J. N. Am. Benthol. Soc., 1993, 12(4):394-405

Microbial respiration on decaying leaves and sticks in a southern Appalachian stream

JENNIFER L. TANK, J. R. WEBSTER, AND E. F. BENFIELD

Department of Biology, Virginia Polytechnic Institute & State University, Blacksburg, Virginia 24061 USA

Abstract. Microbial respiration on sticks and leaves, measured as rate of oxygen uptake, was compared among four sites (2nd-4th order) along Ball Creek/Coweeta Creek, Coweeta Hydrologic Laboratory, North Carolina. Senescent rhododendron and birch leaves were placed in the stream at each site on 21 October 1990. Microbial oxygen uptake rates were measured for both leaf species beginning 15 December 1990 and continuing monthly until leaves were no longer intact (birch—2 mo, rhododendron—7 mo). Oxygen uptake rates also were measured monthly for 1 yr on sticks (1-3 cm diameter) collected from the stream at each site. Oxygen uptake rates (mg O_2/hr) were calculated on the basis of surface area and ash-free dry mass (AFDM). Mean respiration rates per unit surface area of substrate were highest for sticks, followed by rhododendron, then birch, indicating that substrate stability and persistence may affect microbial respiration in streams. When expressed on an AFDM basis, respiration rate was highest for birch, followed by rhododendron, then sticks. Respiration rates were significantly correlated with temperature for both rhododendron leaves and sticks on both an AFDM and surface area basis. Respiration rates on rhododendron also increased with exposure time. Rhododendron leaves represent a long-lasting leaf source for microbial activity in streams. Differences in respiration rates among sites, for both rhododendron leaves and sticks, can be explained primarily by differences in water temperature. The high respiration rate per unit surface area on sticks suggested that small woody debris can play a significant role as a substrate for microbial metabolism.

Key words: microbial respiration, decomposition, leaves, wood, stream.

Forested headwater streams are heavily shaded and depend primarily on riparian organic matter inputs to fuel stream processes (Fisher and Likens 1972, Minshall et al. 1983). Leaves and wood are the major energy inputs to forested headwater streams and are broken down by both abiotic (leaching and physical fragmentation) and biotic processes (microbial and macroinvertebrate consumption). Microorganisms mediate the biotic component of organic matter processing through metabolism, and their presence may increase the palatability and nutritional quality of the substrate as a food source for macroinvertebrates (Cummins 1974). Initial stages of microbial colonization of organic matter usually are dominated by fungi, primarily aquatic hyphomycetes (Bärlocher and Kendrick 1974, Suberkropp and Klug 1976). As fragmentation occurs, fungal biomass typically declines (Suberkropp and Klug 1981), and bacterial numbers increase during the later stages of decay (Suberkropp and Klug 1976).

In our study, microbial respiration on leaves and sticks was examined at four sites along a mountain stream. Stream size, stream temperature, and discharge usually increase downstream, whereas organic matter retention decreases (Vannote et al. 1980). Higher temperatures increase rates of organic matter breakdown by increasing microbial metabolism (Petersen and Cummins 1974, Suberkropp and Klug 1974), and respiration rates were found to increase with temperature by McIntire and Phinney (1965) and Cuffney et al. (1990). Naiman (1983) reported that respiration on coarse particulate organic matter (CPOM) expressed on an ash-free dry mass (AFDM) basis in 1st- to 3rd-order streams in Oregon was best predicted by temperature. Bott et al. (1985) also found that differences in respiration rates among Michigan and Pennsylvania streams were best explained by temperature. In contrast, some other studies showed that respiration per gram of organic matter did not change with increasing stream size (Naiman and Sedell 1980, Minshall et al. 1983, Naiman 1983).

The studies referred to above focused primarily on fine particulate organic matter (FPOM) and leaves, even though woody debris can also be abundant in forested headwater streams (e.g.,

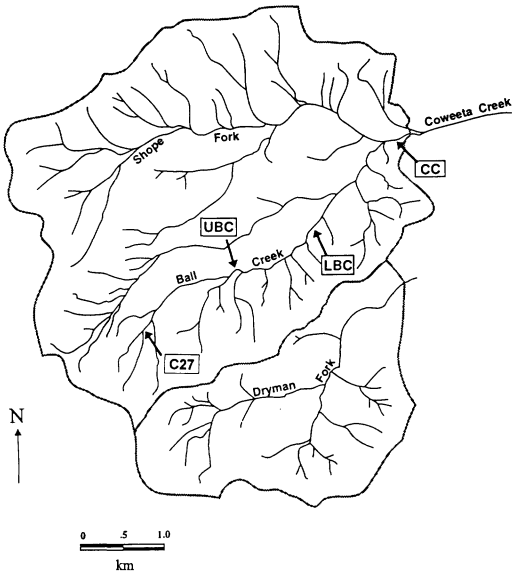

FIG. 1. Basin study sites located at Coweeta Hydrologic Laboratory, Macon Co., North Carolina. Four sites (marked by arrows) were: Catchment 27 (C27), Upper Ball Creek (UBC), Lower Ball Creek (LBC), and Coweeta Creek (CC).

Triska and Cromack 1980). Because wood decomposes much more slowly than leaves, studies of energy dynamics in streams have generally ignored the importance of wood in carbon cycling (Triska and Cromack 1980), even though microbial colonization of wood may be extensive in streams (Aumen et al. 1983, Aumen et al. 1990).

In this study, we ask whether microbial respiration on organic substrata changes along a stream-size gradient. Respiration rates were measured in situ over the course of a year at four sites (2nd–4th order) at elevations of 1070 to 625 m. Substrata representing three kinds of organic matter available to microbial colonists were used: rapidly decomposing leaves (birch); slowly decomposing leaves (rhododendron); and sticks (a highly refractory substrate). Respiration-rate estimates were then extrapolated to stream area so that ecosystem-level patterns of respiration could be compared among sites.

