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Influences of land use on leaf breakdown in southern Appalachian headwater streams: a multiple-scale analysis

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Abstract. Stream ecosystems can be strongly influenced by land use within watersheds. The extent of this influence may depend on the spatial distribution of developed land and the scale at which it is evaluated. Effects of land-cover patterns on leaf breakdown were studied in 8 southern Appalachian headwater streams. Using a GIS, land cover was evaluated at several spatial scales, including the watershed, riparian corridor, and subcorridors that extended upstream in 200-m increments for 2 km. Breakdown rate for American sycamore (*Plantanus occidentalis*) leaf packs varied significantly among sites ($k = 0.0051–0.0180/d$), but fell within the range reported in the literature for sycamore. Leaf breakdown rate increased at sites with high shredder density and biomass. Further, breakdown rate and shredder density and biomass were positively related to mean substrate particle size. Several instream variables were related to watershed-scale features, but leaf breakdown rate was not related to land cover at the watershed scale. Leaf breakdown rate was inversely related to % nonforested land within riparian subcorridors of ~1 km. Results suggest that the distribution of shredders is critical to leaf processing in these streams. In some streams, increased sediment inputs resulting from agricultural activity or residential development in riparian corridors may limit the distribution of shredders and thus influence leaf breakdown rates. Alternatively, near-stream development may alter the quality of allochthonous inputs to streams, and thus indirectly influence the distribution of shredders and instream processing.

Key words: geographical information systems (GIS), shredders, riparian corridor, sedimentation.

Aquatic and terrestrial ecosystems are tightly coupled by the exchange of materials. This relationship is particularly important in forested headwater streams, which depend on allochthonous organic matter as the primary energy source (Fisher and Likens 1973). Leaves entering streams are trapped by retentive structures and broken down through several biological and physical processes (Petersen and Cummins 1974, Webster and Benfield 1986, Gessner et al. 1999). Microbial colonization of leaves marks the beginning of leaf breakdown (Barlöcher and Kendrick 1975, Suberkropp and Klug 1976), followed by invertebrate feeding, which can strongly influence breakdown rates (Sedell et al. 1975, Benfield and Webster 1985, Cummins et al. 1989). Water temperature (Suberkropp et al. 1975), dissolved oxygen (Cummins et al. 1980), availability of inorganic nutrients (Suberkropp and Chauvet 1995), stream geomorphology (Reice 1974, 1980, Meyer 1980), and organic matter retention structures (Rounick and Winterbourn 1983) all may influence the rate of leaf breakdown in streams.

Changes in both the biota and the physicochemical characteristics of streams induced by land-use activities may also influence leaf breakdown (Webster et al. 1995). For example, the presence of toxins or anthropogenic acidification may reduce leaf breakdown rate (Forbes and Magnuson 1980, Carpenter et al. 1983, Mulholland et al. 1987, Griffith and Perry 19939. Logging practices also may affect breakdown rate by increasing the delivery of sediments (Webster and Waide 1982) and dissolved nutrients (Meyer and Johnson 1983) to streams. Benfield et al. (1991) attributed high breakdown rates in streams draining logged watersheds to enhanced physical abrasion generated by a combination of increased sedimentation, loss of instream retention structures, and altered hydrologic regimes. Finally, because of the variation in breakdown rate among leaf species (Petersen and Cummins 1974), vegetation changes that accompany disturbances in the riparian zone may govern the distribution of shredder taxa and influence instream processing (Benfield et al. 1977, Smock and MacGregor 1988, Cummins et al. 1989).

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The extent of land-use impacts on stream ecosystems may depend on the spatial distribution of development in the watershed, and the spatial scale at which this distribution is evaluated (Allan and Johnson 1997). Johnson et al. (1997) found that water chemistry variables in 62 Michigan streams were related to both watershed-scale features (e.g., geology, land cover, and landscape structure) and land--cover patterns within 100-m riparian corridors. The relative importance of both spatial scales varied with season and chemical constituent. Several studies have examined the influence of watershed vs local (or riparian) features on stream ecosystem structure. For example, Richards et al. (1996) found that watershed-scale characteristics, particularly geology and the distribution of row-crop agriculture, governed aspects of stream channel morphology and hydrology. However, the structure of riparian corridors mediated erosional processes and influenced instream sediment-related variables. Using a similar approach, Richards et al. (1997) showed that despite watershed-scale control of channel structure and hydrology, macroinvertebrate species traits were strongly correlated -with local (reach-scale) features. Furthermore, Harding et al. (1998) reported that the history of land-cover patterns at both the watershed and riparian corridor scale are important determinants of macroinvertebrate community structure in North Carolina streams.

