8.8	4.0	6.1
Discharge (l/s)				
Average 1989–93	3.5	3.3	4.9	2.4
Temperature (°C)				
Average 1993–94	11.4	na	na	12.1
Annual degree days	4175	na	na	4433

The objective of this study was to examine the influence of the conversion of riparian vegetation from hardwood to pine on biological processes in headwater streams. Specifically, this study was designed to test whether this landscape-level disturbance altered invertebrate communities, particularly shredders, and leaf litter decomposition dynamics. Thus, benthic invertebrate communities, invertebrate communities inhabiting litterbags, and decomposition of pine and maple litter were examined in headwater streams draining mixed hardwood and white pine monoculture catchments.

Study sites

The four study streams are located at the Coweeta Hydrologic Laboratory (U.S. Forest Service) in the Blue Ridge Province of the southern Appalachian Mountains, Macon county, North Carolina, USA. All streams are first order and drain catchments 1, 17, 18, and 55. Physical characteristics of the study streams are similar (Table 1), and Swank & Crossley (1988)

reported no significant differences in nitrogen and other nutrients among headwater streams draining pine and hardwood catchments at Coweeta. Additionally, Woodall & Wallace (1972) reported similar pH and alkalinity in Coweeta pine and hardwood streams.

Hardwood catchments 18 (H18) and 55 (H55) are relatively undisturbed, and dominant vegetation consists of a mixture of oaks (*Quercus* spp.), Hickories (*Carya* spp.), red maple (*Acer rubrum*), and tulip poplar (*Liriodendron tulipifera*). Additionally, a dense riparian growth of rhododendron (*Rhododendron maximum*) shades streams in these catchments year-round.

Pine catchments 1 (P1) and 17 (P17) were cleared and planted in white pine (*Pinus strobus*) in 1957 and 1956, respectively. P1 was cut and burned (no products removed, but all burned) for 1 year prior to planting with white pine. P17 was also cut prior to planting with white pine, but cut trees were not burned and no products were removed. Following conversion to white pine in both catchments, invading hardwoods have been periodically removed by cutting or chemical treatment. Thus, P1 and P17 currently lack any mature hardwoods, and the riparian rhododenron growth typical of headwater streams at Coweeta is greatly reduced along these streams.

The predominant substratum in all four study streams is a mixture of silt, sand, pebble, and cobble, which is referred to here as mixed substrates. Mixed substrates compose ca. 82 to 92% of the length of all study streams (Table 1). Remaining substrate in each stream is bedrock outcrop. All four study streams are typical of Coweeta headwater streams in that they exhibit high streambed roughness, and retain large amounts of coarse particulate organic matter (Wallace et al. 1995). Additional information on the study streams, other streams at Coweeta, and the entire Coweeta basin is reported by Swank & Crossley (1988).

Methods

Benthic invertebrate sampling

Benthic samples were collected in P1 every other month (6 sampling dates) during 1992. On each sampling date, 4 benthic core ($n = 24$ core samples) and 3 rock outcrop samples ($n = 18$ rock outcrop samples) were collected at previously determined random points along the length of the stream. Core samples were collected by driving a stove pipe coring device (400 cm^2) approximately 10 cm into mixed substrates habitats and removing all material for transport to the laboratory. Rock outcrops were sampled by scraping and brushing a 15 × 15 cm area of rock outcrop into a 250 μm mesh bag held at the downstream edge of the sampled area.

In the laboratory, organic components of benthic samples were elutriated and passed through nested 1 mm and 250 μm sieves. Coarse (>1 mm) and fine (<1>250 μm) fractions were then preserved in a 6–8% formalin solution containing Phloxine B dye. All invertebrates were removed from coarse fractions under a dissecting microscope at 15× magnification. Fine fractions were occasionally sub-sampled (1/2 to 1/32) with a sample splitter (Waters, 1969), before removing invertebrates under a dissecting microscope.

Invertebrates were identified, counted, and measured (total body length) under a dissecting microscope with a graduated stage. Insects were identified to genus and species whenever possible, except for groups such as Chironomidae, which were identified as either Tanypodinae or non-Tanypodinae. Most non-insects were identified to order. Biomass estimates (AFDM) were obtained for all insect taxa and larger non-insect taxa using length-weight regressions derived from animals in the study streams, other streams at Coweeta (Huryn, 1986), or other North Carolina streams (Smock, 1980). Biomass estimates for small non-insect taxa such as Copepoda and Hydracarina were obtained by weighing >50 individuals in each size class and determining mean weight.

All invertebrate taxa were assigned to functional feeding groups according to Merritt & Cummins (1984), or our knowledge of local fauna. Crayfish were divided amongst shredders (1/2), collector-gatherers (1/4), and predators (1/4) according to Huryn & Wallace (1987).

Invertebrate abundance and biomass on mixed substrates and rock outcrop habitats was calculated separately, and habitat-weighted according to the proportion of each habitat in P1. Invertebrate data from P1 during 1992 was compared to invertebrate data from an adjacent hardwood stream (H55) which was collected and processed in exactly the same manner during 1989 and 1990 (see Whiles & Wallace, 1995). Although H55 data from the same year as our investigation of P1 were not available, H55 has served as a reference stream for numerous stream invertebrate investigations spanning many years at Coweeta (e.g. Lugthart & Wallace, 1992; Whiles & Wallace, 1995), and the invertebrate community inhabiting this stream has remained remark-

ably constant from year to year. For example, percent similarity values for functional group abundance and biomass in H55 over four study years which encompassed drought and wet periods (1985, 1986, 1989, 1990) are 97% and 86%, respectively. Because of the temporal continuity in H55, the close proximity of H55 to P1, and similarities in general physical attributes of these two streams, we were confident that differences we observed in invertebrate communities would be a result of differences in catchment management rather than time. Thus, average values from P1 during 1992 were compared with average 1989–1990 values from H55 to compare trends in benthic functional structure and taxonomic composition.

Litter decomposition

Processing rates of red maple and white pine litter were examined in P1 and H55 during 1992–93. In order to substantiate results obtained during the 1992–93 study, processing rates of the same litter types were examined again during 1994–95 in P17 and H18. Red maple litter was collected from undisturbed hardwood catchments at Coweeta just prior to abscission. Senescent white pine litter was collected from white pine catchments at Coweeta by shaking pine bows over a collecting bag. Plastic mesh bags (36 × 20 cm with 5 mm mesh openings) filled with 15 g dry mass leaf material were placed in P1 and H55 on December 16, 1991 and P17 and H18 on December 17, 1993. Because white pine litter easily passed through mesh bags, pine needles were loosely tied together with cotton thread into bundles of 5 g dry mass before placement into bags. Initial mass of litterbags used in each study were corrected for breakage and converted to ash free dry mass (AFDM) at time of placement in streams. Additionally, 4 bags of each litter type were picked up 2 weeks after placement in streams to calculate leaching losses. Replicates of 4–6 bags of each litter type were then collected at 1- to 2-month intervals during the 1992 study (n=20 P1 maple, 30 H55 maple, 30 P1 pine, and 50 H55 pine) and 2- to 3-month intervals during the 1994 study (n=16 P17 maple, 19 H18 maple, 20 P17 pine, and 31 H18 pine), until an average of <5% initial AFDM of each litter type in each stream remained.

