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Are leaf breakdown rates a useful measure of stream integrity along an agricultural landuse gradient?

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Abstract. Biological indicators often are used to assess and manage water quality in anthropogenically altered stream systems. Leaf breakdown has the potential to be a good indicator of stream integrity because it integrates a variety of biological, chemical, and physical conditions. Red maple (*Acer rubrum* L.) leaf breakdown rates were measured along a gradient of agricultural land use in southern Appalachian streams to assess the use of leaf breakdown rates as a measure of stream integrity. Landuse categories included forested, light agriculture, moderate agriculture, and heavy agriculture. Leaf breakdown rates were related to landuse category but did not differ significantly among landuse categories. Nutrient concentration, temperature, and sedimentation increased, and dissolved O_2 decreased along the landuse gradient from forest to heavy agriculture. Macroinvertebrate richness, macroinvertebrate density, and shredder density were the only significant predictors of leaf breakdown rates. We conclude that leaf breakdown rates may not be a useful indicator of stream integrity because of the confounding effects that agricultural land use has on breakdown rates.

Key words: leaf breakdown, stream integrity, shredding macroinvertebrates, agriculture, landuse gradient, southern Appalachians.

Allochthonous inputs of organic matter from surrounding riparian vegetation are an important source of energy to forested streams (e.g., Wallace et al. 1997). Even streams that drain catchments lacking a significant number of trees, such as prairie or agricultural streams, receive organic matter input from the surrounding riparian zone (Stagliano and Whiles 2002, Hagen 2004). Leaves entering streams generally break down via a multi-step process: chemical leaching of soluble compounds, aerobic degradation by microbial organisms (conditioning), physical abrasion, and physical fragmentation by leaf-shredding macroinvertebrates (shredders) (Webster and Benfield 1986). Leaf breakdown in streams is an important ecosystem process that is influenced by a number of factors including water temperature, dissolved O_2, sedimentation, water velocity, leaf species, microbial activity, macroinvertebrate composition, changes in riparian vegetation and surrounding land use, and concentration of dissolved nutrients (e.g., Webster and Benfield 1986, Gessner et al. 1999).

The factors influencing leaf breakdown rates in forested streams are well known, but many of these factors are altered by the conversion of forested land to agriculture. For example, agricultural land use often results in a reduction of riparian vegetation. Loss of vegetation reduces shading, increases insolation, elevates stream temperatures, and lowers dissolved O_2 concentrations (e.g., Quinn 2000, Allan 2004). Nutrient concentrations tend to increase with agricultural land use in response to runoff of fertilizers and excretion by grazing animals adjacent to or directly in the stream (Townsend and Riley 1999). High sedimentation, soil erosion, and bank instability often are associated with agricultural streams (Allan et al. 1997). Movement of sediments, especially during storms, can cause abrasion and physical breakdown of leaf material. In contrast, sediments can bury leaves, resulting in anaerobic conditions, which in turn prevent fungal or macroinvertebrate colonization (Cummins et al. 1980, Webster and Waide 1982, Benfield et al. 2001). In addition, high rates of sedimentation can be detrimental to aquatic biota and can further slow biological fractionation of leaf litter (Zweig and Rabeni 2001).

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Allochthonous material, primarily in the form of leaves, is an important energy source for macroinvertebrates in stream food webs (e.g., Cummins 1974, Minshall et al. 1985), and several studies have shown that macroinvertebrate abundance controls rates of leaf breakdown (Petersen and Cummins 1974, Iversen 1975, Wallace et al. 1982, Dangles et al. 2001). Shredders are particularly important in leaf breakdown and particulate organic matter production in temperate streams (Wallace et al. 1982, Kirby et al. 1983, Benfield and Webster 1985, Sponseller and Benfield 2001). Thus, a reduction in leaf-litter input associated with agricultural land use may reduce shredder biomass and production because of limited food availability. The subsequent loss of shredders may potentially affect leaf breakdown rates (Dance and Hynes 1980, Harding and Winterbourn 1995, Wallace et al. 1997, Sponseller and Benfield 2001).

Several studies suggest using leaf breakdown rates to assess the effects of anthropogenic disturbance on stream ecosystem integrity (e.g., Webster and Benfield 1986). The definition of ecosystem integrity is subject to debate (e.g., Karr 1991) but, for the purpose of our study, ecosystem integrity is a measure of deviation from a desired historic ecosystem state. We define streams with minimal deviation from reference conditions as having high integrity (Bunn and Davies 2000) because reference conditions are chosen to reflect the ecosystem state when free from human disturbance. Macroinvertebrates commonly are used to assess stream integrity (e.g., Lenat and Crawford 1994, Karr 1999) because water quality, particularly temperature, dissolved O_2 concentration, and sedimentation can have direct effects on macroinvertebrate community structure. These assessments tend to rely solely on structural components of stream systems (e.g., species diversity and species richness) even though information on both structural and functional characteristics is important for understanding stream integrity (Minshall 1996, Gessner and Chauvet 2002). Measures of ecosystem function (e.g., nutrient cycling, leaf breakdown, and primary production) have been used as indicators of stream integrity (e.g., Meyer 1997, Bunn et al. 1999, Gessner and Chauvet 2002).

Several studies have suggested using leaf breakdown as a measure of stream integrity (Webster and Benfield 1986, Gessner and Chauvet 2002) because leaf breakdown provides a sensitive, integrated measure of community- and ecosystem-level processes such as allochthonous input, microbial and macroinvertebrate activity, and chemical and physical conditions. However, only a few studies have used leaf breakdown rates to measure stream integrity, whereas numerous studies have incorporated macroinvertebrate indices (e.g., Resh and Jackson 1993, Barbour et al. 1999). Ecosystem function is closely tied to stream integrity; however, it is often unclear how changes in stream structure impact ecosystem function (Bunn et al. 1999). For example, Angermeier and Karr (1994) noted that ecosystem function did not necessarily change in response to shifts in structure (e.g., species diversity). Moreover, studies that have used leaf breakdown to assess stream integrity generally compared leaf breakdown in reference streams vs altered streams rather than along a gradient of integrity (but see Dangles et al. 2004).

The purpose of our study was to determine whether leaf breakdown rates could be used to measure stream integrity along an agricultural landuse gradient. We compared leaf breakdown rates in 12 streams in the southern Appalachians (North Carolina and Georgia). Study stream conditions varied from reference (forested) to heavy agriculture. Forested streams were regarded as having high integrity and were used as reference sites because they represent historic conditions for the agricultural streams we studied. Our hypothesis was that streams with intermediate levels of agriculture (light and moderate) would have faster breakdown rates than reference streams and those with heavy levels of agriculture because of the combined effects of elevated water temperature, high nutrient concentrations, and the presence of shredding macroinvertebrates. Despite a high number of shredding macroinvertebrates in forested streams, we expected slow breakdown rates because of cool temperatures and low nutrient concentrations. We also predicted that heavy-agriculture streams would have slow breakdown rates in response to high sedimentation rates and a paucity of shredders.

