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APPLIED ISSUES

Effects of agriculture on wood breakdown and microbial biofilm respiration in southern Appalachian streams

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SUMMARY

1. Agriculture causes high sediment, nutrient and light input to streams, which may affect rates of ecosystem processes, such as organic matter decay. In the southern Appalachians, socioeconomic trends over the past 50 years have caused widespread abandonment of farmland with subsequent reforestation. Physical and chemical properties of streams in these reforested areas may be returning to pre-agriculture levels thereby creating the potential for recovery of ecosystem processes.
2. We examined wood breakdown and microbial activity on wood substrata in streams with different historical and current agricultural activity in their catchments. We analysed historical (1950) and recent (1998) forested land cover from large areas of the southern Appalachians and categorized streams based on percent forested land cover in these two time periods. Categories included a gradient of current agriculture from forested to heavily agricultural and reforestation from agriculture due to land abandonment. We compared microbial respiration on wood veneer substrata and breakdown of wood veneers among these land-use categories. We also compared temperature, sediment accumulation and nitrogen and phosphorus concentrations.
3. Streams with current agriculture had higher concentrations of dissolved inorganic nitrogen than forested streams. Despite reforestation from agriculture, nitrogen concentrations were also elevated in streams with agricultural histories relative to forested streams. Temperature was also higher in agricultural streams but appeared to recover from historical agriculture through reforestation and stream shading.
4. Wood breakdown rates ranged from 0.0015 to 0.0076 day^{-1} and were similar to other studies using wood veneers to determine breakdown rate. Microbial respiration increased with incubation time in streams up to approximately 150 days, after which it remained constant. Neither wood breakdown nor microbial respiration was significantly different among land-use categories, despite the observed physical and chemical differences in streams based on land-use. Wood breakdown rates could be predicted by microbial respiration indicating microbial control of wood breakdown in these streams. Both breakdown and microbial respiration were negatively correlated with the amount of inorganic sediment accumulated on wood veneers.
5. Higher nutrients and temperature led us to expect faster breakdown and higher microbial respiration in agricultural streams, but sediment in these streams may be limiting microbial activity and breakdown of organic material resulting in little net effect of agriculture on wood breakdown. Wood may not be desirable as a tool for

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functional assessment of stream integrity due to its unpredictable response to agriculture.

Keywords: agriculture, biofilm, decomposition, disturbance, organic matter

Introduction

Streams in forested regions rely heavily on the supply of allochthonous organic material for secondary production (Wallace *et al.*, 1997) and nutrient retention (Webster *et al.*, 2000). This organic matter is subject to a variety of processes including microbial colonization, transport, burial and ingestion. Leaf material is the bulk of allochthonous material reaching small streams (Webster & Meyer, 1997), and many organisms are particularly adapted for processing autumnal input of leaves (Anderson & Sedell, 1979). However, wood is an important structural component of many streams (e.g. Harmon *et al.*, 1986) and is a long-lasting food resource after the rapid breakdown of leaf material. Wood also may be an important resource in streams that do not receive large annual supplies of leaves, such as agricultural streams with altered riparian vegetation or in streams that rapidly process leaf material during winter (Rabeni & Hoel, 2000).

Wood decomposition in streams is primarily achieved through microbial activity (i.e. fungal and bacterial digestion; Sinsabaugh *et al.*, 1992), and extremely active biofilms develop on the surfaces of wood substrata in streams (Golladay & Sinsabaugh, 1991; Tank & Winterbourn, 1995). Substratum quality (i.e. tissue chemistry) can be very important in determining microbial activity and breakdown rate of organic matter in streams (Melillo *et al.*, 1983; Gessner & Chauvet, 1994; Stelzer, Heffernan & Likens, 2003). However, nutrients, primarily nitrogen and phosphorus, in the water column can also control microbial biofilm activity (Howarth & Fisher, 1976; Tank & Webster, 1998; Gulis & Suberkropp, 2003; Niyogi, Simon & Townsend, 2003; Tank & Dodds, 2003), particularly on nutrient-poor organic substrata like wood (Stelzer *et al.*, 2003; Gulis *et al.*, 2004). As a result, elevated nutrient concentrations may increase organic matter breakdown rates (Benfield, Jones & Patterson, 1977; Elwood *et al.*, 1981; Meyer & Johnson, 1983; Suberkropp & Chauvet, 1995; Díez *et al.*, 2002). Elevated temperature may also accelerate microbial activity (Tank, Webster & Benfield, 1993) and result in faster decomposition of organic material in streams (e.g. Paul, Benfield & Cairns, 1978). Catchment disturbances that alter nutrients and temperature may result in faster decomposition of wood in streams (Golladay & Webster, 1988; Spänhoff & Meyer, 2004).

Streams in agricultural areas typically have elevated temperature and nutrients along with altered organic matter supply relative to forested streams (Karr & Schlosser, 1978; Allan, 2004). The altered physicochemical conditions in agricultural streams may cause dramatically different organic matter processing rates, and studies of organic matter dynamics in agricultural streams are becoming more numerous (Benfield *et al.*, 1977; Young, Huryn & Townsend, 1994; Niyogi *et al.*, 2003; Spänhoff & Meyer, 2004; Gulis, Ferreira & Graça, 2006; Hagen, Webster & Benfield, 2006; Paul, Meyer & Couch, 2006). In most cases, leaf breakdown is faster in agricultural streams because elevated nutrients and temperatures increase microbial activity and shredder biomass in leaf packs (Gulis *et al.*, 2006; Hagen *et al.*, 2006; Paul *et al.*, 2006). Agricultural streams do not receive the same amount or type of organic material relative to wooded streams (Stagliano & Whiles, 2002), and wood can often be a major source of available detritus (Rabeni & Hoel, 2000). Therefore, the breakdown of wood may be a key energy pathway in agricultural streams, which makes determining the effect of agriculture on wood decomposition rates particularly important. Historical agriculture has been linked to contemporary biological properties of streams (Harding *et al.*, 1998; Burcher, Valett & Benfield, 2007). Recovery of ecosystem function from historical impacts depends upon the return of factors affecting these processes to pre-disturbance conditions. If physical, chemical and biological effects of agriculture persist in streams following reforestation, ecosystem processes moderated by these properties will not be able to recover.