Study Site

The stream was at Coweeta Hydrologic Laboratory (Macon County, North Carolina, USA) in the eastern part of the southern Appalachian Mountains. The climate is wet and mild with most precipitation in the form of low intensity rainfall (Swank and Crossley 1988). The forest is dominated by oaks (*Quercus* spp.), red maple (*Acer rubrum*), tulip poplar (*Liriodendron tulipifera*), dogwood (*Cornus florida*), and rhododendron (*Rhododendron maximum*) (Swank and Crossley 1988).

Four 100-m reaches were chosen along Ball Creek near the base of Catchment 27 (C27), a 2nd-order stream, to Coweeta Creek (CC), a 4th-order stream formed by the confluence of Ball Creek and Shope Fork (Fig. 1). Upper Ball Creek (UBC) and Lower Ball Creek (LBC) were the mid-elevational sites. Altitude ranged from 1070 m at C27 to 675 m at CC. Stream gradient, width, canopy condition, substratum composition, and mean annual discharge are shown in Table 1.

TABLE 1. Characteristics of study sites along Ball Creek–Coweeta Creek.

	C27	UBC	LBC	CC
Stream order	2	3	3	4
Elevation (m)	1070	922	721	675
Distance from source (m)	950	2600	3850	5550
Gradient (m/m)	0.16	0.17	0.04	0.02
Width (m)	2–5	3–5	4–5	7–8
Canopy	heavy shade	heavy shade	medium shade	partially open canopy
Substratum	cobble, boulder	variable bedrock to sand	mostly large cobble	mostly large cobble
Mean annual discharge (L/s)[a]	20.5	96.8	148.8	590.4
Drainage area (ha)	38.8	206.8	380.5	1561.6

[a] Calculated from Coweeta Hydrologic Laboratory Forest Service data.

Methods

Microbial respiration rates, as indicated by oxygen uptake, were measured monthly at each of the four sites. Respiration rates were determined on two leaf types, sweet birch (*Betula lenta*) and rhododendron (*Rhododendron maximum*), and sticks taken from the stream. Rhododendron and birch leaves were collected just prior to abscission in autumn 1990, air dried, and placed by species into litter bags (5 mm mesh size). Bags were placed in a random array on the stream bed in riffle areas at each of the four sites on 27 October 1990. Microbial respiration was measured monthly starting December 1990 using leaves from randomly selected bags and continued until no intact leaf material remained (2 mo for birch, 7 mo for rhododendron). Microbial respiration also was measured monthly for one year on randomly collected decomposing sticks (1–3 cm diameter) taken from the stream at each site. Sticks decay slowly and have a long residence time in Coweeta streams (Golladay and Webster 1988). Thus it was not practical to introduce fresh sticks and wait for them to attain a state of decomposition comparable to that of most sticks in the stream. Leaves and sticks were incubated at each site except in December, January, and February, when temperature differences among sites were very small (no measurable difference) and all collections were incubated at Upper Ball Creek.

After invertebrates and excess silt had been removed, leaves (removed from bags) or sticks were placed in respiration chambers containing stream water, and oxygen change was measured over a 3–5-h period. Respiration chambers were constructed from opaque PVC pipe (23 cm diameter, 30.5 cm length, 1.6 L volume) equipped with recirculating pumps and YSI Model 5739 polarigraphic oxygen probes. Dissolved oxygen probes were connected to a multi-channel signal conditioner that determined oxygen concentration (Tank and Musson 1993). Six respiration chambers of replicate samples were run simultaneously for each incubation, and the data were recorded on a Campbell 21x datalogger. A chamber containing stream water only was included with each incubation to determine whether the probe consumed significant amounts of oxygen or if water column respiration was appreciable. Dissolved oxygen concentration decreased linearly over the incubation, and the rate of oxygen consumption was therefore determined as the change in oxygen concentration (mg/L) over time (min).

Water temperature was recorded during incubations with a Radio Shack thermistor connected to the datalogger. In addition, stream temperature was recorded every 2 h from December 1990 to December 1991 at the two middle elevation sites, UBC and LBC, using Ryan recording thermographs (J. B. Wallace, University of Georgia, unpublished data). At C27 and CC, thermographs were operating from June 1990 to December 1991. Missing temperature data were estimated by regressing available temperature data for C27 against UBC data and CC against LBC data ($r^2 = 0.99$ for both).

After each incubation, a penetrometer was used to estimate leaf softness (Feeney 1970, Suberkropp and Klug 1981) by determining the weight needed to push a 5 mm diameter rod through the leaf matrix. Eight measurements were made for each leaf sample incubated. Total leaf surface area (m^2) was measured on photocopies of leaves using a digitizer. Stick surface area was estimated from length and diameter measurements. Sticks were assumed to be cylindrical and leaves to be two-dimensionally smooth, thereby underestimating true surface area. All organic material from each chamber was oven dried (48 h for leaves, 1 wk for sticks) at 50°C and weighed. Leaf and stick samples were then ground, and subsamples were weighed and ashed for 35 min at 550°C. The ash was re-wetted, dried at 50°C, and re-weighed. AFDM was calculated as oven dry weight minus ash weight for each chamber. Respiration rates per chamber were expressed on an AFDM and surface area basis. In addition, standing stocks of benthic CPOM (leaves) and wood (small sticks >1 cm and <3 cm in diameter) were estimated for each of the four sites, on seven occasions, from April 1991 to July 1992 (E. F. Benfield, J. R. Webster, J. J. Hutchens, and J. L. Tank, Virginia Polytechnic Institute and State University, unpublished data).

Results

Comparison of respiration rates among substrate types

Mean respiration rates for each substrate are given in Table 2. Birch leaves were skeletonized after 77 d incubation so only two

TABLE 2. Mean (±1 SD) respiration rates for each organic matter type. Respiration is expressed per unit surface area and per g AFDM.