Methods

Site description

Our study was conducted in the southern Appalachian Mountains in Macon County, North Carolina, and Rabun County, Georgia, in the Blue Ridge geological province. The southern Appalachian region is characterized by forested land in the mountains and agriculture in river valleys (SAMAB 1996). The land is not well suited for row crops because of steep hill slopes and high soil erosion rates. Therefore, the primary use of agricultural lands in the southern Appalachians is as pasture for livestock grazing.

The 12 stream sites selected for study were within the Upper Little Tennessee River catchment along a gradient of agricultural land use. Landuse categories included forested, light-agriculture, moderate-agriculture, and heavy-agriculture streams. Stream sites, consisting of 100-m stream reaches that drained

TABLE 1. Ranges of mean values of landuse characteristics of streams in each landuse category (forested: $n = 3$, light agriculture: $n = 2$, moderate agriculture: $n = 3$, heavy agriculture: $n = 4$). See text for an explanation of agricultural influence.

Landuse characteristics	Forested	Light agriculture	Moderate agriculture	Heavy agriculture
3-m riparian tree density (no. trees/ha within 3 m of the stream)	1161–1299	587–772	460–870	0–92
10-m riparian tree density (no. trees/ha within 10 m of the stream)	1179–1620	367–568	70–448	0–63
3-m riparian tree basal area (m^2/ha within 3 m of the stream)	32–47	22–35	11–32	0–5
10-m riparian tree basal area (m^2/ha within 10 m of the stream)	35–37	15–36	2–20	0
Riparian canopy cover (%)	83–86	61–84	37–80	0–13
Stream canopy cover (%)	33–39	27–30	25–32	1–8
Grass ground cover (%)	0	6–17	29–42	67–95
Agricultural influence	0	1	2	2–4

separate tributaries of the Upper Little Tennessee River, were within a 17-km radius and drained catchments of similar bedrock and surface geology (Georgia Geological Survey 1976, North Carolina Geological Survey 1985).

Riparian vegetation along forested streams consisted of a mixed deciduous forest composed primarily of birch (*Betula* sp.), maples (*Acer rubrum* L. and *A. saccharum* Marsh.), oak (*Quercus* sp.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), and yellow poplar (*Liriodendron tulipifera* L.), with a dense understory of rhododendron (*Rhododendron maximum* L.). Riparian vegetation along light-agriculture streams was primarily yellow poplar, yellow buckeye (*Aesculus octandra* Marsh.), and red maple. Riparian vegetation along moderate-agriculture streams was predominantly red maple and alder (*Alnus serrulata* (Ait.) Willd.). The few trees present in heavy-agricultural riparian zones included alder and sycamore (*Platanus occidentalis* L.).

Stream sites were assigned initially to landuse categories based on the influence of agriculture and the extent of forested riparian zone along each study reach (Table 1). Riparian land use is related to leaf breakdown rates, but land use at the catchment scale is not (Sponseller and Benfield 2001). The influence of agriculture was categorized on the basis of the occurrence of active agriculture and livestock grazing along each stream reach (0 = agriculture not present in catchment; 1 = active agriculture present in catchment, no livestock grazing adjacent to stream; 2 = active agriculture in catchment, livestock fenced from stream; 3 = active agriculture in catchment, livestock had historic access to stream; and 4 = active agriculture in catchment, livestock have current access to stream). Extent of forested riparian zone along each stream reach was quantified as riparian tree density (number of trees/ha within 3 and 10 m of the stream), riparian tree basal area (m^2/ha within 3 and 10 m of the stream), % riparian canopy cover, % stream canopy cover, and % grass ground cover (Table 1; methods described by Hagen 2004).

Landuse categories were verified with principle components analysis (PCA). The variables used to quantify the extent of forested riparian zone and agricultural influence (except for 10-m riparian tree basal area) were standardized (mean = 0, SD = 1) and transformed when necessary to meet the assumptions of PCA. Stream scores were plotted on the first 2 principle component axes, and the plot was examined for clusters of streams.

Physicochemical variables

Water samples were collected approximately monthly, December 2002 through September 2003, from each stream reach. On each sampling date, three 60-mL water samples were filtered in the field (Whatman GF/F), stored in acid-washed polyethylene bottles, and frozen until analysis. NO_3-N and NH_4-N were measured 7 times (December 2002 and January, March, April, May, June, and September 2003) using a Technicon Autoanalyzer II (Technicon, Saskatoon, Canada) or Dionex DX500 Chromatography System (Ion Chromatography/High Pressure Liquid Chromatography, Dionex Corporation, Sunnyvale, California). Soluble reactive P (SRP) was measured 5 times (January, March, April, May, and September 2003) using the Technicon Autoanalyzer II. One-half detection limits were used for nutrient concentrations below instrument resolution.

Dissolved O_2 (DO, mg/L) and specific conductance (μS/cm) were measured monthly from October 2002 to September 2003 at each stream site using YSI DO and conductivity probes (Model 55 DO probe and Model 30 conductivity probe, Yellow Springs Instruments, Yellow Springs, Ohio). Stream temperatures were recorded every 4 h from September 2002 to September 2003 using temperature data loggers (HOBO, Pocasset, Massachusetts). Average annual temperature, mean daily temperature, and cumulative degree-days (dd) above 0°C over the duration of the study were calculated.

Streambed sediment distribution was measured using a pebble-count technique described by Bunte and Abt (2001). Within each stream reach, 100 streambed particles were selected at random and the *b*-axis of each particle was measured by passing the particle through a gravelometer, sized by the Wentworth scale (Bunte and Abt 2001). Particles <2 mm were further differentiated visually as silt or sand. Percentage silt and % silt and sand were estimated for each stream reach from the 100 particles collected for the streambed sediment assessment.

Discharge was calculated at 3 locations in each stream during summer baseflow conditions. Velocity was measured with a Marsh–McBirney Flo-Mate Model 2000 flow meter (Marsh–McBirney, Frederick, Maryland) and depth was recorded at 3 to 10 evenly spaced points across the wetted width of each stream. Discharge was calculated as the wetted width of each stream multiplied by its average depth and velocity. The 3 discharge measurements were averaged for each stream reach.