Following collection and transport of litterbags to the laboratory, remaining litter in bags was washed, dried (7 days at 60° C), weighed, ashed (24 h at 500° C), and re-weighed to obtain estimates of AFDM remaining for each collection date. Decay coefficients (-k) and estimates of days to 5% remaining were obtained by regressing the natural log of % AFDM litter remaining against days elapsed. Pairwise comparisons of regression slopes from P1 and H55 during 1992, and P17 and H18 during 1994 were made with a Student's t test ($p<0.05$) (Zar, 1984).

Litterbag invertebrates

Invertebrates in P1 and H55 litterbags were examined on every other litterbag collection date (n=16 maple bags and 20 pine bags from each stream). Invertebrates in P17 and H18 litterbags were examined on two collection dates (15 January and 14 April 1994, n=8 bags of both litter types from each stream). Following collection of litterbags and transport to the laboratory, remaining litter and associated materials in bags were washed over stacked 1 mm and 250 μm sieves. Coarse (>1mm) and fine (<1 mm>250 μum) fractions were then preserved in a 6–8% formalin solution containing Phloxine B dye and processed in the same manner as described above for benthic invertebrates.

Because data were not normally distributed and variances were heterogeneous, Kruskal-Wallis ANOVA on ranks and Dunn's test were used for multiple comparisons of litterbag invertebrate data between streams and litter types (Zar, 1984). The 1992 and 1994 studies were analyzed separately. Because fewer replicate litterbags were examined during the 1994 study, emphasis was placed on litterbag invertebrate data collected during the 1992 study.

Estimates of secondary production of shredder taxa in P1 and H55 litterbags during 1992 were made using the size frequency method (Hamilton, 1969). Values were corrected for cohort production interval (CPI) according to Benke (1979). Variances and 95% confidence intervals for production values of each shredder taxon were calculated according to Krueger & Martin (1980). Pairwise comparisons of individual shredder taxa production in P1 and H55 were made by examining 95% confidence intervals ($p<0.05$) (Zar, 1984).

Results

Benthic invertebrates

Total habitat-weighted invertebrate abundance in H55 was 1.8× greater than that of P1 (Figure 1a). This difference was primarily a result of large differences in total invertebrate abundances in mixed substrates habitats in the two streams, whereas total abundances on

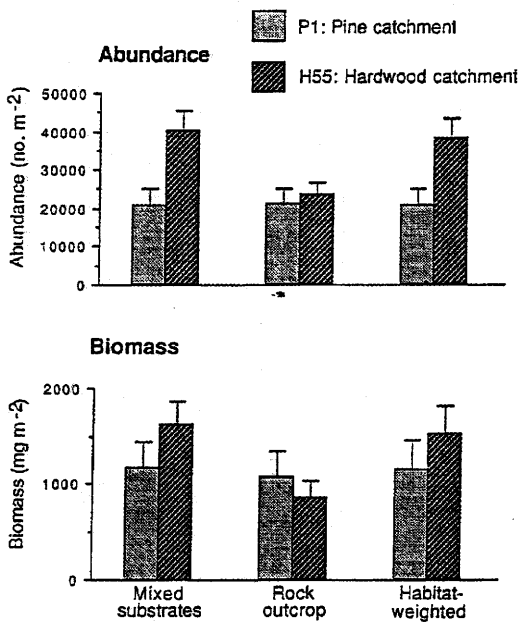

Figure 1. Mean abundance (no. m^{-2}) and biomass (mg AFDM m^{-2}) of total invertebrates in the pine catchment stream (P1) (annual average for 1992 ± standard error) and hardwood catchment stream (H55) (average of 1989–1990 ± standard error) for mixed substrates, bedrock outcrops, and habitat-weighted values.

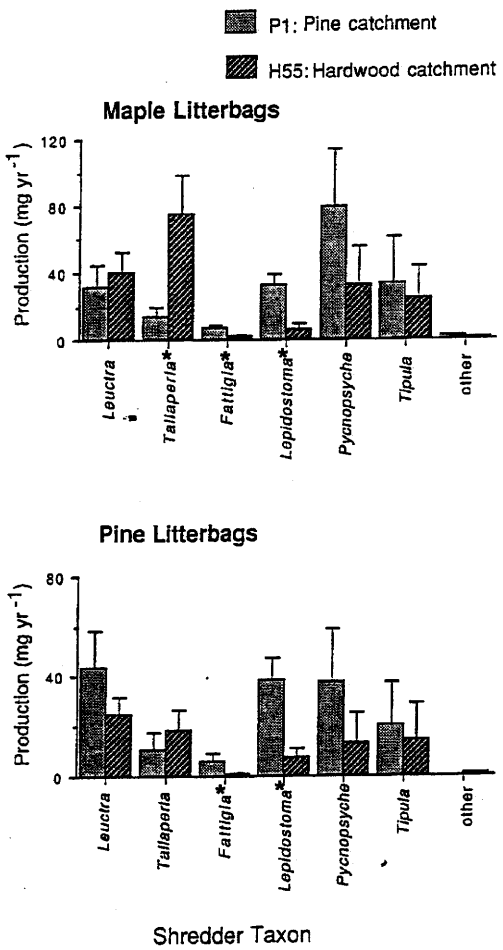

Figure 2. Annual production (mg AFDM $yr.^{-1}$) of shredder taxa during 1992 in pine and maple litterbags from the pine catchment stream (P1) and hardwood catchment stream (H55). * indicates significant difference in individual shredder taxa between streams ($p<0.05$).

rock outcrops in the two streams were similar. A similar pattern was evident for total invertebrate biomass in the two streams (Figure 1b).

Gatherers dominated habitat-weighted invertebrate abundances in both streams (Table 2). However, gatherer abundance in the hardwood stream was 2.3× greater than that of P1, while scraper, shredder, and filterer abundances were somewhat higher in the pine stream than H55. Despite much higher gatherer abundances in H55, gatherer biomass was similar between the two streams. Similarly, although shredder abundance in P1 was 1.7× that of H55, shredder biomass in H55 was 1.6× that of P1 (Table 2). Filterers were the only group exhibiting higher habitat-weighted biomass in the pine stream, and exceeded that of H55 by 2×.