Substrate		mg O_2 m^{-2} h^{-1}	mg O_2 g $AFDM^{-1}$ h^{-1}
Birch (2 mo)[a]	C27	1.48 (0.35)	0.14 (0.03)
	UBC	1.01 (0.10)	0.10 (0.02)
	LBC	1.31 (0.02)	0.13 (0.01)
	CC	1.04 (0.11)	0.10 (0.02)
	Mean[d]	1.23 (0.26)	0.12 (0.02)
Rhododendron (7 mo)[b]	C27	4.44 (1.30)	0.08 (0.03)
	UBC	3.58 (0.99)	0.07 (0.03)
	LBC	5.06 (1.29)	0.10 (0.04)
	CC	4.64 (1.23)	0.10 (0.03)
	Mean[d]	4.42 (1.30)	0.09 (0.03)
Sticks (12 mo)[c]	C27	11.84 (4.61)	0.01 (0.006)
	UBC	11.47 (5.13)	0.01 (0.005)
	LBC	11.09 (3.62)	0.01 (0.004)
	CC	15.58 (6.66)	0.02 (0.007)
	Mean[d]	12.52 (5.36)	0.01 (0.006)

[a] Incubation temperature range = 6.6–9.9°C.
[b] Incubation temperature range = 4.6–16.7°C.
[c] Incubation temperature range = 4.6–18.4°C.
[d] Mean is based on all samples for that substrate type (birch: $n = 11$, rhododendron: $n = 66$, sticks: $n = 97$).

monthly measurements could be made. The range in birch respiration rates was 0.95–1.83 mg O_2 m^{-2} h^{-1} when expressed per unit surface area and 0.08–0.17 mg O_2 g $AFDM^{-1}$ h^{-1} when expressed per g AFDM. Rhododendron leaves were incubated in the stream for 243 d (7 monthly incubations) before fragmentation made it impossible to measure respiration. Ranges in respiration rates for rhododendron were 1.87–6.84 mg O_2 m^{-2} h^{-1}, or 0.03–0.16 mg O_2 g $AFDM^{-1}$ h^{-1}. Respiration rates for sticks taken from the streams each month for a year had a range of 2.93–28.91 mg O_2 m^{-2} h^{-1}, or 0.01–0.03 mg O_2 g $AFDM^{-1}$ h^{-1}.

When microbial respiration was expressed on the basis of AFDM, both leaf types showed respiration rates of about 0.1 mg O_2 g h^{-1}. However, when expressed on a surface-area basis, microbial respiration rates for rhododendron were 2–5× higher than those for birch leaves. In general, respiration expressed per unit surface area varied over a larger range for all organic matter types than did respiration per AFDM. Mean microbial respiration rates for sticks per unit surface area were 10× greater than those for birch leaves and 3× greater than rhododendron (Fig. 2). When expressed on an AFDM basis, the trend was reversed; birch leaves had highest respiration, followed by rhododendron, then sticks (Fig. 2).

Mean respiration rates indicated differences among birch, rhododendron, and sticks, but it is important to note that mean incubation temperatures were different for each substrate type. Birch leaves were measured only in midwinter (mean incubation temperature = 9.2°C); rhododendron leaves were measured in winter, spring, and early summer (mean incubation temperature = 10.9°C); and sticks were measured monthly for a year (mean incubation temperature = 12.5°C). Incubation temperatures de-

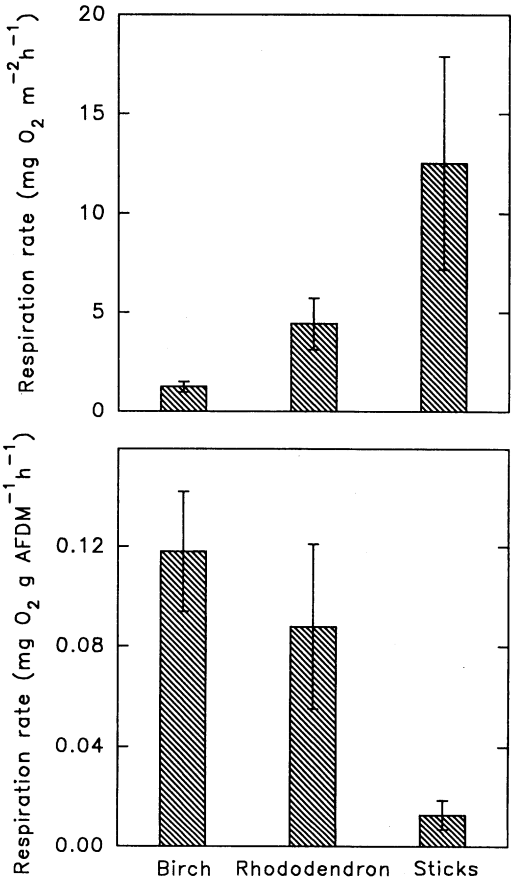

FIG. 2. Mean (±1 SD) respiration rate per unit surface area (upper) and per g AFDM (lower). Means from each substrate type were significantly different ($p < 0.05$).

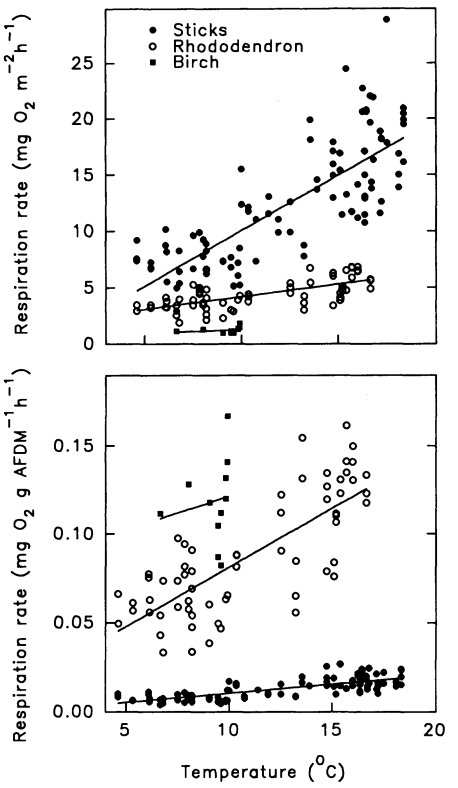

FIG. 3. Respiration per unit surface area vs. incubation temperature (upper), and respiration per g AFDM vs. incubation temperature (lower) plotted for each substrate type. Each point represents a separate chamber incubation.

pend on the duration and timing of decomposition and are therefore ecologically realistic. Analysis of covariance (ANCOVA) followed by comparisons of least squares means (LSM, SAS Institute 1991) showed that mean respiration per AFDM and per unit surface area of birch, rhododendron, and sticks were significantly different ($p < 0.05$) when temperature was included as a covariate in the analysis.