Leaf breakdown

Red maple leaf breakdown was measured over 5 mo beginning November 2002 using the leaf-bag method (Benfield 1996). Red maple is a dominant riparian species at most of the stream sites and, thus, a major contributor of leaf input. Senescent leaves from a single tree were collected shortly after abscission in autumn 2002 and air dried to a constant mass. Leaf bags (4-mm mesh size) were filled with 6.0 g dried leaves, and 12 bags were anchored in riffles in each of the 12 streams during autumn leaf fall in 2002. An additional 5 leaf bags were carried into the field but were never placed in the stream. The leaves in these bags were reweighed upon return to the laboratory to account for handling loss.

Three leaf bags were retrieved at random from each site 4 times throughout the study (after 28, 57, 100, and 147 d) and stored on ice until processing within 48 h of collection. Leaves were rinsed over a 250-µm-mesh sieve to remove sediment and collect aquatic invertebrates. Leaves were dried (50°C) to a constant mass, weighed, ground, subsampled, and ashed (550°C, 45 min) to determine the ash-free dry mass (AFDM) remaining.

A short-term (39-h) leaching study was conducted to account for the initial and rapid loss of soluble compounds from the leaves upon entering the stream. Nine leaf bags, each with 6.0 g dried red maple leaves, were placed in Ball Creek (forested). Three leaf bags were recovered after 12, 24, and 39 h. Four additional leaf bags were taken to the field but never placed in the stream to account for handling loss. AFDM was determined on leaves used in the leaching experiment.

Macroinvertebrates

Macroinvertebrates were preserved in 80% ethanol, counted, and identified to genus when possible (except for Oligochaeta and Chironomidae, which were identified to class and family, respectively). Shredding macroinvertebrates were identified according to Merritt and Cummins (1996) and Voshell (2003). Mean abundance of macroinvertebrates and mean abundance of shredders (ind./leaf bag), total macroinvertebrate and shredder density (ind./g AFDM leaf litter remaining), and macroinvertebrate community richness (total number of taxa/stream) were calculated for each stream.

Statistical analyses

Differences in water chemistry (NO_3-N, NH_4-N, SRP, DO, and specific conductance), annual stream temperature, % silt, and % silt and sand were compared among streams in the 4 landuse categories using 1-way analysis of variance (ANOVA) followed by Tukey's post hoc multiple comparison tests. Differences in macroinvertebrate assemblages (total macroinvertebrate and shredder abundance and density and community richness) were compared among streams in the 4 landuse categories using 1-way ANOVA followed by Tukey's post hoc multiple comparison tests. When the data did not satisfy the assumptions of ANOVA, Kruskal–Wallis tests on rank-transformed data and Dunn's multiple comparison tests were used. Data presented as % were arcsine-square-root transformed to produce a normal distribution (Zar 1999).

Breakdown rates were calculated using a negative exponential decay model (Petersen and Cummins 1974) as the slope of the regression line of ln(% AFDM leaf litter remaining) vs time. Breakdown rates were compared among landuse categories using analysis of covariance (ANCOVA) followed by Tukey's post hoc multiple comparison test.

Regression analyses (simple linear regression and 2^{nd}-order quadratic regression) were used to explore the associations of biological, chemical, and physical factors with breakdown rates. Forward stepwise multiple regression was used to select the best model for predicting leaf breakdown rates among landuse categories.

All statistical analyses were done using SigmaStat for Windows (version 3.00, SPSS, Chicago, Illinois) except for PCA, which was done using Minitab for Windows (Minitab, State College, Pennsylvania), and

ANCOVAs, which were done using Systat 10 for Windows (SPSS, Chicago, Illinois).

Results

Landuse categories

The 1st principal components axis had an eigenvalue of 6.21 and explained 89% of variance, and the 2nd principal components axis had an eigenvalue of 0.42 and explained 6% of total variance. Percentage grass ground cover and 3-m riparian tree basal area were strongly correlated with the 1st principal components axis, whereas 10-m riparian tree density was strongly correlated with the 2nd principal components axis. Based on the ordination, one stream was reclassified from moderate agriculture to heavy agriculture, and another was reclassified from light agriculture to moderate agriculture. This reclassification resulted in an unbalanced design (3 forested streams, 2 light-agriculture streams, 3 moderate-agriculture streams, and 4 heavy-agriculture streams; Fig. 1).

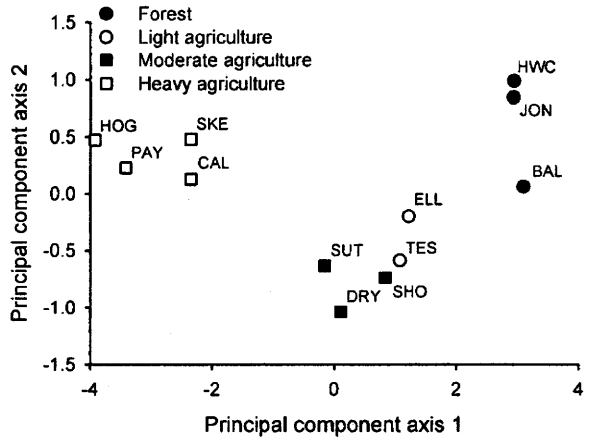

FIG. 1. Principal components analysis of sites showing separation of streams on the basis of landuse characteristics. BAL = Ball Creek, HWC = Hugh White Creek, JON = Jones Creek, ELL = North Prong Ellijay Creek, TES = Tessentee Creek, DRY = Dryman Fork, SHO = North Shope Fork, SUT = Sutton Branch, CAL = Caler Fork, HOG = Hoglot Branch, PAY = Payne Creek, SKE = North Fork Skeenah Creek.

Physicochemical variables

Stream nutrient concentrations generally increased along the landuse gradient from forested to heavy-agriculture streams. Mean NO_3-N increased 4× along the landuse gradient, ranging from 10.9 µg/L in Ball Creek (forested) to 211.0 µg/L in Payne Creek (heavy agriculture). Median NH_4-N increased >2× along the landuse gradient, ranging from ~3 µg/L in forested and light-agriculture streams to ~7 µg/L in moderate- and heavy-agriculture streams (Table 2). Mean SRP concentrations ranged from 1.6 µg/L in Hugh White Creek (forested) to 4.0 µg/L in Sutton Branch (moderate agriculture) and was ~2× higher in agricultural streams than in forested streams (Table 2).