Leuctra spp. (Plecoptera: Leuctridae) numerically dominated (90%) the P1 benthic shredder community (Table 3). Extremely high densities of *Leuctra* spp. in P1 resulted in somewhat higher overall shredder abundances in P1 than H55 (Table 2). *Leuctra* spp. was also the most abundant shredder taxa in H55. However *Leuctra* spp. in H55 comprised only 41% of total shredder abundances, and other shredder taxa such as *Tallaperla* sp. (Plecoptera: Peltoperlidae) and *Lepidostoma* spp. (Trichoptera: Lepidostomatidae) contributed significantly to total shredder abundances in this stream. In contrast, densities of shredder taxa other than *Leuctra* spp. were comparatively low in P1 (Table 3). *Tipula* spp. (Diptera: Tipulidae) was the dominant contributor to shredder biomass in both streams, and the top 3 contributors to shredder biomass were the same between streams (Table 3). However, biomass values for all 3 dominant shredders in P1 were somewhat lower than those in H55.

Table 2. Habitat-weighted average benthic abundance (no./m^2) and biomass (mg/m^2) (± standard error) of functional groups in a pine catchment (P1) in 1992 and hardwood catchment (H55) in 1989–1990. n=number of sampling dates (monthly means used as replicates).

	Pine n=6	Hardwood n=12
Abundance		
Filterers	380 (120)	292 (93)
Gatherers	13567 (2843)	30727 (4957)
Predators	4432 (1117)	4405 (877)
Scrapers	601 (134)	284 (84)
Shredders	1880 (972)	1106 (252)
Total	20860 (4318)	36814 (5086)
Biomass		
Filterers	184 (49)	91 (27)
Gatherers	248 (58)	274 (37)
Predators	274 (92)	519 (111)
Scrapers	33 (10)	30 (7)
Shredders	414 (146)	654 (107)
Total	1152 (311)	1567 (261)

Table 3. Abundance (no/m^2), biomass (mg/m^2) and percent contribution to total shredders of the dominant shredder taxa in streams draining a pine catchment (P1) in 1992 and a hardwood catchment (H55) in 1989–1990.

Pine		%	Hardwood		%
Abundance					
Leuctra spp.	1680.0	90	*Leuctra* spp.	451.0	41
Tallaperla sp.	79.0	04	*Tallaperla* sp.	314.0	28
Molophilus sp.	48.0	03	*Lepidostoma* spp.	127.0	11
Biomass					
Tipula spp.	189.0	46	*Tipula* spp.	263.0	40
Tallaperla sp.	53.0	13	Decapoda	116.0	18
Decapoda	47.0	11	*Tallaperla* sp.	78.0	12
Fattigia pele	41.0	10	*Pycnopsyche* spp.	58.0	09

Litter decomposition

Decomposition of both litter types was significantly higher in pine streams than hardwood streams during both the 1992 and 1994 studies ($p<0.05$) (Table 4). Maple litter decomposed 1.8× (1992 study) to 3.1× (1994 study) faster in pine streams than hardwood streams, and pine litter decomposed ca. 1.6× faster in pine streams than hardwood streams during both studies. For all streams examined during both studies, maple litter decomposed much faster (ca. 3× faster) than pine litter.

Table 4. Decay coefficients (-k ± 95% confidence interval) and days to 95% AFDM loss (± 95% confidence interval) for white pine and red maple litter during the 1992 study of catchments P1 and H55, and the 1994 study of catchments P17 and P18. Coefficients of determination (r^2) and number of litterbags used in each regression (n) are also presented. All regressions were significant at $p<0.01$. Asterisks denote significantly different decay rates of the same litter types between pairs of streams (Student's t-test, $p<0.05$).

Stream/ litter Type	n	r^2	-k ± 95% CI	Days to 95% loss ± 95% CI
1992 Study				
P1 Maple	20	0.84	0.03005 ± 0.0063*	99 ± 17
H55 Maple	30	0.70	0.01598 ± 0.0047*	187 ± 42
P1 Pine	30	0.86	0.00930 ± 0.0015*	322 ± 45
H55 Pine	50	0.82	0.00563 ± 0.0008*	531 ± 65
1994 Study				
P17 Maple	16	0.77	0.03056 ± 0.0097*	98 ± 24
H18 Maple	19	0.88	0.00974 ± 0.0018*	307 ± 47
P17 Pine	20	0.83	0.00933 ± 0.0021*	321 ± 59
H18 Pine	31	0.77	0.00542 ± 0.0011*	553 ± 94

Table 5. Average abundance (no./litterbag) and biomass (mg/litterbag) (± standard error) of invertebrate functional groups in pine and maple litterbags in pine (P1) and hardwood (H55) catchments during 1992. n=number of litterbags examined.

	Maple Bags		Pine Bags	
	P1 n=16	H55 n=16	P1 n=20	H55 n=20
Abundance				
Filterers	18 (7)	10 (2)	10 (2)	16 (5)
Gatherers	802 (106)	1399 (308)	1313 (336)	1277 (302)
Predators	126 (19)	126 (21)	203 (36)	144 (18)
Scrapers	4 (1)	7 (2)	12 (4)	12 (4)
Shredders	105 (21)	118 (26)	164 (35)	100 (20)
Total	1055 (130)	1660 (345)	1702 (397)	1547 (328)
Biomass				
Filterers	2 (1)	2 (1)	4 (1)	4 (1)
Gatherers	16 (7)	8 (1)	14 (2)	9 (2)
Predators	14 (2)	23 (4)	15 (2)	20 (4)
Scrapers	1 (1)	1 (<1)	1 (<1)	1 (<1)
Shredders	45 (7)	37 (7)	25 (6)	12 (2)
Total	78 (9)	70 (8)	60 (8)	46 (7)

Litterbag invertebrates

Total invertebrate abundances in pine and maple bags from P1 and H55 were similar, although biomass values in pine bags, particularly those in the hardwood stream, were generally lower than those of maple (Table 5). A similar pattern was evident in P17 and H18

Table 6. Average abundance (no./litterbag) and biomass (mg/litterbag) (± standard error) of invertebrate functional groups in pine and maple litterbags in pine (P17) and hardwood (H18) catchments during 1994. n=number of litterbags examined.

	Maple Bags		Pine Bags	
	P17	H18	P17	H18
	n=8	n=8	n=8	n=8
Abundance				
Filterers	6 (4)	2 (1)	1 (1)	4 (1)
Gatherers	662 (136)	475 (74)	372 (68)	291 (27)
Predators	94 (33)	71 (22)	68 (17)	46 (12)
Scrapers	1 (<1)	<1(<1)	1 (1)	0 (0)
Shredders	107 (34)	43 (11)	54 (12)	39 (9)
Total	869 (188)	591 (93)	495 (90)	379 (43)
Biomass				
Filterers	<1 (<1)	<1 (<1)	<1 (<1)	1 (<1)
Gatherers	7 (2)	5 (2)	5 (1)	3 (1)
Predators	15 (3)	15 (5)	8 (3)	9 (3)
Scrapers	1 (<1)	<1 (<1)	<1 (<1)	<1 (<1)
Shredders	20 (4)	26 (5)	16 (6)	5 (1)
Total	43 (6)	47 (9)	29 (9)	17 (4)

during 1994 (Table 6). However, because fewer bags were examined, and dates examined were from early in the decomposition process, generally low invertebrate abundance and biomass values were obtained for P17 and H18 during the 1994 study compared to P1 and H55 in 1992 (Tables 5 and 6). In general, bags from both the 1992 and 1994 studies were numerically dominated by collector-gatherers, followed by predators and shredders. Shredders accounted for most biomass in bags from both streams during both studies, except for pine bags from the two hardwood watersheds, where predator biomass exceeded that of shredders. Collector-filterers and scrapers contributed little to abundances and biomass in bags of both litter types in all streams examined (Tables 5 and 6).