Effect of temperature on microbial respiration

Analysis of the continuous temperature data showed that mean daily stream temperatures were significantly different along the elevational gradient: 10.9°C at C27; 11.2°C at UBC; 11.5°C at LBC; and 11.9°C at CC (Duncan's multiple range test, $p < 0.0001$). Highest temperatures occurred in July, whereas lowest temperatures were recorded in February. However, temperatures measured only during incubations showed minimal site differences. C27, at the highest elevation, had a significantly lower mean incubation temperature for the 12 mo of data collection (11.7°C) than the other three sites, which all had mean incubation temperatures around 12.5°C (ANOVA, LSM, $p < 0.0001$).

Microbial respiration increased with increasing incubation temperature for both birch and rhododendron leaves as well as for sticks. Regressions of respiration per unit surface area (m^2) against temperature for sticks ($r^2 = 0.62$, $n = 98$, $p < 0.01$) and rhododendron leaves ($r^2 = 0.43$, $n = 63$, $p < 0.01$) were significantly different from zero (Fig. 3). The regression for birch leaves was not significant, but the temperature range over which birch leaves were incubated was very small. Regressions of microbial respiration per AFDM against temperature were significant for rhododendron leaves ($r^2 = 0.59$, $n = 63$, $p < 0.01$) and sticks ($r^2 = 0.59$, $n = 98$, $p < 0.01$), but were not significant for birch (Fig. 3). Slopes of the relationships between respiration rate and temperature were different between rhododendron leaves and sticks whether expressed on a surface-area or AFDM basis (ANCOVA, $p < 0.0001$) (Fig. 3).

Effect of exposure time on rhododendron microbial respiration

Microbial respiration rates for rhododendron increased with stream exposure time when expressed per unit surface area and per AFDM (Fig. 4). These regressions were significantly different from zero per unit surface area ($r^2 = 0.39$, $n = 63$, $p < 0.01$) and per AFDM ($r^2 = 0.58$, $n = 63$, $p < 0.01$). Birch leaves decomposed quickly and trends in respiration were not statistically significant.

Softness of rhododendron leaves, as measured by decreasing resistance to penetrance (Fig. 5), increased with exposure time ($r^2 = 0.77$, $n = 63$, $p < 0.0001$). In addition, values for the coefficient of variation of penetrance increased with time in the stream ($r^2 = 0.43$, $n = 63$, $p < 0.01$), illustrating the patchy nature of decomposition on each leaf (Fig. 5).

Regressions of microbial respiration rates on rhododendron leaves (both per unit AFDM and surface area) vs. temperature, leaf exposure time, and penetrance were all significantly different from zero ($n = 63$, $p < 0.0001$). Respiration rates on rhododendron leaves expressed per unit surface area or AFDM were related most strongly

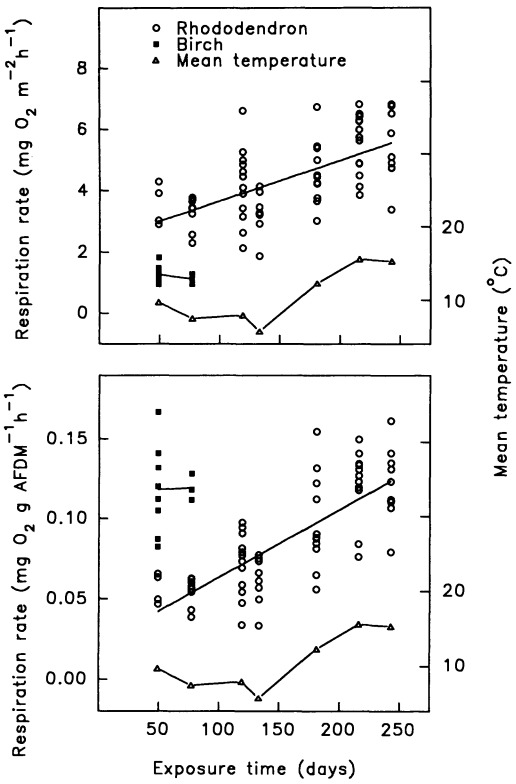

FIG. 4. Leaf respiration rate per unit surface area (upper), and respiration rate per g AFDM (lower) as a function of exposure time. Incubation temperature is also plotted on the y-axis for both graphs.

to temperature (r^2 = 0.43, r^2 = 0.59, respectively). The r^2 values for regressions of respiration per unit surface area and AFDM against exposure time were similar to those for temperature (r^2 = 0.39, r^2 = 0.58, respectively). Pearson correlation coefficients for temperature, exposure time, and penetrance demonstrated that all three variables were correlated ($p < 0.001$). Temperature and exposure time were most strongly correlated despite the fact that temperature was decreasing during the first four months of incubations ($R = 0.77$, $n = 75$).

Generally, respiration (per unit surface area and per AFDM) increased with incubation time, and over the entire exposure period (243 d) temperature accounted for most of the variability in respiration (ANOVA, $p < 0.05$). Stream temperature decreased before day 134 (i.e., during December–March); however, respiration rate continued to increase and regression analysis indicated that exposure time accounted for most of the variability in respiration rates for rhododendron (per AFDM). After day 134, temperature explained most of the variability in respiration rates (per AFDM and surface area).