We used leaf breakdown rate to evaluate the impact of land use on ecosystem function in southern Appalachian headwater streams. This region has been subjected to a variety of land-use disturbances during the last century, including extensive logging, agriculture, and more recently, residential development (Yarnell 1998). Our objective was to determine how changes in ecosystem processes are related to the spatial distribution of land use within watersheds. Because several physical, chemical, and biological factors can mediate leaf breakdown, we predicted that disturbances operating at different spatial scales would act concurrently to influence breakdown rates. Our approach was to 1st determine which physicochemical and/or biological factors had the strongest influence on leaf breakdown rate. We then sought to discern the spatial scale(s) over which land-cover patterns relate to those features or processes that drive breakdown rate in streams.

Methods

Study site

The study was conducted in the Upper Roanoke River Basin (URRB) in southwestern Virginia (Fig. 1) at the interface of the Appalachian Valley and Ridge and Blue Ridge physiographic provmces. The URRB is topographically and geologically diverse, and is characterized by Precambrian and Cambrian metamorphics and clastics at high elevations and Cambrian and Ordovician carbonates at low elevations (Waller 1976). Land-use patterns in the URRB vary among watersheds but are generally characterized by a mixture of small livestock farms, and residential areas that are variable in age. Eight watersheds, with 2nd- or 3rd-order streams, were selected for study. Watersheds ranged in elevation from 325 to 575 m, and in area from 278 to 1014 ha. Fifty-meter stream reaches were selected in each watershed for study sites. Benthic habitat at all streams was dominated by particles ranging from silt to cobbles, though the relative proportion of these size classes varied among sites.

Land-use quantification

A geographical information system (Arcview 3.1, ESRI, Inc., Redland, California) was used to yuantify land cover within each watershed. Digital land-cover information for the Roanoke Valley was obtained from a preliminary land-cover map of Virginia, produced through the Virginia Gap Analysis Project (VAGAP) for 1992 (Morton 1998). This statewide data set was generated from 14 Landsat thematic mapper scenes, and classified using both unsupervised and enhanced supervised methods (Morton 1998). Pixels provided 30 x 30 m resolution and included information from 7 land-use categories: deciduous forest, coniferous forest, mixed forest, shrub / scrubland, herbaceous (mostly agriculture), open water, and disturbed (areas lacking vegetation). We categorized the data into *forest* and *nonforest*. The forest category included all forest types, but was dominated by the deciduous class. The nonforest category included both agricultural areas and urban/ suburban areas. Morton (1998) used aerial videography to acquire reference data and assess the overall accuracy of the land-cover data, which was 81%.

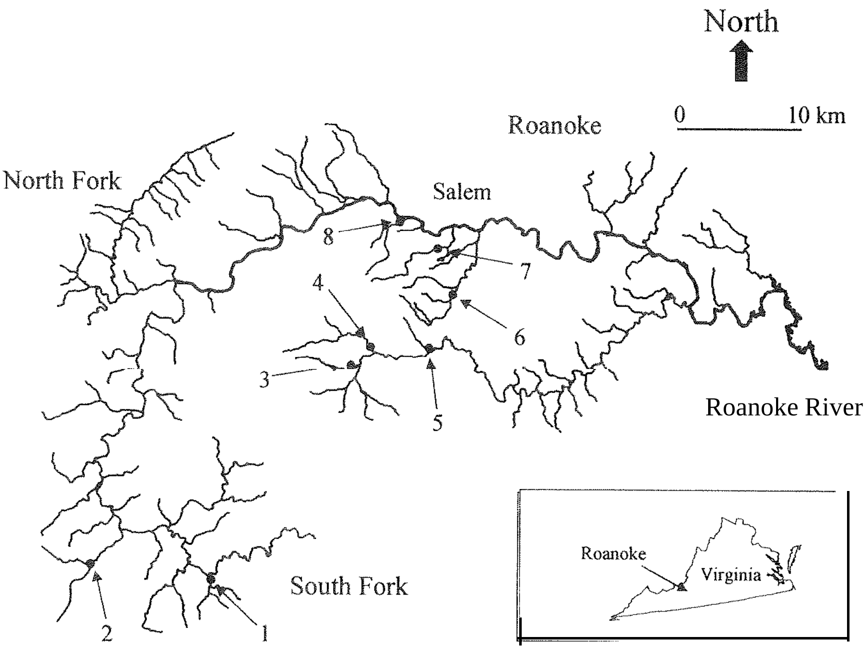

FIG. 1 **Upper Roanoke** River Basin, showing North and South Fork subbasins, and selected study sites. 1 = Powers Branch, 2 = Purgatory Tributary, 3 = Martins Creek, 4 = Little Back Creek, 5 = Greenbriar Branch, 6 = Mudlick Creek, 7 = Barnhardt Creek, 8 = Franklin Creek. Map does not include 1st-order channels.