Streams in the southern Appalachians have suffered from many anthropogenic insults over the past several centuries including mining, logging and agriculture (Yarnell, 1998). Agriculture in the region is

now primarily pasture and small row-crop activities, primarily in bottomland. Large areas in the southern Appalachians have converted from agriculture to forest due to changes in regional socioeconomic factors (Wear & Bolstad, 1998). Logging, once a major land-use in the southern Appalachians, is currently only a minor disturbance in the region but may become significant as second-growth forest matures. Many areas are undergoing suburban development along with reforestation on historically agricultural land (Wear & Bolstad, 1998; Burcher *et al.*, 2007). In-stream sediment concentrations and biological communities in southern Appalachian streams have been related to current and historical agriculture (Harding *et al.*, 1998; Burcher & Benfield, 2006). We used spatial and temporal patterns of reforestation of agricultural land to determine the impact of historical and current agriculture on breakdown and microbial biofilm activity of wood in southern Appalachian streams.

The objectives of this study were: (i) to determine physical and chemical conditions of streams along an agricultural disturbance gradient and (ii) to compare wood breakdown and respiration of associated microbes among streams with different land-uses (present and past) to assess the role of physical and chemical parameters in organic matter processes. We predicted that elevated nutrients and temperature in agricultural streams will cause higher microbial activity on wood substrata with subsequently faster breakdown rates.

Methods

Study sites

This study was conducted in the Blue Ridge Physiographic Province of the southern Appalachians (Fig. 1, inset). The Blue Ridge Province is a topographically complex region that escaped glaciation and is characterized by residual saprolitic ultisol and inceptisol soils (Isphording & Fitzpatrick, 1992). Micaceous schist and granitic gneiss dominate the region's geology resulting in streams with slightly acidic water and low concentrations of dissolved ions (Simmons & Heath, 1982).

Land-cover database development and site selection

We developed a database of land cover (% forest) in 1950 and 1998 for second and third-order catchments in our study area (Grayson County, Virginia; Buncombe, Macon and Madison Counties, North Carolina) using a geographic information system (GIS). We delineated riparian zones for streams in each catchment by buffering 50 m on each side of stream vectors (100 m total width) for the entire stream length. Land

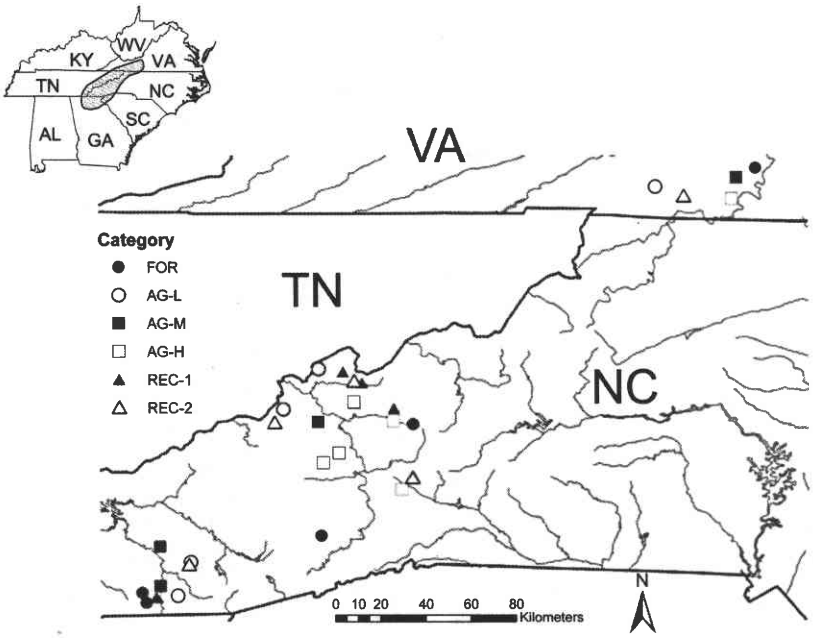

Fig. 1 Map showing study sites in the southern Appalachians (gray area on inset) with names of states abbreviated (AL = Alabama, GA = Georgia, KY = Kentucky, NC = North Carolina, SC = South Carolina, TN = Tennessee, VA = Virginia, WV = West Virginia). Study sites are categorized according to historical and current land cover (% forest) at different spatial scales (category abbreviations described in text).

cover was determined for each catchment and its respective riparian zone by overlaying these spatial zones on a land cover map from each year and quantifying the % forest cover. We designed this study to explore changes in streams as a result of agricultural land-use and subsequent reforestation and sought to control factors unrelated to anthropogenic impacts, such as geology, topography and altitude. Therefore, we considered only those catchments with areas between 5 and 30 km^2 and stream outlet altitudes between 600 and 1000 m as eligible sites. Filtering all catchments using catchment size and altitude decreased the pool of potential catchments from over 6500 to approximately 500.