Total shredder abundance and biomass was similar between streams and litter types during both studies, except for pine bags from hardwood streams. In both hardwood streams, total shredder biomass in pine bags was significantly lower than that of maple bags ($p<0.05$) (Tables 7,8).

Differences in shredder community composition between streams and litter types were evident during both studies. In maple bags examined during the 1992 study, abundance and biomass of trichopteran shredders in P1 was significantly higher ($p<0.05$) than that of H55 (Table 7). This difference was due to significantly higher values for *Lepidostoma* spp. and *Fattigia pele* (Trichoptera: Sericostomatidae) ($p<0.05$), and somewhat higher values for *Pycnopsyche* spp. (Trichoptera: Limnephilidae) (see appendix). Trichopteran shredder abundance and biomass in maple bags from the pine stream was again significantly higher than those from the hardwood stream during the 1994 study ($p<0.05$) (Table 8). However, due to smaller sample sizes during this study, fewer significant differences in individual taxa were observed. During the 1994 study, *Lepidostoma* abundance and biomass values were again significantly higher in the pine stream ($p<0.05$), and *Fattigia* values were somewhat higher in P17 than H18 (see appendix).

Similar patterns in trichopteran shredder abundances and biomass between streams were evident in pine litterbags during both studies. Values for total trichopteran shredders and many individual trichopteran shredder taxa were significantly higher in pine bags from pine streams than hardwood streams ($p<0.05$) (Tables 7 and 8, see appendix). Total trichopteran shredder biomass in pine bags from P17 during the 1994 study, although 3× higher than pine bags from H18, was not significantly higher ($p>0.05$) (Table 8).

In contrast to many trichopteran shredders, *Tallaperla* sp. (Plecoptera: Peltoperlidae) was more abundant in bags from hardwood watersheds. *Tallaperla* abundance and biomass was significantly higher ($p<0.05$) in maple bags collected from H55 than those from P1 during the 1992 study (see appendix). During 1994, *Tallaperla* abundance was again significantly higher in maple bags from the hardwood stream than the pine stream. *Tallaperla* biomass in 1994 showed the same trend, but was not significant (see appendix). *Tallaperla* biomass in maple bags from the hardwood streams also tended to be higher (significantly during the 1992 study) than that of pine bags from both streams. Abundance and biomass of the smaller and generally more abundant shredding plecopteran, *Leuctra* spp., did not differ markedly between streams and/or litter types (see appendix). Thus, differences in total plecopteran shredder abundances were not evident during either study. However, total plecopteran shredder biomass in maple bags from both hardwood streams was significantly higher than that of pine bags from hardwood streams ($p<0.05$) (Tables 7,8). Additionally, total plecopteran biomass in maple bags from hardwood streams was >2× and 1.5× higher than that of maple bags in P1 during 1992, and P17 during 1994, respectively.

Table 7. Average abundance (no./litterbag) and biomass (mg/litterbag) (± standard error) of shredder taxa in maple and pine bags placed in a pine catchment (P1) (n=16 maple bags and 20 pine bags), and a hardwood catchment (H55) (n=16 maple bags and 20 pine bags) during 1992. Values for each taxonomic group with different superscript letters are significantly different ($p<0.05$, Kruskal-Wallis ANOVA on ranks and Dunn's test).

	Maple bags		Pine bags	
Shredder taxon	P1	H55	P1	H55
Abundance				
Trichopteran shredders	28.6 (4.9)^{a}	11.7 (2.8)^{b}	28.5 (4.6)^{a}	8.0 (2.4)^{b}
Plecopteran shredders	73.1 (19.6)^{a}	104.3 (26.3)^{a}	134.7 (33.1)^{a}	91.2 (19.4)^{a}
Dipteran shredders	2.9 (1.2)^{a}	2.2 (0.9)^{a}	1.0 (0.4)^{a}	0.6 (0.2)^{a}
Total shredders	104.6 (20.9)^{a}	118.2 (26.0)^{a}	164.2 (35.3)^{a}	99.8 (20.0)^{a}
Biomass				
Trichopteran shredders	23.2 (6.6)^{a}	7.6 (3.0)^{bc}	12.7 (3.4)^{ab}	3.2 (1.3)^{c}
Plecopteran shredders	12.3 (2.7)^{ab}	27.0 (6.0)^{a}	11.0 (3.7)^{ab}	6.6 (1.6)^{b}
Dipteran shredders	9.0 (4.9)^{a}	2.7 (1.0)^{a}	1.7 (0.8)^{a}	2.5 (1.2)^{a}
Total Shredders	44.5 (7.2)^{a}	37.2 (7.0)^{a}	25.4 (5.6)^{ab}	12.2 (2.2)^{b}

Table 8. Average abundance (no./litterbag) and biomass (mg/litterbag) (± standard error) of shredder taxa in maple and pine bags placed in a pine catchment (P17) (n=8 maple bags and 8 pine bags), and a hardwood catchment (H18) (n=8 maple bags and 8 pine bags) during 1994. Values for each taxonomic group with different superscript letters are significantly different ($p<0.05$, Kruskal-Wallis ANOVA on ranks and Dunn's test).

	Maple bags		Pine bags	
Shredder taxon	P17	H18	P17	H18
Abundance				
Trichopteran shredders	26.0 (7.2)^{a}	5.6 (0.9)^{b}	27.1 (5.5)^{a}	3.5 (1.0)^{b}
Plecopteran shredders	80.8 (29.6)^{a}	36.8 (11.2)^{a}	26.8 (10.5)^{a}	34.9 (9.0)^{a}
Dipteran shredders	0.1 (0.1)^{a}	0.1 (0.1)^{a}	0.1 (0.1)^{a}	0.3 (0.3)^{a}
Total shredders	106.9 (34.1)^{a}	42.5 (11.2)^{a}	54.0 (11.8)^{a}	38.6 (8.7)^{a}
Biomass				
Trichopteran shredders	8.0 (3.4)^{a}	7.8 (2.8)^{a}	8.1 (5.6)^{a}	2.7 (1.0)^{a}
Plecopteran shredders	12.1 (4.8)^{ab}	18.5 (5.1)^{b}	5.4 (2.8)^{ac}	1.9 (0.4)^{ac}
Dipteran shredders	0.0 (0.0)^{a}	0.0 (0.0)^{a}	2.5 (2.5)^{a}	0.4 (0.4)^{a}
Total Shredders	20.2 (4.3)^{a}	26.3 (4.6)^{a}	16.0 (6.0)^{ab}	4.9 (1.4)^{b}

The only other shredder taxa collected during both studies were dipterans such as *Tipula* spp. and *Molophilus* sp. (Diptera: Tipulidae). Combined, dipteran shredders constituted a relatively small portion of shredder abundances and biomass during both studies, and no significant differences in dipteran shredders were observed amongst litter types and streams during either study.