This level of accuracy may not hold for riparian corridors, which are more difficult to classify, particularly in mountainous areas. Our accuracy assessment for riparian corridors from 25 locations across 5 watersheds with the greatest land-cover heterogeneity found ~75% of the streamside pixels were correctly classified. Of the streamside pixels classified as nonforest, 50% had thin strips of riparian vegetation but otherwise lacked forested areas. Incorrect classifications encountered in this assessment generally occurred when pixels classified as forest had small residences but were otherwise heavily forested.

Watersheds were delineated using a watershed delineator (Texas Natural Resource Conservation Commission, Austin, Texas © 1997), which uses neighborhood functions with data from US Geologic Survey (USGS) digital elevation maps (DEMs) to quantify the surface area contributing to drainage through a given point. The outputs were converted to *watershed polygons,* which included the entire drainage area upstream of the sampling reach. Within each watershed polygon, a 60-m *riparian corridor polygon* was created (30 m on both sides of the channel), beginning at the sampling reach and extending the entire length of the stream. To assess the influence of riparian land cover at specific distances upstream of the study reach, riparian corridors were subdivided longitudinally into *subcorridors* (Fig. 2), which began with an initial polygon of 60 X 200 m and increased longitudinally by 200-m increments (i.e., 60 X 400 m, 60 X 600 m, etc.) until 2 km of upstream length were included. For each study site, associated watershed, riparian corridor, and subcorridor polygons were overlaid onto the digital land-cover data. It is important to note that the 2-km subcorridor polygon did not represent the entire longitudinal distance for any streams in the study. Percentages for each land-cover category were quantified within the polygons. Regression analysis was used to relate leaf breakdown rate and physicochemical variables to land-cover patterns at the watershed, riparian corridor, and subcorridor scales. A sequential Bonferroni correction (Rice 1989) was used when multiple bivariate comparisons were performed between several independent variables (e.g., land cover at all spatial scales) and a single dependent variable. Percent nonforest values

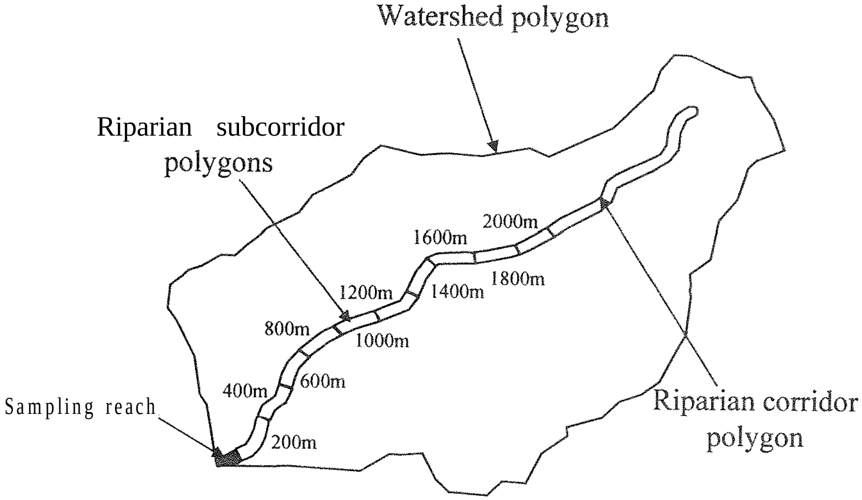

FIG. 2. Spatial scales ($n = 12$) used to analyze land-cover patterns in the study watersheds. Subcorridor polygons extend longitudinally in 200-m increments for 2 km (i.e., 60 X 200 m to 60 X 2000 m).

were transformed (arcsine square root) for statistical analyses.

Physical and chemical characterizations

Physical and chemical characteristics were measured for each stream from January to May 1999. Triplicate water samples were collected monthly from each site, passed through glass-fiber filters (Whatman GFF, Gelman Type AE), and frozen before analysis of dissolved constituents. Samples were analyzed for NH,-N using the phenate method (Soloranzo 1969) and NO,-N by colorimetric techniques following reduction by Cd (Wood et al. 1967) on a Technicon Auto-analyzer. PO,-P was analyzed as soluble reactive P (SRI') using the molybdate colorimetric method (Murphy and Riley 1962, Wetzel and Likens 1991). Alkalinity, hardness, and specific conductance were measured once using standard laboratory protocol (APHA 1998) and a YSI Model 30 / 50-conductivity meter. Temperature was recorded monthly until data loggers (HOBO”, Pocasset, Massachusetts) were installed in March 1999, after which temperature was recorded hourly. Discharge was measured at least monthly at each site using velocity determined with an electronic flow meter (FLOW-MATE, Marsh-McBirney, Inc., Frederick, Maryland) and cross-sectional area (Gore 1996). Mean substrate particle size (MI'S) of course substrates was determined from randomly selected particles using a USGS gravelometer (Wolman 1954). MI'S was calculated from 100 particles along 50-m reaches (MI'S reach) and from 50 particles along the 10-m areas where leaf packs were placed (MPS site).