Effect of site differences in microbial respiration rates on rhododendron leaves and sticks

Mean microbial respiration rates for leaves and sticks calculated for each site showed no general longitudinal trends (Table 2). However, rhododendron respiration per surface area at UBC was significantly lower than at all other sites (LSM following ANOVA, $p = 0.0064$) and respiration per AFDM at UBC was lower than at LBC and CC (LSM, $p < 0.01$). When temperature or exposure time was included in the analysis along with site, the statistical model was significant, and mean respiration rates (per surface area and AFDM) for UBC were again lower

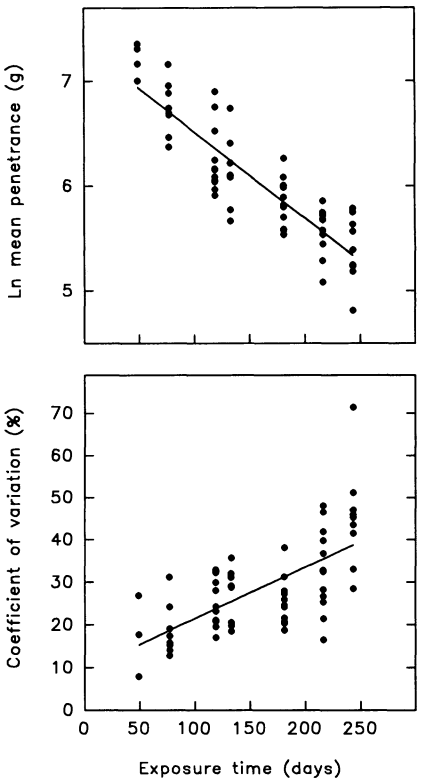

FIG. 5. Penetrance (upper) for rhododendron leaves as a function of exposure time. Penetrance is expressed as weight (g) required to penetrate the leaves. Ln of mean penetrance (from 8 leaves per chamber) is plotted against leaf exposure time. Variability in penetrance (lower) is plotted as a function of exposure time.

than at all other sites (LSM, $p < 0.0001$). When penetrance was included in the analysis of variance with site, respiration rates (per surface area and AFDM) at UBC were different only from LBC (LSM, $p < 0.001$).

Analysis of variance using site alone showed that stick respiration rates per unit surface area at CC were higher at all other sites (LSM, $p < 0.01$). When temperature was included in the analysis, both site and temperature had significant effects ($p < 0.0001$), and mean respiration at CC was higher than at all other sites (LSM, $p < 0.01$). When stick respiration was expressed per unit AFDM, analysis of variance showed that respiration rates at C27 were significantly different from those at UBC and LBC (LSM, $p < 0.05$). When temperature was included in the analysis, both site and temperature had significant effects ($p < 0.0001$); respiration at CC was different from that at LBC, and the rate at C27 was different from those at UBC and LBC (LSM, $p < 0.01$).

Annual standing stocks of leaves and sticks, calculated from weighted means from each of three habitat types, decreased with increasing stream size (except for sticks at UBC), and leaf biomass generally was higher than corresponding stick biomass (except at C27 where wood dominated annually) (Table 3A). Mean annual respiration rates for each site (mg O_2 g AFDM^{-1} h^{-1}) for sticks and rhododendron leaves were applied to annual standing stocks of leaves and sticks to obtain estimates of respiration rates per area of streambed at each site (Table 3B). Leaf respiration rates were probably underestimated because we used rates for rhododendron which decompose more slowly than other common leaves found at this site. In our study, respiration rates for leaves were 6–37× greater than for sticks. Wood standing stocks were highest at C27 (Table 3A) and therefore wood respiration contributed the most to total benthic respiration at this headwater site. Annually, sticks accounted for 56% of the standing stock and contributed 14% to total respiration of coarse benthic organic matter (CBOM).

Discussion

Petersen and Cummins (1974) described a processing continuum in which there is a hierarchy of leaf species ranked in order of decomposition rate in streams. Similarly, we might expect respiration rates to vary as a function of leaf type. Findlay et al. (1986) found that a rapidly decomposing leaf type (alligatorweed) had a greater rate of microbial respiration than did a more refractory leaf type (oak). Furthermore, leaves with different decay rates should theoretically harbor peak microbial biomass after different lengths of exposure in a stream (Findlay and Arsuffi 1989), a prediction supported by our results. Overall, mean respiration rate per unit AFDM was higher for birch leaves than for rhododendron leaves. The maximum respiration rate for birch measured during an incubation was very close to the rhododendron maximum (0.17 vs. 0.16 mg O_2 g AFDM^{-1} hr^{-1}), but the birch peak occurred much earlier than rhododendron and at a lower temperature.

Expressing respiration per unit AFDM is an inappropriate way to compare biological activity on organic matter with different densities and surface area : volume ratios. Respiration rates per unit AFDM on rhododendron and birch leaves were very similar even though respiration rates on birch leaves were only measured during December and January. In contrast, respiration rates expressed per unit surface area were higher for rhododendron than for birch. Rhododendron leaves are much thicker than birch leaves, and despite decomposing more slowly, they supported an active microbial community that may have been more active than that on birch as indicated by our respiration data. Rhododendron leaves may also have supported a higher density of fungal mycelia than did thinner leaves like birch, and therefore had higher respiration rates per unit surface area. High microbial activity on wood has been attributed to substrate stability and persistence (Aumen et al. 1990, Golladay and Sinsabaugh 1991), and perhaps this concept can also be applied to slow-decomposing leaf species such as rhododendron.

A positive relationship between respiration rate and stream exposure time was found for rhododendron but not for birch leaves, which decomposed very rapidly. Maximum respiration rates on birch leaves were recorded on day 50 and had generally decreased by day 77. Findlay and Arsuffi (1989) found that fungal hyphal biomass (82–96% of total microbial biomass) and spore production peaked on sycamore leaves within 30 d and that respiration rates tripled in 2 wk, before declining in the third week of

TABLE 3. Estimates of annual standing stocks and respiration of sticks and leaves at study sites along Ball Creek–Coweeta Creek. A. Standing stocks are expressed in g AFDM/m^2 streambed. Mean standing stocks are calculated as weighted means based on samples taken from each habitat type (cobble riffle, sandy reach, bedrock) at each site. Percentages of total standing stock of CBOM at each site are given in parentheses (E. F. Benfield, J. R. Webster, J. J. Hutchens, and J. L. Tank, Virginia Polytechnic Institute and State University, unpublished data). B. CBOM respiration is expressed in mg O_2 m^{-2} streambed h^{-1}. Values were calculated from standing stocks (g AFDM substrate/m^2 streambed) and mean annual rhododendron and stick respiration rates (mg O_2 g $AFDM^{-1}$ substrate h^{-1}) at each site (Table 2). Percentage of total CBOM respiration for each site is given in parentheses.