DO was significantly higher in light-agriculture streams than in heavy-agriculture streams ($p = 0.01$; Table 2). Specific conductance and stream temperature increased significantly along the landuse gradient from forested to heavy-agriculture streams (Table 2). Annual stream temperature (September 2002–September 2003) ranged from 10.7°C in Ball Creek (forested) to 14.4°C in Payne Creek (heavy agriculture). Over the entire study, November 2002 to April 2004 (148 d), average stream temperature was coldest in North Prong Ellijay Creek (light agriculture, 6.4°C) and warmest in Payne Creek (heavy agriculture, 8.9°C). The number of degree days (dd) ranged from 939 in North Prong Ellijay Creek to 1316 in Payne Creek (Table 3); however, dd did not differ among landuse categories.

Streambed sediment distribution was related to land use. Heavy-agriculture streams had significantly greater % silt than forested and light-agriculture streams ($p = 0.009$; Table 2). Likewise, % silt and sand was substantially lower in forested streams than in moderate- and heavy-agriculture streams ($p = 0.002$; Table 2). Width, depth, velocity, and discharge did not differ among landuse categories. Average discharge was 0.30 m^3/s (range: 0.02–0.76 m^3/s) with no pattern among landuse categories (Table 2).

Leaf breakdown

Red maple leaves lost 20% of initial dry mass within the first 12 h of the leaching study. The initial leaf mass used when determining breakdown rates was corrected from 6.0 g to 4.2 g AFDM to account for loss of leaf mass caused by handling (11%) and leaching (20%). Red maple leaf breakdown rates ranged from 0.0053 to 0.0180/d and 0.0007 to 0.0030/dd across all study streams (Table 3). Leaf breakdown was significantly related to landuse category (ANOVA, rate/d: $p = 0.001$, rate/dd: $p < 0.001$; Fig. 2A, B). However, Tukey's multiple comparison tests failed to find any significant differences among individual landuse categories. Breakdown rates tended to be faster in light- and moderate-agriculture streams than in forested and heavy-agriculture streams (Fig. 2A, B).

Macroinvertebrates

Total macroinvertebrate and shredder density and abundance were significantly related to landuse category. Macroinvertebrate abundance (Fig. 3A),

TABLE 2. Mean (±1 SE) chemical and physical characteristics for streams in each landuse category (forested: $n = 3$, light agriculture: $n = 2$, moderate agriculture: $n = 3$, heavy agriculture: $n = 4$). Means with different superscripts were significantly different ($p < 0.05$). $p < 0.05$ indicates variable differed significantly among landuse categories. SRP = soluble reactive P.

Variable	Forest	Light agriculture	Moderate agriculture	Heavy agriculture	p
NO_3-N (μg/L)	30.4 (19.4)	65.2 (12.1)	80.7 (55.5)	134.6 (33.1)	0.28
NH_4-N (μg/L)[a]	3.2 (3.1–3.3)	2.9 (2.8–3.0)	5.0 (2.5–15.5)	7.4 (6.4–12.4)	0.12
SRP(μg/L)	1.7 (0.1)	3.8 (0.0)	2.9 (0.5)	3.4 (0.7)	0.17
Dissolved O_2 (mg/L)	7.42 (0.01)^{AB}	7.72 (0.12)^{A}	7.13 (0.08)^{AB}	6.90 (0.16)^{B}	0.01
Specific conductance (μS/cm)	14.1 (3.0)^{A}	25.6 (7.3)^{AB}	21.9 (3.2)^{AB}	32.3 (2.8)^{B}	0.03
Temperature (°C)	10.9 (0.1)^{A}	11.6 (0.0)^{AB}	12.1 (0.2)^{B}	13.7 (0.2)^{C}	<0.001
Silt (%)	1.7 (0.3)^{A}	4.0 (4.0)^{A}	21.3 (6.0)^{AB}	28.0 (6.9)^{B}	0.009
Silt and sand (%)	12.3 (0.7)^{A}	17.5 (5.5)^{AB}	34.0 (6.4)^{BC}	42.0 (2.9)^{C}	0.002
Width (m)	3.7 (1.1)	5.8 (0.3)	3.7 (1.2)	2.0 (0.6)	0.14
Depth (m)[a]	0.13 (0.09–0.22)	0.23 (0.18–0.27)	0.16 (0.12–0.19)	0.16 (0.15–0.16)	0.37
Velocity (m/s)[a]	0.56 (0.21–0.74)	0.48 (0.47–0.48)	0.47 (0.27–0.75)	0.59 (0.46–0.77)	0.85
Discharge (m^3/s)	0.43 (0.14)	0.61 (0.15)	0.22 (0.08)	0.16 (0.04)	0.09

[a] Did not meet assumptions of analysis of variance; median (range) shown

macroinvertebrate density (Fig. 3B), and shredder density (Fig. 3D) generally were higher in light- and moderate-agriculture streams than in forested and heavy-agriculture streams. Total macroinvertebrate abundance ranged from 34.7 to 85.2 ind./leaf bag (Fig. 3A). The abundance of macroinvertebrates in leaf bags in light-agriculture streams was 1.7× higher than in forested and heavy-agriculture streams ($p = 0.02$; Fig. 3A). Macroinvertebrate density in leaf bags ranged from 17.5 ind./g AFDM leaf litter remaining in Hoglot Branch (heavy agriculture) to 108.3 ind./g AFDM leaf litter remaining in North Prong Ellijay Creek (light agriculture). Mean macroinvertebrate density in light- and moderate-agriculture streams was ~2 to 3× higher than in forested and heavy-agriculture streams ($p < 0.001$; Fig. 3B). Abundance of shredding macroinvertebrates ranged from 0.3 to 18.1 ind./leaf bag, with significantly fewer shredders in heavy-agriculture streams than in streams in other landuse categories ($p = 0.001$; Fig. 3C). Mean shredder density ranged from 0.1 ind./g AFDM leaf litter remaining in Hoglot Branch to 16.5 ind./g AFDM leaf litter remaining in North Prong Ellijay Creek. Shredder density was significantly lower in heavy-agriculture and forested streams than light- and moderate-agriculture streams ($p < 0.001$; Fig. 3D).

Macroinvertebrate abundance and density in leaf bags increased throughout the study, with significantly higher abundances after 100 d in the streams than after 28 and 57 d ($p < 0.001$; Fig. 4A, B). Throughout the study, macroinvertebrate abundance and density were consistently highest in light-agriculture streams and lowest in forested and heavy-agriculture streams ($p < 0.001$; Fig. 4A, B). Shredder abundance in forested and moderate-agriculture streams increased throughout the course of the study (Fig. 4C). On day 147, forested and heavy-agriculture streams consistently had the lowest densities of total macroinvertebrates (Fig. 4B)

TABLE 3. Red maple leaf breakdown rates in 12 streams with different land use. dd = degree days. r^2 refers to the fit of the exponential decay model; $p < 0.05$ for all breakdown rates/d and for all breakdown rates/dd.