These 500 catchments were categorized based on the extent of present and past agriculture in their basins using the following scheme:

Forested (FOR) >98% forest in all years;

Light agriculture (AG-L) 90–95% forest in all years;

Moderate agriculture (AG-M) 70–80% forest in all years;

Heavy agriculture (AG-H) <60% forest in all years;

Recovery stage 1 (REC1) <60% forest in 1950, >75% forest in 1998;

Recovery stage 2 (REC2) <75% forest in 1950, >90% forest in 1998.

We used four categories (FOR, AG-L, AG-M, AG-H) to represent the gradient of agriculture currently present in catchments across the region. Intensities of agriculture varied dramatically, but AG-H streams had no woody vegetation in riparian zones, AG-M streams had heterogeneous landscapes and AG-L streams were primarily forested and had intact woody vegetation along streams. Streams from these categories were also used as positive (forested) and negative (agricultural) controls for comparing streams in different stages of recovery following historical agriculture. Recovery stages were based on the historical extent of agriculture in catchments and the amount of forested land cover currently present.

We selected five streams from each category and attempted to distribute the sites within categories across the study region (Fig. 1). We identified a 100-m stream reach on each stream (second or third order) for the study. Our actual sampling sites did not match catchment outlets used in the original land-cover analysis, so we generated catchment boundaries, riparian zones and riparian zones within 1 and 2 km upstream of our study reach to assess land cover immediately upstream. We then re-analysed land cover from 1950 and 1998 using % forest cover. We used extensive reconnaissance and landowner interviews to ensure that catchments properly matched the *a priori* categorization, particularly for REC1 and REC2 sites. We used current and historical values of % forest at all spatial scales in a principal component analysis to validate land-use categories.

Physical and chemical characteristics

Physical and chemical characteristics were measured for each stream from November 2000 to October 2001. Triplicate water samples were collected every 2 months from each site, filtered in the field using pre-soaked membrane filters (0.45-μm pore size) and frozen before analysis. Samples were analysed for NO_3-N and PO_4-P using a Dionex DX500 ion chromatograph (Dionex Corporation, Sunnydale, CA, U.S.A.) and NH_4-N using the indophenol blue method and a fluorometer (Holmes *et al.*, 1999). Nitrate and ammonium values were combined to represent dissolved inorganic nitrogen (DIN). Specific conductance was measured every 2 months using a field probe (YSI Model 30 conductivity meter). Alkalinity was measured once at the beginning of the study using acid titration (APHA, 1998). Discharge was measured every 2 months at each site using velocity determined with an electronic flow meter (FLO-MATE Model 2000; Marsh-McBirney, Inc., Frederick, MD, U.S.A.) and cross-sectional area. Temperature was recorded every 6 h during wood incubation (November 2000 through August 2001) using data loggers (HOBO Temp; Onset Corporation, Bourne, MA, U.S.A.). Temperature data were converted to daily means, which were then used to calculate cumulative degree-days (above 0 °C).

Wood breakdown and microbial respiration

We cut white oak wood veneer into strips (2.5 × 15 cm, henceforth called sticks) and mounted five sticks onto plastic mesh using cable ties (Tank & Webster, 1998). Seven sets of sticks were anchored in riffle sections over similar gravel/cobble substratum in each stream in late November 2000 using a cable secured to a stake on the stream bank. Stick sets were spaced approximately 0.5 m apart along the cable in each stream. Five sets were transported to each site

and returned to the laboratory as controls for handling losses and to determine initial ash-free dry mass (AFDM) and microbial respiration. Sets of five sticks were retrieved after 41, 130, 203 and 269 days from each stream, placed in containers filled with stream water and transported on ice to the laboratory.

Sticks were handled gently in the laboratory and were processed without removing biofilms and accumulated sediments. The centre section (4 × 2.5 cm) of each stick was removed to determine microbial biofilm respiration. The remainder of each stick was dried (50 °C) to constant weight and ashed at 500 °C to determine AFDM. Following the respiration assay, AFDM was determined for the entire stick, including the section used for respiration. In addition, ash remaining after combustion was weighed to quantify the amount of inorganic sediment accumulating on sticks (mg cm^{-2}) during incubation in streams. Breakdown rate (k) was calculated for each stream by regressing the natural log of percent AFDM remaining against incubation time and degree-days (Petersen & Cummins, 1974). Using degree-days did not improve the fit of decay models (no significant difference in r^2 for models using days or degree-days), so we used breakdown rates calculated by days to compare land-use categories. Wood breakdown rates were compared among land-use categories using one-way ANOVA.

Microbial respiration was measured on sticks using a carbon dioxide production assay in the laboratory. Each assay used five sticks per site along with a control for each stream (20 mL of filtered stream water with no wood). Each stick was placed into a 40-mL EPA vial with 20 mL of filtered stream water from its respective stream. Samples were equilibrated to incubation temperature (average ambient stream temperature on the retrieval date) in the dark prior to sealing the vials with Teflon-coated silicon caps. Samples were then incubated in the dark for 18 h. After incubation, 1-mL gas samples were collected from the vial headspace and saved in pre-vacuumed borosilicate glass containers. Gas samples were analysed for CO_2 using a gas chromatograph equipped with a thermal conductivity detector (SRI-8610 Gas Chromatograph; SRI Instruments, Torrance, CA, U.S.A.). Headspace CO_2 concentrations were converted to water CO_2 concentrations using Henry's law. Sticks used in the respiration assay were oven dried and ashed to determine AFDM. We calculated microbial respiration rate by dividing control-adjusted CO_2 production by stick surface area and AFDM. Respiration values were compared using two-way ANOVA with land-use categories and sampling date as factors. We used regression to explore relationships between stream physicochemistry, sediment accumulation, breakdown rates and biofilm respiration.