Shredder production in litterbags

Total shredder production in P1 (197 mg AFDM yr.$^{-1}$) and H55 (181 mg AFDM yr.$^{-1}$) maple bags was similar. However, production of individual taxa in the two streams varied. For example, *Tallaperla* sp. showed the highest production of all shredders in maple litterbags from the hardwood stream, and was significantly higher ($p<0.05$) than *Tallaperla* sp. production in maple bags from P1 (Figure 2). In contrast, *Pycnopsyche* spp. was the most productive shredder in maple bags from the pine stream, and production of two other trichopteran shredders, *Lepidostoma* spp. and *Fattigia pele*, was significantly higher in maple bags from P1 than H55. Thus, trichopteran shredders accounted for ca. 60% of shredder production in maple bags from the pine stream, and only 22% of shredder production in H55 maple bags. Plecopteran shredders (primarily *Tallaperla* in H55 and *Leuctra* in P1) accounted for 63%

of shredder production in maple bags from the hardwood stream, and only 23% of shredder production in P1 maple bags. *Leuctra* spp. and dipteran shredder production in maple bags was similar between streams (Figure 2).

Total shredder production in pine bags from P1 (156 mg AFDM yr^{-1}) was slightly lower than that of P1 maple bags, but greatly exceeded that of H55 pine bags (78 mg AFDM yr^{-1}). Total shredder production in H55 pine bags was < 50% that observed in H55 maple bags, and production of all shredder taxa in H55 pine bags was generally lower than that observed in H55 maple bags (Figure 2). As observed in maple bags, *Lepidostoma* spp. and *Fattigia pele* production in P1 pine bags was significantly higher ($p<0.05$) than that of H55 pine bags, and trichopteran shredders made up >50% of shredder production in P1 pine bags (Figure 2). In pine bags from the hardwood stream, plecopteran shredders constituted 55% of shredder production, whereas trichopteran shredders accounted for only 25% of total shredder production.

Discussion

The major difference between shredder communities in pine and hardwood streams observed during this study was the proportion of trichopteran and plecopteran shredders in each. Shredder communities in litterbags from pine streams were dominated by trichopterans such as *Lepidostoma* spp., *Pycnopsyche* spp., and *Fattigia pele*, whereas plecopteran shredders such as *Tallaperla* sp. were less important than in undisturbed hardwood streams. Trichopterans are often a dominant component of streams in northern and western regions of North America, where pine and other conifers dominate forests (e.g. Grafius & Anderson, 1979; Grafius & Anderson, 1980; Molles, 1982). Whiles et al. (1993) recently demonstrated that *Lepidostoma* spp. readily consumed normally refractory rhododendron litter. Additionally, Friberg & Jacobsen (1994) noted that a sericostomatid trichopteran, *Sericostoma personatum*, was a less selective shredder than the amphipod, *Gammarus pulex*, and attributed this difference to larger mandibles, decreased mobility, and lower respiration of *Sericostoma* compared to *Gammarus*. These features of shredding trichopterans may be important factors in pine streams at Coweeta. Trichopteran shredders at Coweeta, and in other regions where pine and other conifers naturally dominate forests, appear quite capable of utilizing relatively poor detritus resources such as pine and other conifer needles as food. Additionally, trichopteran shredders may incorporate refractory litter materials into their cases. *Lepidostoma* spp. and *Pycnopsyche* spp. cases collected from pine streams during this study were primarily constructed of pine needles, bark, and wood fragments (Whiles & Wallace, personal observation).

Feeding and case making activities of caddisflies are major decomposition pathways in many headwater streams, and may represent the most important invertebrate-mediated decomposition mechanism in streams draining pine catchments at Coweeta. Chung et al. (1993) observed that litter decomposition rates following an insecticide disturbance coincided most closely with trichopteran shredder dynamics. Whiles et al. (1993) observed unusually rapid litter decomposition rates in disturbed streams where *Lepidostoma* densities were high and other shredders were poorly represented. Further, high laboratory feeding rates for *Lepidostoma* on both refractory and labile litter types have also been documented (Whiles et al., 1993). Thus, the higher proportion of trichopteran shredders in pine streams may be the most important mechanism underlying rapid decomposition rates observed during this study.

Pine needles normally decompose slowly, and are generally considered to be a low quality detritivore food resource in aquatic (Friberg & Jacobsen, 1994) and terrestrial (Taylor et al., 1989; Klemmedson, 1992) systems. This is primarily a result of pine needles having relatively low nutrient (nitrogen and phosphorus) values (Taylor et al., 1989; Klemmedson, 1992), and a high lignin content (Berg & Staaf, 1980, Taylor et al., 1989; Klemmedson, 1982). In contrast, red maple litter is quite labile, and one of the faster decomposing litter types in undisturbed Coweeta streams (Chung et al., 1993; Whiles et al., 1993). Shredder communities inhabiting streams draining pine catchments at Coweeta are apparently quite capable of exploiting low quality pine litter as a food and case making (trichopteran shredders) resource, as consistently faster rates of pine litter decomposition were obtained from pine streams. This is most likely a result of the relative scarcity of high quality litter resources in pine streams as compared to hardwood streams. Undisturbed headwater streams at Coweeta generally have plentiful accumulations of deciduous leaf detritus present year-round (Wallace et al., 1995), whereas little or none of this material is ever evident in pine streams at Coweeta (Whiles & Wallace, personal observation). Shredders which persist in streams draining pine watersheds

we examined at Coweeta apparently have few alternative resources, and must exploit pine litter, regardless of palatability or nutritional quality. During a previous study at Coweeta, faster decomposition rates of normally refractory litter types such as rhododendron were observed in a stream draining a clear-cut catchment, and this was attributed to lack of alternative resources for inhabitant shredders (Webster & Waide, 1982). Reduced availability of high quality detritus in pine streams must be further decreased by rapid shredder consumption of this scarce resource.

The ability of shredders to consume a variety of food resources has been demonstrated in numerous studies. Friberg & Jacobsen (1994) recently investigated feeding plasticity of two invertebrate shredders, and demonstrated the ability of both an amphipod and sericostomatid trichopteran shredder to feed on a variety of food types, including least preferred Sitka spruce needles. Their study also demonstrated that the food type most available in the streams where these shredders exist (conditioned *Fagus* leaves) was not preferred.