	C27	UBC	LBC	CC
A. Annual standing stocks				
Sticks	76.10 (56%)	5.96 (16%)	16.67 (38%)	9.63 (34%)
Leaves	58.85 (44%)	32.01 (84%)	27.34 (62%)	19.00 (66%)
B. CBOM respiration				
Sticks	0.76 (14%)	0.06 (3%)	0.17 (6%)	0.19 (9%)
Leaves	4.71 (86%)	2.24 (97%)	2.73 (94%)	1.90 (91%)

decomposition. In contrast, rhododendron leaves in our study showed no decline in respiration rate over 7 mo.

Hanson et al. (1984) found that a negative exponential model incorporating exposure time and accumulated temperature best described leaf decomposition rates. Similarly, we found some interaction between rhododendron respiration rate and both exposure time and temperature. Suberkropp and Klug (1981) found the density of aquatic hyphomycetes to be higher for leaves incubated at colder stream temperatures and that the fungi were therefore adapted for high growth in autumn when substrata became available. We observed microbial respiration rates to rise over time despite initially declining stream temperature. This apparently anomalous relationship may be attributed to hyphomycete activity.

Respiration on decomposing sticks found in the stream was higher (per unit surface area) than that of decomposing leaves (of known age and species). Stick respiration, when expressed on an AFDM basis, was much lower than respiration rates for the two leaf types, but reporting respiration on a mass basis underestimates microbial activity, which is often substantial and restricted to the outer surface of wood (Aumen et al. 1983, Petersen et al. 1989). When stick respiration was expressed per unit surface area, it was 10× higher than for birch and 3× higher than for rhododendron.

Sticks found in streams are often heavily grooved, providing a complex surface for colonization in contrast to the relatively smoother surface of leaves. Small woody debris (<10 cm diameter) has a high surface-to-volume ratio, decomposes more quickly than larger wood, and may contribute substantially to energy flow in woodland stream systems (Triska and Cromack 1980). As a microbial substrate, small woody debris can be thought of as an intermediate between large woody debris and leaf litter on a decomposition continuum (Triska and Cromack 1980). Organic surfaces, such as wood, are not just a surface for colonization (as in epilithic biofilms) but also provide a metabolic substrate (Golladay and Sinsabaugh 1991). Golladay and Sinsabaugh (1991) found that biofilm biomass was greater on white birch sticks than on leaves and attributed this to the greater physical stability of wood in terms of location and residence time in the stream. As new layers of wood are exposed at the surface, fresh substrate becomes available for microbial colonization. In addition, hyphae and/or bacteria may penetrate further into wood than leaves as a result of grooves. The high respiration rates (per unit surface area) measured on sticks in this study suggest the presence of a well developed microbial community on small woody debris in Coweeta streams.

Oxygen consumption by organic matter is a result of chemical oxidation and respiration by organisms. Temperature affects both processes as well as the diffusion rate of oxygen and reducing substances across the water-substrate interface (Hargrave 1969). Previous studies have

TABLE 4. Benthic respiration rates (per g AFDM) in North American streams. All measurements were made by oxygen uptake in chambers.

Stream	Order	Respiration rate (mg O_2 g $AFDM^{-1}$ d^{-1})	Notes	Reference
McKenzie River System, Oregon	1-7	0.17	CPOM metabolism, same for all sites	Naiman and Sedell (1980)
Beaver Creek, Quebec	2	0.05-0.35	CPOM <10 cm diameter, per g dry weight	Naiman (1983)
White Clay Creek, Pennsylvania	3	10-17	trays of natural substrate, measured 1 day in August	Bott et al. (1978)
Beaver Creek, Quebec	2	0.11 0.11	wood <10 cm CPOM	Naiman et al. (1986)
C53, C54, C55 North Carolina	1	0.03-0.44 0.59-2.65	wood CPOM	Cuffney et al. (1990)
Ball Creek-Coweeta Creek, North Carolina	1-4	2.40-3.36 1.68-2.40 0.24-0.48	birch leaves rhododendron leaves sticks <5 cm diameter	This study

indicated that microbial respiration rates on different substrates should respond similarly to changes in temperature. Chamier and Dixon (1982) found that the same "fungal consortia" colonized all litter types in a particular stream, although Suberkropp and Klug (1976) found that the taxonomic composition may change over time. Although the rate of colonization of different kinds of organic matter may vary because of differences in organic matter chemistry, the positive relationship between respiration and temperature should have the same rate of increase. Respiration on rhododendron leaves and sticks was measured at a range of temperatures in our study and increased with temperature, but slopes of the increase were different between rhododendron leaves and sticks. Because sticks were of variable age and species, levels of decomposition during respiration measurements were unknown and this may account for the slope differences. In addition, rhododendron leaf surface area was probably overestimated during the later months of decomposition because we were unable to account for areas of leaf that may have been devoid of epidermis as a result of invertebrate feeding. When digitizing we assumed that all leaf material present was available for microbial colonization. Overestimating leaf surface area in the later months of decomposition resulted in lower estimates for respiration rates during a period of higher temperatures.

No general trend in respiration rates on leaves and sticks was seen among sites. Overall, variability in respiration rates at the four sites, for both rhododendron leaves and sticks, was primarily a function of temperature and incubation time. Other site differences (e.g., discharge, canopy openness, etc.) apparently did not have significant effects on respiration rates. Despite a lack of general trends, a few specific site differences were observed. Rhododendron leaves had a significantly lower mean rate of respiration at UBC (2nd order) than at the other three sites. This may have been a result of placing leaf packs in slower flowing areas where sedimentation and occasional burying of some leaf packs may have retarded biofilm development and, hence, microbial respiration.

A different pattern was found for sticks, where respiration rates were significantly higher at the most downstream site (CC) than at the other three sites. This difference could have been a function of the age of the sticks. Discharge was highest at CC, and the stream was wider and had fewer backwater areas than upstream sites. It was the least retentive of the four site (J. R. Webster, VPI & SU, and A. Covich, University of Oklahoma, unpublished data), and all sticks found there were firmly lodged in a few large, long-term debris dams. Their well decomposed (punky and grooved) appearance suggested that these sticks may have had a more strongly developed biofilm than sticks from the more tran-

TABLE 5. Benthic respiration rates (per m^2 of streambed) in North American streams. All measurements were made by oxygen uptake in chambers (except where noted).