Land use	Stream name	Stream code	Breakdown rate (/d)	r^2	Breakdown rate (/dd)	r^2	Cumulative dd
Forested	Ball Creek	BAL	0.0059	0.98	0.0009	0.93	963
	Hugh White Creek	HWC	0.0075	0.95	0.0011	0.99	1088
	Jones Creek	JON	0.0113	0.96	0.0018	1.00	974
Light agriculture	North Prong Ellijay Creek	ELL	0.0180	0.90	0.0030	0.98	939
	Tessentee Creek	TES	0.0114	0.97	0.0017	0.98	1018
Moderate agriculture	Dryman Fork	DRY	0.0121	0.90	0.0018	0.96	1071
	North Shope Fork	SHO	0.0138	0.94	0.0018	0.97	1199
	Sutton Branch	SUT	0.0140	0.90	0.0020	0.97	1095
Heavy agriculture	Caler Fork	CAL	0.0083	0.99	0.0011	0.94	1092
	Hoglot Branch	HOG	0.0053	0.94	0.0007	0.99	1079
	Payne Creek	PAY	0.0093	0.96	0.0010	0.92	1316
	North Fork Skeenah Creek	SKE	0.0115	0.88	0.0015	0.96	1232

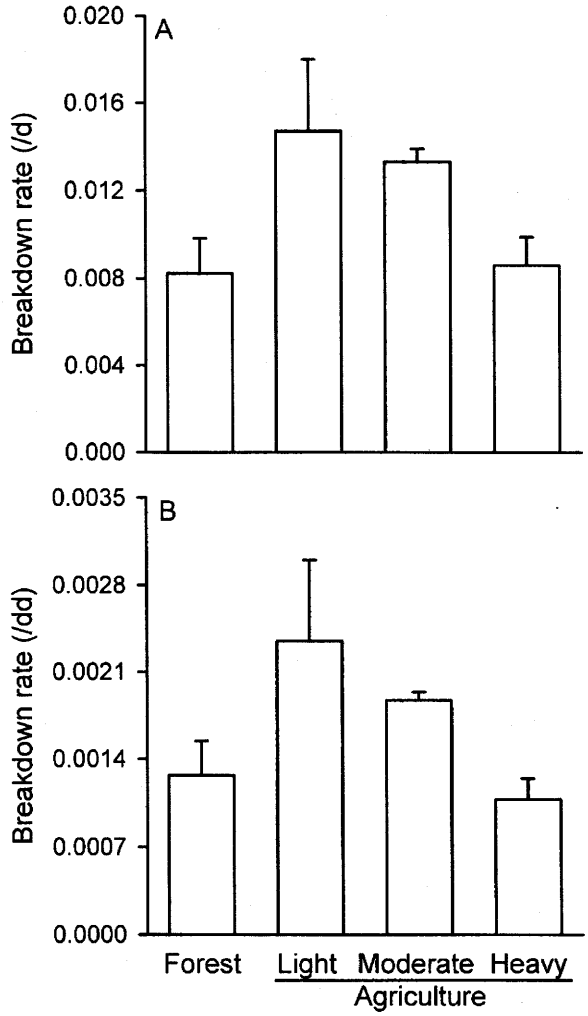

FIG. 2. Mean (+1 SE) leaf breakdown rate per day (A) and leaf breakdown rate per degree day (dd; B) in streams along an agricultural landuse gradient.

and shredding invertebrates (Fig. 4D). Both macroinvertebrate and shredder density increased with days in stream in each landuse category (Fig. 4B, D).

The shredder assemblage varied considerably among landuse categories. *Tallaperla* sp. (Plecoptera) were abundant in forested streams, whereas *Tipula* sp. (Diptera) were common shredders in light- and moderate-agriculture streams (Fig. 5). *Lepidostoma* (Trichoptera), *Pycnopsyche* (Trichoptera), and *Leuctra* (Plecoptera) also were abundant in forested, light-agriculture, and moderate-agriculture streams (Fig. 5). Heavy-agriculture streams were characterized by few shredding macroinvertebrates. Macroinvertebrate taxa richness varied from 16 taxa in Hoglot Branch (heavy agriculture) to 40 taxa in Tessentee Creek (light agriculture) but was not significantly related to landuse category ($p > 0.05$). Macroinvertebrate richness (Fig. 6A), macroinvertebrate density (Fig. 6B), and shredder density (Fig. 6C) were significant predictors of leaf breakdown rates. The strongest model produced by forward stepwise regression analysis using all measured variables included NO_3-N concentration, stream temperature, % silt, and shredder density. Furthermore, based on forward stepwise regression, shredder density was the best predictor of breakdown rates in all landuse categories assessed ($r^2 = 0.33$, $p < 0.05$).

Discussion

Effects of agriculture on leaf breakdown

Our results show that leaf breakdown is not a useful indicator of stream integrity along an agricultural landuse gradient because breakdown rates did not vary significantly among individual landuse categories and did not show a trend consistent with the landuse gradient that was reflected in other variables. Leaf breakdown rates were significantly related to landuse category, but multiple comparison tests failed to find any significant difference between any pairs of landuse categories. Low sample size and high variation in breakdown rates among streams within the same landuse category effectively masked any differences among landuse categories.

The influence of multiple confounding factors on leaf breakdown rates also may have limited the effectiveness of leaf breakdown as an indicator of stream integrity. Huryn et al. (2002) measured no difference in red maple breakdown rates between forested and agricultural streams and attributed this result to the antagonistic influences of shredding macroinvertebrates and nutrients (NO_3-N and SRP). That is, landuse categories with low nutrient concentrations tended to have large numbers of shredders (e.g., forested streams), whereas landuse categories with high nutrient concentrations tended to have few shredders (e.g., agricultural streams) (Huryn et al. 2002).