Results of this study differ from other recent investigations of riparian forest disturbance and stream processes. For example, Tuchman & King (1993) observed higher litter decomposition but lower shredder biomass in litterbags from Michigan headwater stream reaches bordered by agriculturally perturbed riparian zones, compared to reaches bordered by undisturbed forest. They attributed higher decomposition rates to discharge abrasion at agricultural sites, as discharge was higher and more variable at these sites and shredders were relatively scarce. In contrast, because of higher annual rainfall interception and higher dormant season transpiration, pine streams at Coweeta generally display lower discharge than those draining similar hardwood catchments (Swank et al., 1988). Of the three streams examined during our study which drain similar sized areas at Coweeta (P1, P17, H18), those draining pine catchments, where decomposition was faster, have lower average discharge (see Table 1). Therefore, unlike Tuchman & King (1993), results of this study cannot be attributed to differences in discharge, and shredders were well represented in litterbags from pine catchments. These observations suggest somewhat similar disturbances (alteration of riparian zones) may differentially influence different stream systems. Disturbance associated with conversion to pine monoculture at Coweeta has not decimated aquatic invertebrates, but resulted in taxonomic changes in the shredder community.

Differences in detritus resources in pine and hardwood streams at Coweeta are undoubtedly a major factor influencing differences in shredder communities. In turn, differences in shredder communities appear to be the primary mechanism behind differences in decomposition rates. Although temperature differences have recently been implicated as a mechanism for variation in litter processing rates (Boulton & Boone, 1991), warmer temperatures are generally associated with higher processing rates (e.g. Short & Smith, 1989). The pine stream we monitored temperature in (P1) had a lower average annual temperature and accumulated fewer degree days than the adjacent hardwood stream (P55) (see Table 1). Thus, if temperature differences were taken into account, decomposition rates in pine streams would be even faster than those in hardwood streams.

Physical habitat differences resulting from past and present management practices may also be influencing invertebrate communities and ecosystem processes in pine streams at Coweeta. Original logging and removal of hardwoods took place in catchments P1 and P17 ca. 35 years ago, and many major direct effects on the physical environments associated with logging activities (e.g. open canopy and massive sedimentation) are no longer evident. Although others have attributed absence or low abundance of invertebrate species in streams draining conifer plantations to water chemistry and structural habitat differences from native forest streams (Ormerod et al., 1990; Ormerod et al., 1993; Weatherley et al., 1993), water chemistry differences between pine and hardwood streams at Coweeta are minimal (Woodall & Wallace, 1972; Swank & Crossley, 1988). However, some physical habitat differences between pine and hardwood streams examined during this study are evident. The general lack of an understory in both pine catchments may result in higher sediment inputs and habitat differences compared to streams draining undisturbed catchments with lush understory growth. In particular, P1 substrate composition is skewed toward smaller particle sizes (see Table 1), and large expanses of silt overlying coarser substrates are present in this stream. Higher sedimentation in pine streams may result in altered habitat availability and burial of organic materials, further reducing available detritus. Additionally, because catchment P1 was burned prior to planting in pine, coarse woody debris on the forest floor of this catchment is relatively scarce (Whiles & Wallace, personal observation). Lack of woody debris may contribute to sedimentation of streams draining pine catchments and reduced

stream habitat heterogeneity, as woody debris has been shown to influence sediment dynamics and habitat heterogeneity in both forests (Harmon et al., 1986) and streams (Harmon et al., 1986; Golladay et al., 1987; Wallace et al., 1996).

Interestingly, results of the 1992 benthic analysis of P1 and H55 rock outcrop and mixed substrate invertebrate communities closely agree with those of a previous study examining the effects of clear cutting on stream invertebrate communities at Coweeta. Gurtz & Wallace (1984) observed less negative impact on bedrock outcrop invertebrate communities than mixed substrate communities during massive sedimentation of a stream following catchment logging. Similarly, differences in benthic invertebrate abundances between P1 and H55 were evident in mixed substrate habitats, but not more physically stable, high gradient rock outcrops. Collector-filterers and scrapers, which both prefer bedrock outcrop habitats, were the only two functional groups displaying higher abundances and biomass in P1 compared to H55. Thus, Gurtz & Wallace's observations on the relationship between physical and biological stability may apply to P1 35 years after cessation of logging activities.

Although long-term alteration of riparian vegetation is certainly a chronic landscape-level disturbance, differences in invertebrate communities observed during this study were surprisingly subtle. However, an important consideration is the close proximity (e.g. <300 m) of undisturbed hardwood catchments to pine streams examined during this study. Both pine catchments examined during this study are surrounded by relatively undisturbed hardwood catchments which may serve as invertebrate source areas for pine streams. Future studies which examine growth rates, survivorship, and fecundity of invertebrate communities in streams draining pine plantations may reveal if these systems represent 'sinks' supplemented by nearby undisturbed source areas.

Our results suggest that pine streams at Coweeta appear to support a reasonably abundant and viable shredder community, with the relative proportions of trichopteran and plecopteran shredders as the major difference compared to undisturbed catchments. However, these seemingly subtle differences in shredder communities have an obvious and significant impact on ecosystem-level processes such as decomposition dynamics. Thus, although this landscape-level disturbance appears to have a relatively subtle influence on stream dwelling invertebrate communities, vital ecosystem-level processes associated with organic matter dynamics and energy flow have been significantly influenced.

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References

Anderson, N. H. & J. R. Sedell, 1979. Detritus processing by macroinvertebrates in stream ecosystems. Ann. Rev. Ent. 24: 351–377.

Barrett, J. W. (ed.), 1994. Regional silviculture of the United States. John Wiley & Sons, New York.

Benke, A. C., 1979. A modification of the Hynes method for estimating secondary production with particular significance for multivoltine populations. Limnol. Oceanogr. 24: 168–174.

Blair, J. M., R. W. Parmalee & R. L. Wyman, 1994. A comparison of the forest floor invertebrate communities of four forest types in the northeastern U.S. Pedobiologia 38: 146–160.

Boulton, A. J. & P. I. Boone, 1991. A review of methodology used to measure leaf litter decomposition in lotic environments: time to turn over a new leaf? Aust. J. mar. Freshwat. Res. 42: 1–43.

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

Cummins, K. W., J. R. Sedell, F. J. Swanson, G. W. Minshall, S. G. Fisher, C. E. Cushing, R. C. Peterson & R. L. Vannote, 1983. Organic matter budgets for stream ecosystems: problems with their evaluation, In Barnes, J. R. & G. W. Minshall (eds), Stream Ecology: Application and Testing of General Ecological Theory. Plenum Press, New York: 299–353.