Stream	Order	Respiration rate (g O_2 m^{-2} d^{-1})	Notes	Reference
McKenzie River system, Oregon	1-7	0.03-0.35	highest in 1st- and 2nd-order streams	Naiman and Sedell (1980)
Augusta Creek, Michigan				King and Cummins (1989a, 1989b)
Site 1,	1	0.6	wooded	
Site 2,	1	0.5	wooded	
Site 3,	2	1.8	meadow	
Site 4,	3	1.9	cleared	
Site 5,	3	0.8	wooded	
Chippewa River, Michigan	3	0.3	measured over sediments	Brown and King (1987)
Beaver Creek, Quebec	2	0.02-0.23	CPOM <10 cm diameter	Naiman (1983)
White Clay Creek, Pennsylvania	1-4	1.11-2.17	FPOM and *Cladophora*	Bott et al. (1985)
Augusta Creek, Michigan	1-4	0.71-2.88	primarily *Potomageton*	
Hubbard Brook, New Hampshire	1-2	0.03-0.4	CO_2 production in chambers, RQ = 0.85	Hedin (1990)
Artificial streams, Oregon	—	0.3-2.5	laboratory streams	McIntire and Phinney (1965)
Beaver Creek, Quebec	2	0.03	wood <10 cm	Naiman et al. (1986)
		0.01	benthic CPOM	
White Clay Creek, Pennsylvania	3	2.5-3.4	trays of natural substrate	Bott et al. (1978)
Stillhouse Brook, C54	1	2.2	trays of natural substrate	T. F. Cuffney and J. B. Wallace, University of Georgia, unpublished data
Satellite Brook, C55, North Carolina	1	1.9		
Ball Creek-Coweeta Creek, North Carolina	1-4	0.04-0.12	leaves[a]	This study
		0.001-0.02	sticks[a]	

[a] Based on rhododendron leaves, and sticks <5 cm in diameter.

sient debris dams at other sites. Other differences in respiration rates among sites seen only for stick respiration per unit AFDM may be a result of variability in the wood density of sticks found at each site. Sticks supporting an equally developed biofilm may vary in density and therefore have very different respiration rates (per g AFDM) that would not be demonstrated if respiration was expressed per surface area.

Mean daily respiration rates (per g AFDM) obtained in this study are compared with those from other North American studies in Table 4. Except for the study by Bott et al. (1978), respiration estimates from the two Coweeta studies (this study, Cuffney et al. 1990) fall at the high end of the range. The much higher respiration rates for White Clay Creek, Pennsylvania (Bott et al. 1978), were recorded at high summer temperatures in an open-canopy reach.

Although respiration rate may not change significantly with stream order, standing stocks of leaves or sticks often decline as stream order increases. Naiman (1983) found that because the CPOM standing stock decreased in a downstream direction, community metabolism per unit area of stream bottom also declined. Extrapolation of our microbial respiration rates on sticks and rhododendron leaves to annual standing stocks of sticks and leaves at our four sites along an elevational gradient gave similar results. Calculated respiration rates per area of streambed for sticks and leaves generally decreased with increasing stream size. In a study examining benthic metabolism in various biomes, Bott et al. (1985) also found that respiration was highest in the headwater site as a result of a larger standing stock of detritus.

Respiration rates per m^2 streambed for the Ball Creek-Coweeta Creek continuum were generally low compared with respiration re-

ported for other streams (Table 5) (Webster et al., in press). This difference may be due to several factors. First, we based our leaf respiration estimates on rhododendron; because other faster decomposing leaf types, with higher rates of respiration (e.g., birch), were not included in the analysis, we may have underestimated total leaf respiration in the stream. Second, we used respiration estimates for only two organic matter types, leaves and sticks; we did not include respiration on fine particulate organic matter or aufwuchs respiration. In addition, respiration rate estimates from most studies in Table 5 were measured using trays of benthic substrata (leaves, sticks, FPOM, and rocks of various sizes) rather than separate organic matter types.

Higher standing stocks of leaves and high rhododendron respiration rates per g AFDM resulted in the leaf respiration rate (per m^2 of streambed) contributing more to the total CBOM respiration than stick respiration. Although, at the headwater site (C27), where wood was most abundant, stick respiration contributed 14% of total CBOM respiration. Despite low respiration rates per unit AFDM, wood played a significant role in total CBOM respiration because of its high standing stock. Hedin (1990) described wood as a "focal site of metabolic activity in headwater streams". He referred primarily to the role of debris dams in retention of fine particulate organic matter, but his definition can also be applied to the metabolic activity of the microbial community colonizing wood itself, thereby expanding the importance of wood beyond its structural characteristics.

Acknowledgements

We thank Rob Cook, John Hutchens, and Caroline Weicking for their assistance in completing the field and laboratory aspects of this study. We also appreciate the cooperation from the staff at Coweeta Hydrologic Laboratory. Nick Aumen, Gary Lamberti, Rosemary Mackay, Mike Winterbourn, and an anonymous reviewer helped to improve the manuscript. This research was supported by grants from Sigma Xi and the Long Term Ecological Studies Program of the National Science Foundation.

Literature Cited

AUMEN, N. G., P. J. BOTTOMLEY, G. M. WARD, AND S. V. GREGORY. 1983. Microbial decomposition of wood in streams: distribution of microflora and factors affecting ^{14}C lignocellulose mineralization. Applied Environmental Microbiology 46: 1409–1416.

AUMEN, N. G., C. P. HAWKINS, AND S. V. GREGORY. 1990. Influence of woody debris on nutrient retention in catastrophically disturbed streams. Hydrobiologia 190:183–192.

BÄRLOCHER, F., AND B. KENDRICK. 1974. Dynamics of the fungal populations on leaves in a stream. Journal of Ecology 62:761–791.