Elevated N and P concentrations increase breakdown rates (e.g., Robinson and Gessner 2000), and agricultural land use often is associated with high nutrient concentrations. In our study, nutrient concentrations generally increased along the gradient from forested to heavy-agriculture land uses. Elevated NO_3-N and NH_4-N concentrations in the moderate- and heavy-agriculture streams probably were caused primarily by fertilizer application and cattle grazing in the riparian zone (e.g., del Rosario et al. 2002), although N-fixing alder trees in the riparian zone

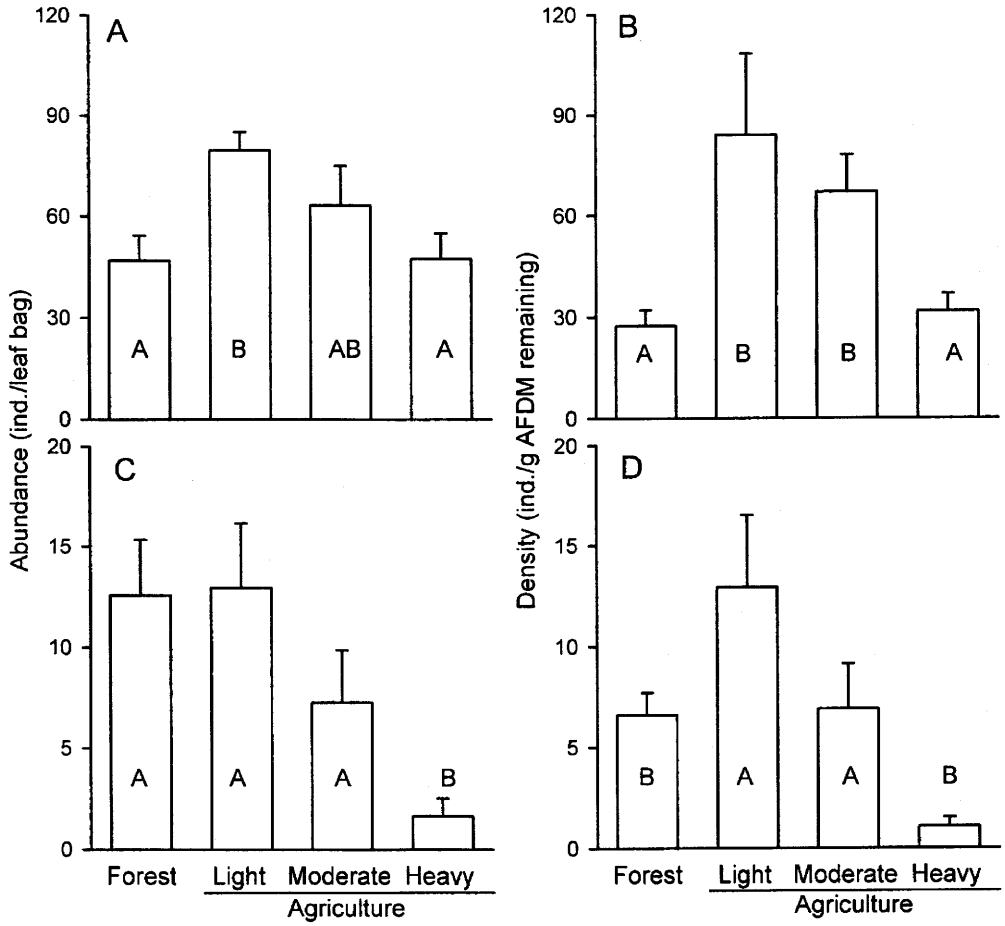

FIG. 3. Mean (+1 SE) macroinvertebrate abundance (A) and density (B) and shredder abundance (C) and density (D). $n = 2$ to 4 streams in each landuse category. Different letters indicate significant differences among landuse categories ($p < 0.05$). AFDM = ash-free dry mass.

may also have had some effect (Gregory et al. 1991). In forested and light-agriculture streams, faster leaf breakdown rates were correlated with higher NO_3-N, higher SRP, and lower NH_4-N concentrations. However, we found no correlation between breakdown rate and nutrient concentration in moderate- and heavy-agriculture streams.

Macroinvertebrate density, shredder density, and macroinvertebrate richness were the only significant predictors of leaf breakdown rates along the agricultural landuse gradient. This result is consistent with several studies that showed the importance of macroinvertebrates and shredders to leaf breakdown (e.g., Benfield and Webster 1985, Jonsson et al. 2001, Sponseller and Benfield 2001, Huryn et al. 2002, Hutchens and Wallace 2002). The positive effect of agricultural land use on shredder abundance in light- and moderate-agriculture streams probably was a response to increased light, elevated water temperatures, high nutrients, and adequate food supplies and habitat associated with intermediate levels of agricultural land use (Quinn 2000, Allan 2004). However, warm temperatures, high nutrient concentrations, low DO, and high rates of sedimentation most likely contributed to the decline in shredder abundance and density in heavy-agriculture streams. Low shredder abundance and density in heavy-agriculture streams also may have been a response to reductions in the quantity and diversity of riparian vegetation (Benfield et al. 1977).

Shredder density was the strongest predictor of leaf breakdown rates along the agricultural landuse gradient. However, shredder abundance and density were significantly lower in heavy-agriculture streams than in light- or moderate-agriculture streams. This result suggests that factors such as microbial degradation