DeLong, M. D. & M. A. Brusven, 1994. Allochthonous input of organic material from different riparian habitats of an agriculturally impacted stream. Envir. Mgmt 18: 59–71.

Dobson, M. & A. G. Hildrew, 1992. A test of resource limitation among shredding detritivores in low order streams in England. J. anim. Ecol. 61: 69–77.

Egglishaw, H. J. & D. W. Mackay, 1967. A survey of the bottom fauna of streams in the scottish highlands. Part III: Seasonal changes in the fauna of the three streams. Hydrobiologia 30: 305–334.

Fisher, S. G. & G. E. Likens, 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecol. Monogr. 43: 421–439.

Friberg, N. & D. Jacobsen, 1994. Feeding plasticity of two detritivore-shredders. Freshwat. Biol. 32: 133–142.

Gee, J. H. R., 1988. Population dyamics and morphometrics of *Gammarus pulex* L.: evidence of seasonal food limitation in a freshwater detritivore. Freshwat. Biol. 19: 333–343.

Golladay, S. W., J. R. Webster & E. F. Benfield, 1987. Changes in stream morphology and storm transport of seston following watershed disturbance. J. North am. Benthol. Soc. 6: 1–11.

Grafius, E. & N. H. Anderson, 1979. Population dynamics, bioenergetics, and the role of *Lepidostoma quercina* Ross (Trichoptera:

Lepidostomatidae) in an Oregon Woodland stream. Ecology 60: 433–441.

Grafius, E. & N. H. Anderson, 1980. Population dynamics and the role of two species of *Lepidostoma* (Trichoptera: Lepidostomatidae) in an Oregon coniferous forest stream. Ecology 61: 808–816.

Gurtz, M. E. & J. B. Wallace, 1984. Substrate-mediated response of stream invertebrates to disturbance. Ecology 65: 1556–1569.

Hamilton, A. L., 1969. On estimating annual production. Limnol. Oceanogr. 14: 771–782.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack, Jr & K. W. Cummins, 1986. Ecology of coarse woody debris in temperate systems. In McFadyen, A. & E. D. Ford, (eds), Advances in Ecological Research. Volume 15. Academic Press, New York: 133–302.

Huryn, A. D., 1986. Secondary production of the macroinvertebrate community of a high-elevation stream in the southern Appalcahian Mountains. Ph.D. thesis. University of Georgia, Athens, Georgia, U.S.A.

Huryn, A. D. & J. B. Wallace, 1987. Production and litter processing by crayfish in an Appalchian Mountain stream. Ecology 68: 1932–1942.

Hynes, H. B. N., 1975. The stream and its valley. Verh. Int. Ver. Theor. Angew. Limnol. 19: 1–15.

Klemmedson, J. O., 1992. Decomposition and nutrient release from mixtures of Gambel Oak and Pondersoa Pine leaf litter. Forest Ecol. Mgmt 47: 349–361.

Krueger, C. C. & F. B. Martin, 1980. Computation of confidence intervals for the size-frequency (Hynes) methodof estimating secondary production. Limnol. Oceanogr. 25: 773–777.

Lugthart, G. J. & J. B. Wallace, 1992. Effects of disturbance on benthic functional structure and production in mountain streams. J. North am. Benthol. Soc. 11: 138–164.

Merritt, R. W. & K. W. Cummins (eds), 1984. An introduction to the aquatic insects of North America, 2nd edn. Kendall/Hunt, Dubuque, Iowa.

Molles, M. C. Jr, 1982. Trichopteran communities of streams associated with aspen and conifer forests: long-term structural change. Ecology 63: 1–6.

Mulholland, P. J., J. W. Elwood, J. D. Newbold & L. A. Ferren, 1985. Effect of a leaf-shredding invertebrate on organic matter dynamics and phosphorus spiralling in heterotrophic laboratory streams. Oecologia 66: 199–206.

Naiman, R. J. & J. R. Sedell, 1979. Characterization of some particulate organic matter transported by some Cascade Mountain streams. J. Fish. Res. Bd Can. 36: 17–31.

Ormerod, S. J., S. D. Rundle, E. C. Lloyd & A. A. Douglas, 1993. The influence of riparian management on the habitat structure and macroinvertebrate communities of upland streams draining plantation forests. J. appl. Ecol. 30: 13–24.

Ormerod, S. J., N. S. Weatherly & W. J. Merrett, 1990. The influence of conifer plantations on the distribution of the golden ringed dragonfly *Cordulegaster boltoni* (Odonata) in upland Wales. Biol. Conserv. 53: 241–251.

Otto, C., 1974. Growth and energetics in a larval population of *Potomophylax cingulatus* (Steph.) (Trichoptera) in a south Swedish stream. J. anim. Ecol. 43: 339–361.

Short, R. A. & P. E. Maslin, 1977. Processing of stream litter by a detritivore: effect on nutrient availability to collectors. Ecology 58: 935–938.

Short, R. A. & S. L. Smith, 1989. Seasonal comparison of leaf processing in a Texas stream. Am. Midl. Nat. 121: 219–224.

Smock, L. A., 1980. Relationships between body size and biomass of aquatic insects. Freshwat. Biol. 10: 375–383.

Stewart, K. W. & B. P. Stark, 1988. Nymphs of North American stonefly genera. The Thomas Say Foundation. Ent. Soc. Am. 460 pp.

Swank, W. T. & D. A. Crossley, Jr. (eds), 1988. Forest Hydrology and Ecology at Coweeta. Springer Verlag, New York: 469 pp.

Swank, W. T., L. W. Swift, jr. & J. E. Douglas, 1988. Streamflow changes associated with forest cutting, species conversions, and natural disturbances. In Swank, W. T. & D. A. Crossley, Jr (eds), Forest Hydrology and Ecology at Coweeta. Springer Verlag, New York: 469 pp.

Sweeney, B. W., 1993. Effects of streamside vegetation on macroinvertebrate communities of white clay creek in eastern North America. Proc. Acad. nat. Sci. Philad. 144: 291–340.

Sweeney, B. W. & R. L. Vannote, 1986. Growth and production of a stream stonefly: influence of diet and temperature. Ecology 67: 1396–1410.

Taylor, B. R., D. Parkinson & W. F. J. Parsons, 1989. Nitrogen and lignin content as predictors of litter decay rates: a microcosm test. Ecology 70: 97–104.

Tuchman, N. C. & R. H. King, 1993. Changes in mechanisms of summer detritus processing between wooded and agricultural sites in a Michigan headwater stream. Hydrobiologia 268: 115–127.

Wallace, J. B. & A. C. Benke, 1984. Quantification of wod habitat in subtropical coastal plain streams. Can. J. Fish. aquat. Sci. 41: 1643–1652.