BOTT, T. L., J. T. BROCK, C. E. CUSHING, S. V. GREGORY, D. KING, AND R. C. PETERSEN. 1978. A comparison of methods for measuring primary productivity and community respiration in streams. Hydrobiologia 60:3–12.

BOTT, T. L., J. T. BROCK, C. S. DUNN, R. J. NAIMAN, R. W. OVINK, AND R. C. PETERSEN. 1985. Benthic community metabolism in four temperate stream systems: an inter-biome comparison and evaluation of the river continuum concept. Hydrobiologia 123:3–45.

BROWN, S. S., AND D. K. KING. 1987. Community metabolism in natural and agriculturally disturbed riffle sections of the Chippewa River, Isabella County, Michigan. Journal of Freshwater Ecology 4:39–51.

CHAMIER, A. C., AND P. A. DIXON. 1982. Pectinases in leaf decomposition by aquatic hyphomycetes I: field study of the colonization-pattern of aquatic hyphomycetes on leaf packs in a survey stream. Oecologia 52:109–115.

CUFFNEY, T. F., J. B. WALLACE, AND G. J. LUGTHART. 1990. Experimental evidence quantifying the role of benthic invertebrates in organic matter dynamics of headwater streams. Freshwater Biology 23:281–299.

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

FEENEY, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology 51:565–581.

FINDLAY, S. G., AND T. L. ARSUFFI. 1989. Microbial growth and detritus transformations during decomposition of leaf litter in a stream. Freshwater Biology 21:261–269.

FINDLAY, S. G., P. J. SMITH, AND J. L. MEYER. 1986. Effect of detritus addition on metabolism of river sediment. Hydrobiologia 137:257–263.

FISHER, S. G., AND G. E. LIKENS. 1972. Stream ecosystem: organic energy budget. BioScience 22: 33–45.

GOLLADAY, S. W., AND R. L. SINSABAUGH. 1991. Biofilm development on leaf and wood surfaces in a boreal river. Freshwater Biology 25:437–450.

GOLLADAY, S. W., AND J. R. WEBSTER. 1988. Effects of clearcut logging on wood breakdown in Appalachian mountain streams. American Midland Naturalist 119:143–155.

HANSON, B. J., K. W. CUMMINS, J. R. BARNES, AND M. W. CARTER. 1984. Leaf litter processing in aquatic systems: a two variable model. Hydrobiologia 111:21–31.

HARGRAVE, B. T. 1969. Similarity of oxygen uptake by benthic communities. Limnology and Oceanography 14:801–805.

HEDIN, L. O. 1990. Factors controlling sediment community respiration in woodland stream ecosystems. Oikos 57:94–105.

KING, D. K., AND K. W. CUMMINS. 1989a. Autotrophic-heterotrophic community metabolism relationships of a woodland stream. Journal of Freshwater Ecology 5:205–218.

KING, D. K., AND K. W. CUMMINS. 1989b. Factors affecting autotrophic-heterotrophic relationships of a woodland stream. Journal of Freshwater Ecology 5:219–230.

MCINTIRE, C. D., AND H. K. PHINNEY. 1965. Laboratory studies of periphyton production and community metabolism in lotic environments. Ecological Monographs 35:237–258.

MINSHALL, G. W., R. C. PETERSEN, K. W. CUMMINS, T. L. BOTT, J. R. SEDELL, C. E. CUSHING, AND R. L. VANNOTE. 1983. Interbiome comparison of stream ecosystem dynamics. Ecological Monographs 53:1–25.

NAIMAN, R. J. 1983. The annual pattern and spatial distribution of aquatic oxygen metabolism in boreal forest watersheds. Ecological Monographs 53:73–94.

NAIMAN, R. J., AND J. R. SEDELL. 1979. Benthic organic matter as a function of stream order in Oregon. Archiv fur Hydrobiologie 87:404–422.

NAIMAN, R. J., AND J. R. SEDELL. 1980. Relationship between metabolic parameters and stream order in Oregon. Canadian Journal of Fisheries and Aquatic Sciences 37:834–847.

NAIMAN, R. J., J. M. MELILLO, AND J. E. HOBBIE. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). Ecology 67:1254–1269.

PETERSEN, R. C., AND K. W. CUMMINS. 1974. Leaf processing in a woodland stream. Freshwater Biology 4:345–368.

PETERSEN, R. C., K. W. CUMMINS, AND G. M. WARD. 1989. Microbial and animal processing of detritus in a woodland stream. Ecological Monographs 59:21–39.

SAS INSTITUTE, INC. 1991. SAS user's guide: statistics, version 6. 4th edition. SAS Institute, Inc., Cary, North Carolina.

SUBERKROPP, K. F., AND M. J. KLUG. 1974. Decomposition of deciduous leaf litter in a woodland stream. I. A scanning electron microscopic study. Microbial Ecology 1:96–103.

SUBERKROPP, K. F., AND M. J. KLUG. 1976. Fungi and bacteria associated with leaves during processing in a woodland stream. Ecology 57:707–719.

SUBERKROPP, K. F., AND M. J. KLUG. 1981. Degradation of leaf litter by aquatic hyphomycetes. Pages 761–776 *in* D. T. Wicklow and G. C. Carroll (editors). The fungal community. M. Dekker, New York.

SWANK, W. T., AND D. A. CROSSLEY (editors). 1988. Forest hydrology and ecology at Coweeta. Springer Verlag, New York.

TANK, J. L., AND J. C. MUSSON. 1993. An inexpensive chamber apparatus for multiple measurements of dissolved oxygen uptake or release. Journal of the North American Benthological Society 12:406–409.

TRISKA, F. J., AND K. CROMACK. 1980. The role of wood debris in forests and streams. Pages 171–190 *in* R. H. Waring (editor). Forests: fresh perspectives from ecosystem analysis. Oregon State University Press, Corvallis.

VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

WEBSTER, J. R., J. B. WALLACE, AND E. F. BENFIELD. In press. Organic processes in streams of the eastern United States. *In* C. E. Cushing, G. W. Minshall, and K. W. Cummins (editors). River and stream ecosystems. Elsevier, Amsterdam.

Received: 23 November 1992
Accepted: 13 September 1993