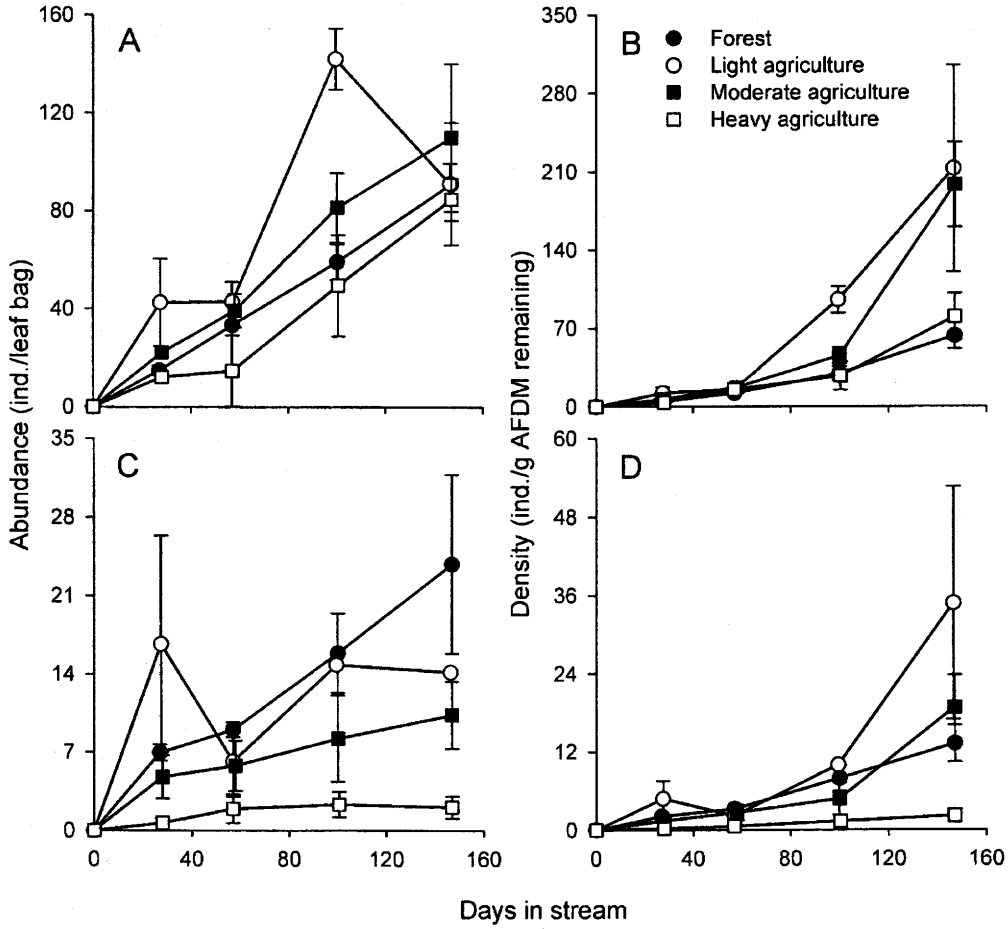

FIG. 4. Mean (±1 SE) macroinvertebrate abundance (A) and density (B) and shredder abundance (C) and density (D) over time in streams in different landuse categories. Error bars on some dates are too small to be seen. AFDM = ash-free dry mass.

and fragmentation by physical breakage dominate the leaf breakdown process in heavy-agriculture streams (Benfield et al. 1977, Bird and Kaushik 1992, Tuchman and King 1993, Young et al. 1994).

The leaf-bag method is an established technique used to measure leaf breakdown rates (e.g., Boulton and Boon 1991). However, this technique may have limitations when used in agricultural streams. For example, the leaf-bag method may overestimate breakdown rates if the bags attract colonizing macroinvertebrates by providing a more palatable food source and more suitable habitat than is present in natural leaf packs in agricultural streams. Thus, macroinvertebrate and shredder abundance, density, and richness may be estimated accurately for leaf bags, but leaf-bag assemblages may over-represent the macroinvertebrate assemblage at the reach scale (Webster and Waide 1982, Tuchman and King 1993).

Breakdown as a measure of stream integrity

Several studies suggest using leaf breakdown as an indicator of stream integrity because leaf breakdown is an integration of multiple stream characteristics (Webster and Benfield 1986, Gessner and Chauvet 2002). Gessner and Chauvet (2002) provided a method for assessing stream integrity using leaf breakdown rates. In their method, streams with breakdown rates above or below rates measured in pristine sites receive a low score. Niyogi et al. (2003) applied this method and found faster breakdown rates in agricultural streams than in pristine streams. Thus, Gessner and Chauvet's (2002) method accurately depicted agricultural streams as having poor stream integrity (Niyogi et al. 2003). However, in our study, leaf breakdown rates did not vary along the agricultural landuse gradient. When we applied Gessner and Chauvet's (2002) method to our data and calculated stream

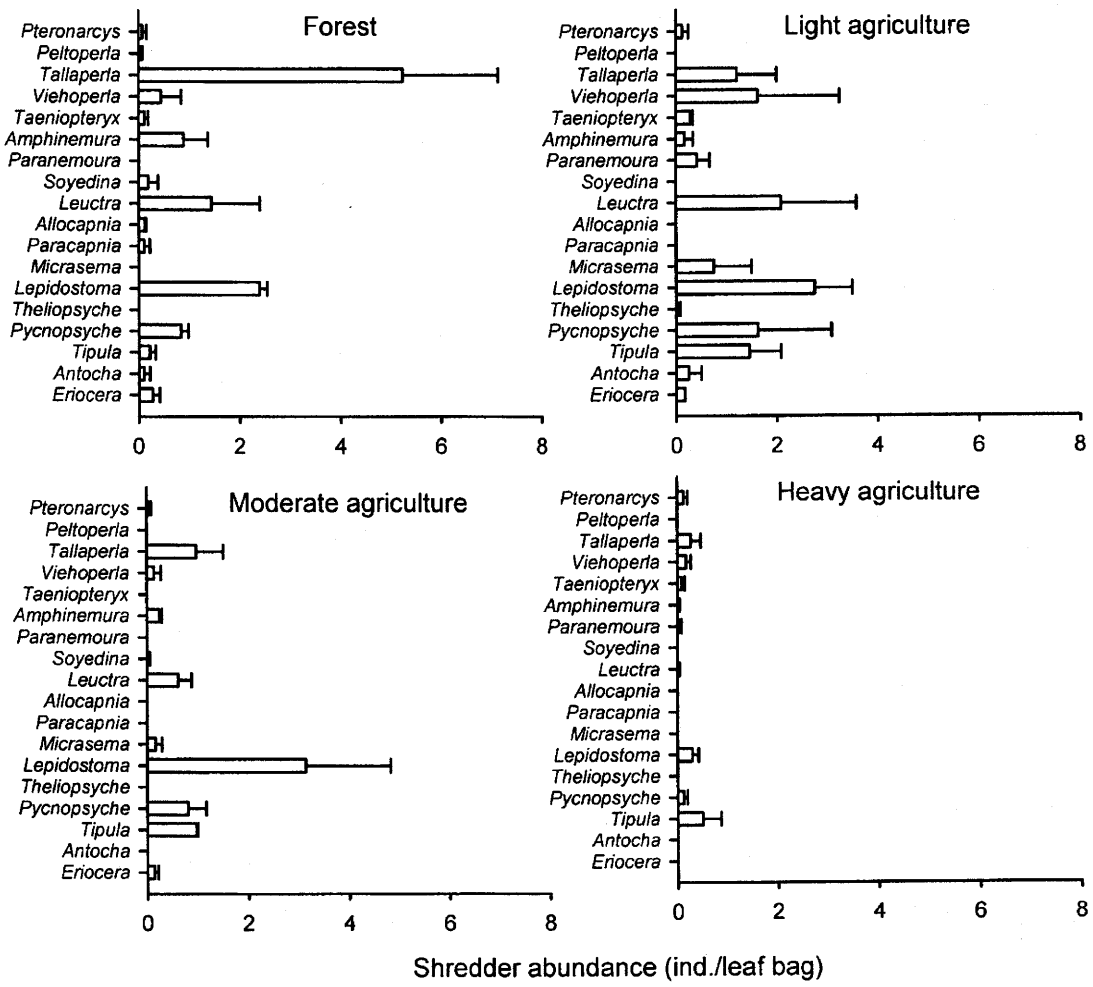

FIG. 5. Mean (+1 SE) shredder abundance for each landuse category. Values were calculated from mean stream values.

integrity scores, light- and moderate-agriculture streams generally received lower scores than heavy-agriculture streams. Heavy-agriculture streams and forested streams received similar scores because leaf breakdown rates in heavy-agriculture streams were similar to rates in forested streams. Niyogi et al. (2003) also reported similar integrity scores among several forested streams and one agricultural stream. Niyogi et al. (2003) attributed this result to sedimentation that slowed leaf breakdown rates in the agricultural stream, and they stressed that caution was necessary when using breakdown rates to assess stream integrity.