Results

Land cover

Principal component analysis using historical and current land cover at these spatial scales was able to separate sites into groups that conformed to our land cover categories (Fig. 2). Based on the ordination, two sites did not match their *a priori* categories due to realigning spatial boundaries to specific sampling reach. We switched these sites from their previous categories to groups identified by the ordination (one site in REC1 to AG-M and one site in AG-M to AG-H, Fig. 2). This resulted in six streams in AG-H and four streams in REC1. We correlated land cover data with values on the first two principal components to determine which parameters were driving the distribution of sites on the ordination (Table 1). Percent forest cover (means for each category) in each spatial

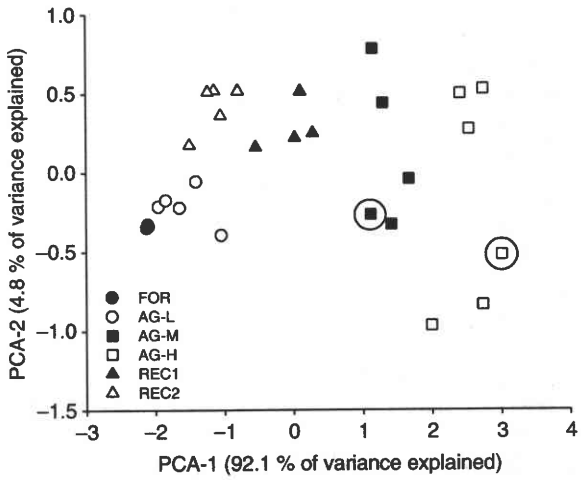

Fig. 2 Principal component analysis of sites using historical (1950) and current (1998) land cover (% forest) within several spatial scales (whole catchment, 100-m riparian zone, 100-m riparian zone 1 and 2 km upstream of sampling site). Circled symbols indicate those sites that were originally in different categories (see text for details).

Table 1 Pearson product moment correlations between land cover at different scales (CAT = whole catchment, RIP = 100-m riparian corridor for entire stream length, 2km-RIP = 100-m riparian zone 2 km upstream of sampling site and 1-km-RIP = 100-m riparian zone 1 km upstream of sampling site) and site scores for the first two principal component axes

Land Cover	PCA-1	PCA-2
CAT-1950	**−0.952**	0.282
CAT-1998	**−0.932**	−0.232
RIP-1950	**−0.936**	0.248
RIP-1998	**−0.937**	−0.257
2km-RIP-1950	**−0.907**	**−0.853**
2km-RIP-1998	**−0.865**	**−0.794**
1km-RIP-1950	**−0.776**	**−0.829**
1km-RIP-1998	**−0.869**	**−0.780**

Values shown are correlation coefficients (r, $N = 30$) with strongest correlations in bold ($P < 0.0001$). The first and second principal component axes explained 92.1% and 4.8% of the variance among sites respectively.

zone and year are given in Table 2. Based on analysis of eigen values, the first principal component explained 92.1% of the variance and was most significantly correlated with % forest at the catchment (CAT) and riparian (RIP) spatial scales (Table 1). The second principal component contained much less information (4.8% of variance) and was correlated most strongly with land cover at subcorridor spatial scales (Table 1). Therefore, land cover at broad spatial scales primarily separated sites on the ordination.

Physical and chemical characteristics

Altitude at our study sites ranged from 576 to 861 m a.s.l. and was not significantly different among categories (Table 3). Catchment area ranged from 3.21 to 21.31 km^2. AG-L and AG-M catchments were significantly larger than FOR and REC2 catchments (ANOVA, Tukey's pairwise comparison, $P < 0.05$), but stream discharge was not different among categories. Mean discharge was 65 L s^{-1} but ranged from 29.1 to 101.9 L s^{-1} among study sites. Specific conductance ranged from 11.9 to 98.4 μS cm^{-1} and was highest in AG-L streams (ANOVA, Tukey's, $P < 0.05$). Alkalinity

Table 2 Historical and current land cover (% forest) within different spatial scales for categories used in this study. The spatial scales used are indicated by CAT (whole catchment), RIP (100-m riparian corridor), 2km-RIP (100-m riparian zone 2 km upstream of sampling site) and 1-km-RIP (100-m riparian zone 1 km upstream of sampling site)

Spatial scale	FOR (n = 5)	AG-L (n = 5)	AG-M (n = 5)	AG-H (n = 6)	REC1 (n = 4)	REC2 (n = 5)
CAT-1950	99.9 ± 0.1	87.5 ± 3.0	60.0 ± 6.3	52.7 ± 6.5	79.6 ± 5.2	77.6 ± 7.8
CAT-1998	99.3 ± 0.3	94.9 ± 1.9	83.6 ± 2.8	74.1 ± 4.8	94.9 ± 1.0	94.8 ± 1.1
RIP-1950	99.8 ± 0.2	84.2 ± 3.1	42.0 ± 8.0	29.3 ± 3.8	57.5 ± 8.4	75.5 ± 6.9
RIP-1998	99.9 ± 0.1	96.3 ± 0.9	72.2 ± 5.2	58.4 ± 2.3	85.4 ± 3.0	94.6 ± 2.0
2km-RIP-1950	99.7 ± 0.3	74.6 ± 3.8	13.7 ± 4.7	11.3 ± 5.1	40.4 ± 11.6	71.7 ± 6.1
2km-RIP-1998	96.8 ± 1.2	89.2 ± 3.0	47.7 ± 5.2	32.2 ± 6.6	76.7 ± 4.9	91.2 ± 1.4
1km-RIP-1950	99.1 ± 0.9	58.6 ± 12.2	12.6 ± 3.8	9.6 ± 3.5	29.0 ± 11.7	62.4 ± 6.3
1km-RIP-1998	96.6 ± 1.3	78.1 ± 12.1	43.8 ± 4.2	25.5 ± 7.5	66.4 ± 4.9	84.4 ± 3.7

Values are mean ± 1SE.