Wallace, J. B., J. W. Grubaugh & M. R. Whiles, 1996. The influence of coarse woody on stream habitats and invertebrate biodiversity. In McMinn, J. W. & D. A. Crossley, Jr (eds), Biodiversity and Coarse Woody Debris in Southern Forests. Gen. Tech. Report SE-94. Asheville, NC: U.S. Department of Agriculture, Forest Service, Southeastern Forest Experiment Station.

Wallace, J. B., D. H. Ross & J. L. Meyer, 1982. Seston and dissolved organic carbon dynamics in a southern Appalachian stream. Ecology 63: 824–838.

Wallace, J. B., M. R. Whiles, S. Eggert, T. F. Cuffney, G. J. Lugthart & K. Chung, 1995. Long-term dynamics of coarse particulate organic matter in three small Appalachian Mountain streams. J. North am. Benth. Soc. 14: 217–232.

Waters, T. F., 1969. Subsampler for dividing large samples of stream invertebrate drift. Limnol. Oceanogr. 14: 813–815.

Weatherley, N. S., E. C. Lloyd, S. D. Trundle & S. J. Ormerod, 1993. Management of conifer plantations for the conservation of stream macroinvertebrates. Biol. Conserv. 63: 171–176.

Webster, J. R. & J. B. Waide, 1982. Effects of forest clearcutting on leaf breakdown in a sothern Appalachian stream. Freshwat. Biol. 12: 331–344.

Whiles, M. R. & J. B. Wallace, 1995. Macroinvertebrate production in a headwater stream during recovery from anthropogenic disturbance and hydrologic extremes. Can. J. Fish. aquat. Sci. 52: 2402–2422.

Whiles, M. R., J. B. Wallace & K. Chung, 1993. The influence of Lepidostoma (Trichoptera: Lepidostomatidae) on recovery of leaf-litter processing in disturbed headwater streams. Am. Midl. Nat. 130: 356–363.

Woodall, W. R. & J. B. Wallace, 1972. The benthic fauna in four small southern Appalachian streams. Am. Midl. Nat. 88: 393–407.

Zar, J. H., 1984. Biostatistical Analysis. 2nd edn. Prentice-Hall, Englewood Cliffs, New Jersey.

Appendix 1. Average abundance (no./litterbag) and biomass (mg/litterbag) (± standard error) of individual shredder taxa in maple and pine bags placed in catchments P1 (pine catchment, n=16 maple bags and 20 pine bags) and H55 (hardwood catchment, n=16 maple bags and 20 pine bags) during 1992, and P17 (pine catchment, n=8 maple bags and 8 pine bags) and H18 (hardwood catchment, n=8 maple bags and 8 pine bags) during 1994. Values for each taxonomic group with different superscript letters are significantly different ($p<0.05$, Kruskal-Wallis ANOVA on ranks and Dunn's test).

Shredder taxon	Maple bags		Pine bags	
	Pine Catchments	Hardwood Catchments	Pine Catchments	Hardwood Catchments
1992 study				
Abundance				
Fattigia pele	2.4 (0.7)^{a}	0.8 (0.5)^{b}	1.7 (0.7)^{ab}	0.2 (0.1)^{b}
Lepidostoma spp.	23.7 (4.8)^{a}	9.9 (2.7)^{b}	25.8 (4.7)^{a}	7.3 (2.4)^{b}
Pycnopsyche spp.	2.5 (0.8)^{a}	0.9 (0.3)^{ab}	1.1 (0.2)^{ab}	0.6 (0.2)^{b}
Leuctra spp.	70.9 (19.8)^{a}	82.7 (22.7)^{a}	129.7 (33.2)^{a}	77.8 (17.2)^{a}
Tallaperla sp.	2.3 (0.7)^{a}	21.6 (5.7)^{b}	5.0 (2.5)^{a}	13.5 (4.8)^{ab}
Tipula spp.	2.4 (1.2)^{a}	1.0 (0.4)^{a}	0.7 (0.3)^{a}	0.3 (0.1)^{a}
Biomass				
Fattigia pele	2.8 (1.1)^{a}	0.7 (0.5)^{bc}	2.3 (0.7)^{ab}	0.2 (0.2)^{c}
Lepidostoma spp.	3.5 (0.9)^{a}	0.4 (0.1)^{bc}	3.9 (1.3)^{ab}	0.7 (0.3)^{c}
Pycnopsyche spp.	16.9 (5.7)^{a}	6.5 (3.1)^{ab}	6.4 (2.7)^{ab}	2.3 (1.3)^{b}
Leuctra spp.	4.2 (1.6)^{a}	5.8 (1.7)^{a}	6.8 (2.4)^{a}	3.6 (1.1)^{a}
Tallaperla sp.	8.1 (2.6)^{a}	21.1 (5.6)^{b}	4.3 (2.3)^{a}	3.0 (0.8)^{a}
Tipula spp.	8.7 (4.9)^{a}	2.4 (1.0)^{a}	1.7 (0.8)^{a}	2.4 (1.2)^{a}
1994 Study				
Abundance				
Fattigia pele	2.1 (1.0)^{a}	0.1 (0.1)^{a}	0.8 (0.3)^{a}	0.1 (0.1)^{a}
Lepidostoma spp.	18.0 (6.7)^{a}	2.3 (0.9)^{b}	23.5 (5.2)^{a}	2.1 (0.8)^{b}
Pycnopsyche spp.	5.9 (2.3)^{a}	3.3 (0.5)^{a}	2.9 (0.9)^{a}	1.3 (0.4)^{a}
Leuctra spp.	74.4 (31.6)^{a}	16.1 (8.8)^{a}	19.1 (11.1)^{a}	12.4 (4.9)^{a}
Tallaperla sp.	6.4 (2.6)^{a}	20.6 (3.2)^{b}	7.6 (2.0)^{ab}	22.5 (7.5)^{b}
Tipula spp.	0.0 (0.0)^{a}	0.0 (0.0)^{a}	0.1 (0.1)^{a}	0.1 (0.1)^{a}
Biomass				
Fattigia pele	2.8 (1.6)^{a}	0.7 (0.7)^{a}	0.8 (0.7)^{a}	1.0 (1.0)^{a}
Lepidostoma spp.	0.5 (0.2)^{a}	0.0 (0.0)^{b}	0.7 (0.2)^{a}	0.3 (0.2)^{ab}
Pycnopsyche spp.	4.7 (3.2)^{a}	7.1 (2.5)^{a}	6.5 (5.5)^{a}	1.5 (0.6)^{a}
Leuctra spp.	1.6 (0.7)^{a}	0.5 (0.4)^{a}	0.4 (0.2)^{a}	0.3 (0.1)^{a}
Tallaperla sp.	10.5 (5.2)^{ab}	18.0 (5.2)^{b}	5.0 (2.6)^{ab}	1.5 (0.5)^{a}
Tipula spp.	0.0 (0.0)^{a}	0.0 (0.0)^{a}	2.5 (2.5)^{a}	0.3 (0.3)^{a}