We must conclude from our calculation of high integrity scores in heavy-agriculture streams that either 1) heavy-agricultural land use does not reduce stream integrity, or 2) leaf breakdown rates are not a useful measure of stream integrity. The negative effects of agricultural land use on stream ecosystem water quality, habitat, and macroinvertebrate assemblages have been documented repeatedly (e.g., Harding et al. 1999, Quinn 2000, Allan 2004). In our study, heavy-agriculture streams showed evidence of low integrity including warm temperatures, high nutrient concentrations, low DO, high sedimentation, and an altered macroinvertebrate community. Sites were placed into landuse categories that reflected a decline in stream integrity along the landuse gradient from forested to heavy-agriculture streams, and heavy-agriculture streams were defined a priori as having the highest level of agricultural disturbance indicated by extent of riparian forest and livestock grazing. Thus, an accurate assessment of stream integrity should identify heavy-agriculture streams as having low integrity, and we argue that leaf breakdown rates were not a useful measure of stream integrity along an agricultural landuse gradient.

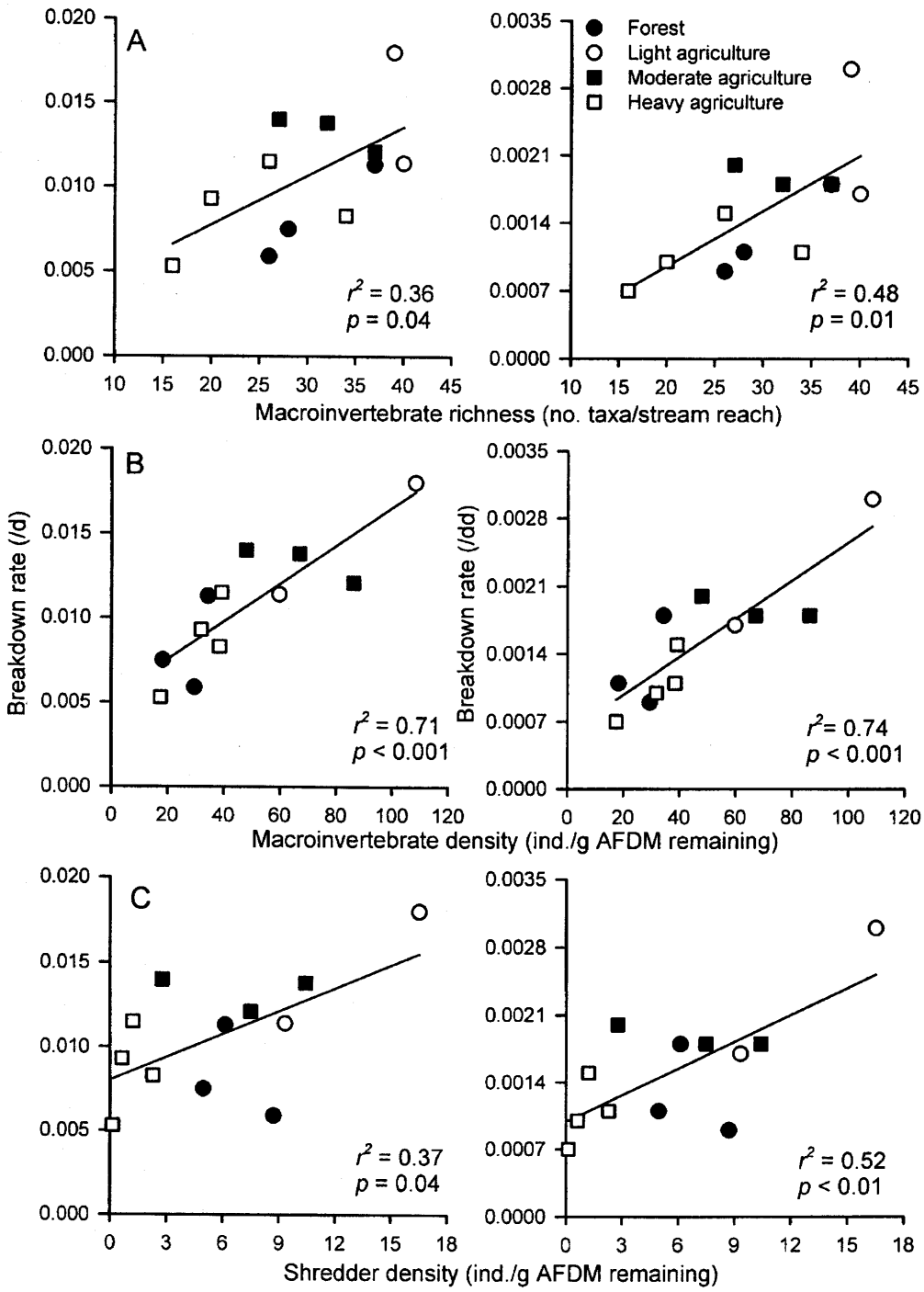

FIG. 6. Relationship between leaf breakdown rates (/d and /degree day [dd]) and macroinvertebrate richness (A), macroinvertebrate density (B), and shredder density (C).

Leaf breakdown rates may not be a useful indicator of stream integrity because of high variability in breakdown rates within individual landuse categories. Numerous factors influence leaf breakdown, so natural variability will exist even among reference streams. Natural variability may limit the effectiveness of leaf breakdown rates as a measure of stream integrity because it may mask variability specifically

associated with agricultural land use. Furthermore, studies that have shown higher leaf breakdown rates in response to agricultural land use (Young et al. 1994) were limited in that they compared leaf breakdown rates in reference streams to rates in one level of agricultural land use rather than assessing leaf breakdown along a gradient of land use from forest to heavy-agriculture (Benfield et al. 1977, Dance and Hynes 1980, Tuchman and King 1993). In our study, the complex influence of agriculture on leaf breakdown emerged when rates were evaluated along a gradient of land use. Agricultural land use does not simply result in elevated levels of leaf breakdown. Instead, our study suggests that agricultural land use has both positive and negative effects on leaf breakdown. The result is similar breakdown rates along the landuse gradient. Thus, leaf-bag breakdown rates are a measure of stream process that must be interpreted in the context of other structural and functional variables associated with the stream category being studied.

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