Table 3. Physical and chemical characteristics of study sites by category (abbreviations in text)

	FOR (n = 5)	AG-L (n = 5)	AG-M (n = 5)	AG-H (n = 6)	REC1 (n = 4)	REC2 (n = 5)
Altitude (m a.s.l.)	767 (25)	710 (44)	641 (32)	676 (24)	754 (45)	776 (37)
Catchment area† (km^2)	6.18^a (1.49)	14.03^{bc} (1.75)	18.42^c (0.92)	13.11^{abc} (2.47)	6.67^{ab} (1.54)	6.00^a (1.67)
Discharge (L s^{-1})	69.6 (4.2)	91.7 (3.9)	63.6 (7.6)	62.1 (10.4)	66.6 (9.1)	62.9 (6.2)
Specific conductance† (μS cm^{-1})	20.1^a (2.8)	72.1^c (9.0)	31.6^{ab} (4.8)	38.0^{ab} (4.0)	58.7^{bc} (10.9)	52.9^{bc} (10.0)
Alkalinity‡ (mg $CaCO_3$ L^{-1})	5.4^a (0.5)	7.4^{ab} (1.3)	13.0^b (1.5)	13.7^b (2.4)	11.5^{ab} (1.6)	10.6^{ab} (1.1)
DIN† (μg L^{-1})	93.2^a (33.9)	108.7^a (36.6)	420.1^{ab} (126.6)	642.6^b (110.7)	286.8^{ab} (89.6)	244.2^a (55.1)
PO_4-P (μg L^{-1})	3.6 (0.2)	8.2 (3.9)	10.8 (4.0)	8.2 (1.8)	11.3 (2.6)	9.5 (2.5)
Degree-days† (above 0 °C)	2543^a (62)	2600^{ab} (109)	3013^c (88)	3158^c (117)	2844^{bc} (88)	2546^{ab} (49)

Values are means with standard errors in parentheses.
Means with different letters are significantly different ($P < 0.05$).
†Differences determined using one-way ANOVA and Tukey's pairwise comparisons.
‡Differences determined using Kruskal–Wallis ANOVA on Ranks and Dunn's pairwise comparisons.

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ranged from 4 to 21 mg $CaCO_3$ L^{-1} among our sites and was significantly lower in FOR streams compared with AG-M and AG-H streams (Kruskal–Wallis ANOVA on Ranks, Dunn's pairwise comparison, $P < 0.05$).

Dissolved inorganic nitrogen (DIN) ranged from 20.97 to 1118 μg L^{-1} among our sites (Table 3). DIN was significantly higher in AG-H streams than in FOR, AG-L and REC2 streams (Table 3; ANOVA, Tukey's pairwise comparison, $P < 0.05$). DIN values for AG-M and REC1 streams fell between values for AG-H and REC2 streams. Phosphorus (PO_4-P) ranged from 3 to 25 μg L^{-1} and was not significantly different among categories. Many PO_4-P values were at or below the detection limit for the analytical method used (2.0 μg L^{-1}). Cumulative degree-days above 0 °C from November 2000 to August 2001 ranged from 2172 to 3218. Degree-days were significantly higher in AG-H and AG-M streams compared to FOR, AG-L, and REC2 streams (Table 3; ANOVA, Tukey's pairwise comparison, $P < 0.05$). Degree-days were also significantly higher in REC1 streams than FOR streams, but the difference between REC1 streams and other categories was not significant.

Wood breakdown and microbial respiration

Wood breakdown rate ranged from 0.0015 to 0.0076 day^{-1} among all sites. Breakdown rates were slowest in FOR streams and fastest in REC1 streams, but there were no significant differences among categories (Fig. 3; ANOVA, $P = 0.341$). Microbial respiration on wood increased with time in all streams (Fig. 4; two-way ANOVA, $P < 0.001$) and appeared to level off around 0.003 mg CO_2 cm^{-2} h^{-1} or 0.1 mg CO_2 g $AFDM^{-1}$ h^{-1} after approximately 130 days. Microbial respiration did not differ among land-use categories, either overall or on individual retrieval dates. Respiration on wood not incubated in the streams (i.e. initial conditions) was negligible (<0.0001 mg CO_2 g $AFDM^{-1}$ h^{-1}), and respiration on all retrieval dates was higher than initial conditions. Respiration was significantly higher on days 130, 203 and 269 than on day 41 (Fig. 4; two-way ANOVA, $P < 0.05$). Within each category, microbial respiration was significantly lower on day 41 than on days 130, 203 and 269 for all categories except AG-H. Respiration in AG-H streams more than doubled from day 41 (0.0439 mg CO_2 g $AFDM^{-1}$ h^{-1}) to day 269 (0.0975 mg CO_2 g $AFDM^{-1}$ h^{-1}), but this difference

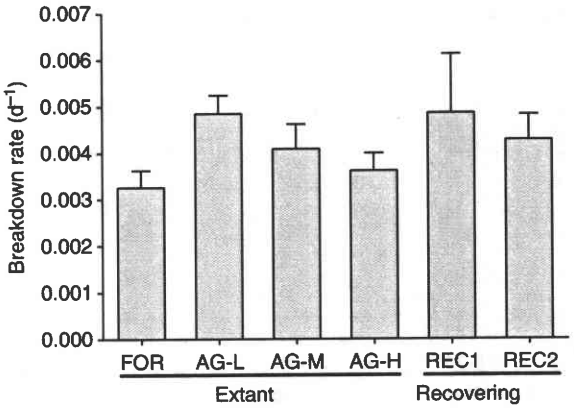

Fig. 3 Mean breakdown rates (day^{-1}) of wood in each category (+1SE). Extant categories represent streams with no change over time from current land-use patterns in their catchments. Recovering categories represent streams with agricultural histories but significant amounts of reforestation over the past 50 years. Breakdown rates were not significantly different among categories (one-way ANOVA, $P > 0.05$). Category abbreviations described in text.

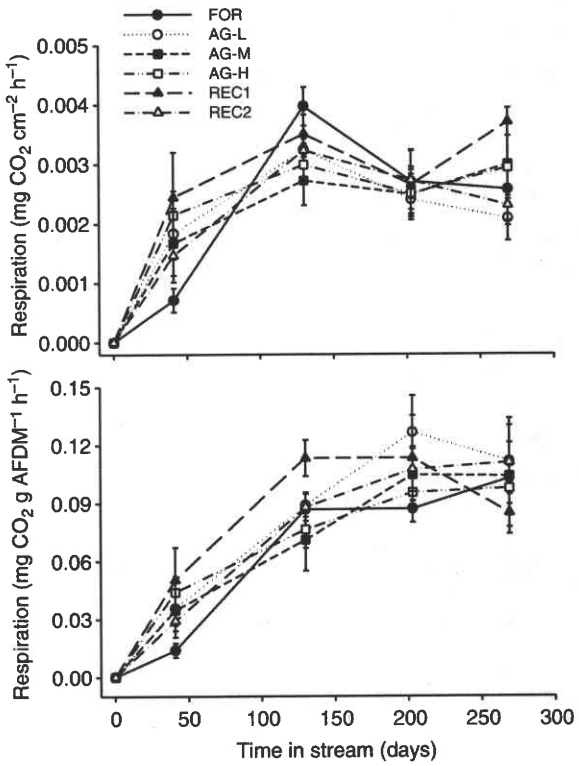

Fig. 4 Mean respiration rates of microbial biofilm on wood after incubation in streams expressed per unit area and per unit mass. Initial rates (day 0) were determined using handling loss controls. Other values are mean ± 1SE for each category on each sampling date. Category abbreviations described in text.

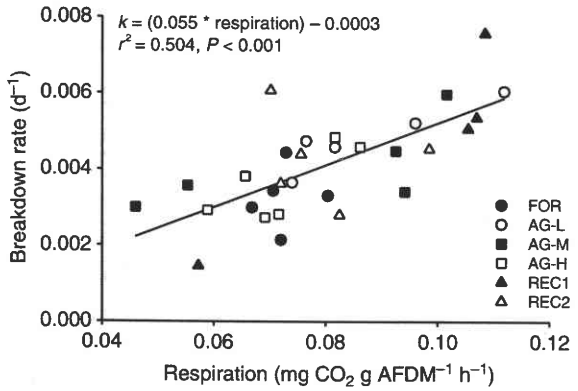

Fig. 5 Wood breakdown rate (day^{-1}) as a function of microbial respiration (mg CO_2 g AFDM^{-1} h^{-1}) on the last wood retrieval. Relationship analysed using simple linear regression. Category abbreviations described in text.

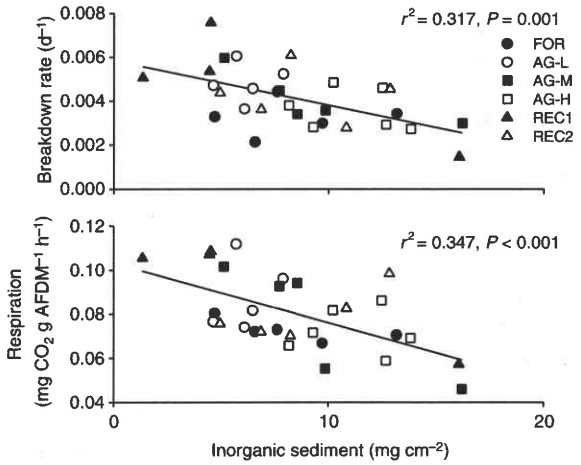

Fig. 6 Wood breakdown rates (day^{-1}) and microbial respiration (mg CO_2 g AFDM^{-1} h^{-1}) as functions of the amount of inorganic sediment (mg cm^{-2}) accumulated on wood substrates during incubation in streams. Relationships were analysed using simple linear regression. Category abbreviations described in text.

was not significant due to high variability among streams.

Wood breakdown rates were not correlated with land-use at any spatial scale or in either year. Breakdown rates also were not significantly related to nutrients or temperature. Microbial respiration rates were not correlated with land-use at any spatial scale or in either year or with water chemistry or temperature. However, wood breakdown rate was correlated with microbial respiration (Fig. 5; $r^2 = 0.504$, $P < 0.001$), suggesting that microbes likely play a critical role in determining wood breakdown rates. Accumulated sediment on sticks ranged from 1.4 to 41.8 mg cm^{-2} across all sites on last stick retrieval and was not significantly different among land-use categories. However, amount of sediment was negatively correlated with both breakdown rate and microbial respiration (Fig. 6; $r^2 = 0.317$, $P = 0.001$; $r^2 = 0.347$, $P < 0.001$).

Discussion

Nutrient and temperature responses to agriculture

Streams influenced by agriculture had elevated concentrations of nutrients and warmer temperature regimes than long-term forested streams. Streams in different land-use categories were not significantly different in altitude or discharge making land-use the most likely factor causing physical and chemical differences among streams. Many studies have demonstrated elevated nutrients and temperature in agricultural streams (e.g. Karr & Schlosser, 1978; Peterjohn & Correll, 1984; Lowrance *et al.*, 1985; review by Allan, 2004). Historical agriculture seems to have a persistent effect on water chemistry. DIN concentrations in REC2 streams were between values for streams in categories with similar past (AG-M) or present (AG-L) extents of agriculture. Elevated nutrient concentrations in streams have lasted for decades following logging (e.g. Swank & Vose, 1997) and experimental agriculture (Meyer & Johnson, 1983) in the southern Appalachians. With the addition of fertiliser and soil compaction in agricultural areas, nutrients may remain elevated in streams recovering from agriculture, perhaps having even longer recovery times than logging. Reforestation on abandoned agricultural land takes longer than reforestation from logging for many reasons (Myster & Pickett, 1994), and this may result in a longer legacy of effects in historically agricultural streams. However, forest development in historically agricultural catchments was likely dense enough to prevent warm temperature regimes found in agricultural streams. Swift (1983) showed that stream temperature recovers quickly (within 5 years) during reforestation from clear-cutting. Fifty years appears to be enough time for streams to reach a pre-agriculture temperature regime as a result of reforestation, despite the likelihood of delayed forest growth on abandoned agricultural land.

Effects of agriculture on wood breakdown and microbial respiration

Wood breakdown has been extensively studied in forested streams of the southern Appalachians. Our range of wood breakdown rates (0.0015–0.0076 day^{-1}) was similar to other studies using wood veneers to assess breakdown (Tank & Webster, 1998; Simon & Benfield, 2001; Gulis *et al.*, 2004) but was much faster than breakdown of natural sticks (Golladay & Webster, 1988; Webster *et al.*, 1999; Spänhoff & Meyer, 2004). Accelerated breakdown of wood veneers has been attributed to the high surface area to volume ratio of veneers compared with natural sticks or larger wood pieces (Tank & Webster, 1998; Spänhoff & Meyer, 2004). Wood breakdown rates are generally slower as size of wood pieces increases, whether using natural sticks or milled wood (e.g. Melillo *et al.*, 1983; Golladay & Webster, 1988; Sinsabaugh *et al.*, 1992; Díez *et al.*, 2002; Spänhoff & Meyer, 2004). The breakdown rates we measured were similar to those found using small natural sticks.

Wood breakdown was generally faster in streams with low or moderate amounts of agriculture than in streams with forested or heavy agricultural land uses. The gradient of agriculture used in our study, except for the recovering streams, was similar to that used by Hagen *et al.* (2006), who found that leaf breakdown rates were faster in streams with low to intermediate amounts of agriculture than in forested reference or intensively agricultural streams. Eutrophication by agricultural inputs to streams tends to increase breakdown rates of wood (Spänhoff & Meyer, 2004), but extreme eutrophication may actually cause a decrease in organic matter breakdown rates due to other pollutants or sediment (Lecerf *et al.*, 2006). As a result, leaf breakdown rates were unimodal along the gradient of agriculture and eutrophication used by Hagen *et al.* (2006) and Lecerf *et al.* (2006). Without a clear pattern of wood breakdown rates along our gradient of current agriculture, it is difficult to predict how historical agriculture would affect wood breakdown. Breakdown rates were highly variable among streams in recovering categories, but REC2 streams tended to be slower than REC1 streams, which may suggest that organic matter breakdown rates are recovering from past agricultural effects.

Microbial respiration in our study (*c.* 3–4 μg CO_2 cm^{-2} h^{-1} after 100 days incubation in streams) was similar to values reported for other studies using wood veneers (*c.* 4 μg CO_2 cm^{-2} h^{-1}, Tank & Webster, 1998) but higher than studies using natural wood substrata (*c.* 0.35 μg CO_2 cm^{-2} h^{-1}, Tank *et al.*, 1993). Compared to streams from nutrient-enrichment experiments, our mass-specific microbial respiration rates from wood veneers (0.07–0.11 mg CO_2 g $AFDM^{-1}$ h^{-1} after 100 days) were similar to values for non-enriched reference streams (0.07 mg CO_2 g $AFDM^{-1}$ h^{-1} after 55 days, Stelzer *et al.*, 2003; *c.* 0.1 mg CO_2 g $AFDM^{-1}$ h^{-1} after 90 days, Gulis *et al.*, 2004) but much lower than respiration in enriched streams in nutrient-addition experiments (*c.* 0.23 mg CO_2 g $AFDM^{-1}$ h^{-1} after 55 days, Stelzer *et al.*, 2003; *c.* 0.25 mg CO_2 g $AFDM^{-1}$ h^{-1} after 90 days, Gulis *et al.*, 2004). Most studies of wood decomposition in streams show a strong correlation between microbial activity and decomposition rates. Microbial respiration was positively correlated with wood breakdown rate and accounted for *c.* 50% of carbon lost from sticks during the incubation period.

Factors controlling breakdown rate and microbial respiration

We expected higher nutrients and temperature to stimulate microbial activity and hence to increase breakdown rate because microbes are primarily responsible for wood breakdown in streams (Sinsabaugh *et al.*, 1992). Rates of microbial respiration and decomposition have been linked to nutritional content of organic matter (Tank *et al.*, 1993) or to stream nutrient concentrations (Tank & Webster, 1998; Gulis & Suberkropp, 2003; Stelzer *et al.*, 2003; Gulis *et al.*, 2004). Furthermore, microbial respiration on wood is enhanced by dissolved nutrients more than on leaves because wood is a more nutrient-poor substratum (Stelzer *et al.*, 2003; Gulis *et al.*, 2004). Nutrient concentrations in enrichment studies were similar to those measured in agricultural streams in the present study (Stelzer *et al.*, 2003: NO_3-N 196 μg L^{-1}; SRP 30 μg L^{-1}; Gulis *et al.*, 2004: DIN 380 μg L^{-1}, SRP 46 μg L^{-1}) but resulted in higher microbial respiration rates. Higher microbial respiration rates on tussock grass in agricultural streams in New Zealand were attributed to elevated nutrient concentrations (Niyogi *et al.*, 2003). However, nutrient enrichment by agriculture did not appear to result in higher respiration rates in agricultural streams in our

study. Higher water temperature may also stimulate microbial activity on organic matter (Tank *et al.*, 1993) and increase organic matter breakdown rates in streams (Paul *et al.*, 1978; Short & Ward, 1980). Indeed, our agricultural streams accumulated more degree-days during wood incubation than our forested streams, but neither wood breakdown nor microbial respiration was correlated with temperature.

Inorganic material on wood substrata was negatively correlated with both breakdown rate and microbial respiration, which suggests that sediment accumulation may have reduced microbial activity and decomposition rate. As biofilms develop, microbes exude a polysaccharide matrix that protects cells, facilitates intercellular communication and allows for extracellular enzyme activity (Lock, 1993; Ben-Ari, 1999). Unfortunately, this matrix also creates a sticky surface on wood that may trap sediment particles, which reduces availability of oxygen and dissolved nutrients to microbes (Herbst, 1980). Many of the sticks we collected, especially from agricultural streams, were covered in silt and fine sand. Sticks with dense sediment accumulations were often blackened and smelled of hydrogen sulphide, indicating hypoxic conditions on the wood surface, which would likely inhibit microbial activity.

Increased sediment transport and deposition is characteristic of agricultural streams (Waters, 1995; Allan, 2004), so we expected sediment accumulations on wood substratum to be higher as amount of agriculture increased in catchments. However, accumulated sediment was highly variable within land-use categories and not correlated with land cover. The high variability of sediment accumulation on wood could potentially be attributed to differences in catchment land use among streams within land-use categories, including different types or intensities of agriculture (e.g. row crop versus pasture), distributions of agriculture in catchments (i.e. proximity to sampling location), or historical disturbances on the landscape (e.g. logging).

The negative influence of sediment on organic matter decomposition rates (Herbst, 1980; Webster & Waide, 1982; Rounick & Winterbourn, 1983) may negate the stimulatory effects of higher nutrient concentrations or warmer temperatures in streams with disturbed catchments. If nutrient enrichment and warmer temperatures accompany land use, microbial processes may be stimulated enough to increase decomposition rates in agricultural streams (Niyogi *et al.*, 2003; Gulis *et al.*, 2006) or to compensate for loss of shredding macroinvertebrates resulting in similar breakdown rates in reference and impacted streams (Benfield *et al.*, 1977; Huryn *et al.*, 2002). On the other hand, if nutrients, temperature and sediment are higher, breakdown rates in impacted streams might be similar to reference streams because of lower nutrients and temperatures (Niyogi *et al.*, 2003; Hagen *et al.*, 2006) or may be even lower than reference streams because of lower shredder abundance (Sponseller & Benfield, 2001). Agricultural streams had higher nutrients and temperature in our study, leading us to expect higher microbial biofilm activity and faster breakdown. However, some of our agricultural streams also had high sediment load, which may inhibit microbial activity on wood substrata. As a result, there was no net result of agriculture on wood breakdown because accumulation of sediment appears to eliminate the effects of higher nutrients and temperature.

The ambiguity of agriculture's effect on wood decomposition and respiration by microbes on wood makes it difficult to draw conclusions about the resistance or resilience of organic matter processes to agriculture. Recovery of organic matter decomposition following reforestation from past agriculture depends on the legacy of the historical land use on physical and chemical stream conditions. Reforested streams with elevated nutrient concentrations but low sediment loads might have elevated microbial respiration and wood decomposition rates, as was shown by Meyer & Johnson (1983). However, streams with sediments remaining from previous land uses might have low microbial activity and wood decomposition rates, as seen in REC streams with high sediment accumulations.

Since Bunn & Davies (2000) and Gessner & Chauvet (2002) advocated functional measurements, including organic matter decomposition, to assess stream ecosystem health, many studies have explored the effects of land use on leaf breakdown. These studies generally support the concept of functional assessment using breakdown rates but also caution about the potential confounding and contradictory effects that land use can have on breakdown rates (Niyogi *et al.*, 2003; Hagen *et al.*, 2006). In particular, the similarity of breakdown rates in undisturbed reference and heavily

disturbed streams (Hagen *et al.*, 2006; Lecerf *et al.*, 2006; present study) casts doubt on the usefulness of leaf breakdown to assess stream functional integrity. If low-nutrient concentrations limit breakdown of organic matter in reference streams but high sediment loads limit breakdown in highly impacted streams (Niyogi *et al.*, 2003; Hagen *et al.*, 2006), the net effect of human disturbance on decomposition could be null. Because wood breakdown is mediated by surface microbial biofilms, it could be particularly sensitive to the various changes in stream conditions caused by land uses. Streams with different land uses (agriculture versus urban) may have similar breakdown rates but differ dramatically in the mechanisms affecting breakdown rates (Paul *et al.*, 2006). The complexity of interacting factors that affect wood decomposition, particularly in streams affected by human activities, and the variability among streams, even without land use (Spänhoff & Meyer, 2004), suggest that wood breakdown and microbial biofilm processes may not be suitable for biomonitoring of agricultural impact of streams.

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