Leaf breakdown

Breakdown rate for American sycamore (*Plantanus occidentalis*) was determined using litterbags placed at the 8 sites in January 1999. Sycamore was selected because it dominates riparian corridors in developed watersheds in this region (Benfield et al. 1977) and was present at all study sites. Abscised sycamore leaves were collected in autumn 1998 and air-dried to a constant weight. Approximately 8 g of leaf material were placed into plastic mesh bags (mesh size = 5 mm). Fifteen litterbags were anchored in riffles by tying them to a length of cable attached to a stake in the streambed. Three additional packs were taken to each site to serve as controls for handling loss and to determine initial ash-free dry mass (AFDM). Three leaf packs per site were retrieved randomly after 13, 45, 70, 105, and 130 d, placed immediately into plastic bags, and returned to the laboratory on ice. Leaf material was washed to remove sediments and macroinvertebrates, and oven dried (50°C) to a constant weight. Individual packs were ground by a Wiley mill, subsampled, and ashed at 500°C to determine AFDM. Remaining

TABLE 1. Land-cover patterns in the 8 study watersheds. Values are the % of nonforested land within each scale category. Subcorridor values are the % of nonforested land within a polygon of 60-m width and progressively greater distances upstream from the sampling reach. *Entire riparian corridor* includes riparian areas for the entire length of the watershed. LBC = Little Back Creek.

	Powers	Greenbriar	LBC	Purgatory	Barnhardt	Mudlick	Franklin	Martins
Scale								
Watershed	7.50	34.20	8.37	13.88	19.31	41.47	19.66	20.31
Entire riparian corridor	1.20	19.17	10.79	1.28	26.41	34.70	19.86	56.28
Subcorridors (m)								
Sample reach	0.00	0.00	100.00	0.00	100.00	0.00	18.18	50.00
200	0.00	14.29	23.08	0.00	92.86	85.71	84.62	75.00
400	0.00	6.67	IO.04	0.00	46.43	07.86	67.86	83.33
600	0.00	3.65	9.76	0.00	61.90	76.19	79.07	88.89
800	0.00	3.51	7.02	3.85	60.71	79.66	73.77	92.00
1000	0.00	4.29	7.25	3.12	55.88	80.82	77.00	92.19
1200	0.00	13.41	h.02	2.56	57.32	68.97	80.46	88.61
1400	0.00	19.15	5.21	2.17	62.50	59.41	74.00	85.87
1600	0.00	18.52	4.50	1.90	61.1I	56.25	67.83	83.96
1800	0.00	25.41	4.00	1.69	56.56	51.59	60.47	77.50
2000	0.00	22.79	3.65	1.54	51.1 I	49.29	54.55	77.6 l

ground material was pooled by site and analyzed for total Kjeldahl N (TKN) using micro-Kjeldahl digestion (APHA 1998). C:N ratios were determined for leaf packs assuming C constitutes 48% of AFDM. Leaf breakdown rate (k/d) was calculated as the slope of the line derived from the regression of natural log % AFDM remaining against time (Petersen and Cummins 1974). Regression analysis was used to test the null hypothesis that $k = 0$, and an analysis of covariance (ANCOVA) with a dummy variable technique (Kleinbaum et al. 1988) and Bonferroni correction was used to compare breakdown rates among sites.

Macroinvertebrates washed from leaf packs were preserved in 80% ethanol, and shredders (sensu Cummins 1973, Merritt and Cummins 1996) were separated and identified to genus following Merritt and Cummins (1996), Stewart and Stark (1993), and Wiggins (1996). After identification, shredders from each pack were combined, oven dried (50°C), and weighed on a microbalance (Mettler Toledo MT5). Because preservation in ethanol reduces invertebrate dry mass, these data were only used as comparative measures of invertebrate biomass. Shredder density and biomass per remaining leaf pack AFDM were compared among sites using a multivariate analysis of variance (MANOVA) on log-transformed data followed by separate univariate ANOVAs with Tukey's post-hoc multiple comparisons. All statistical procedures were performed on SAS (version 7, SAS Institute, Cary, North Carolina).

Results

Land-use quantification

The magnitude and distribution of nonforested areas within watersheds, riparian corridors, and subcorridors varied considerably among sites (Table 1). Moreover, several sites showed vastly different land-cover patterns when the spatial scale of analysis was shifted from the watershed to the riparian corridor. Land-cover patterns derived from subcorridors indicated that some watersheds had a high % of nonforested area located within several hundred meters upstream of the sampling reach. At Franklin Creek, for example, 19.7% and 19.9% of the land was nonforest at both the watershed and riparian corridor scales, respectively. However, within the 1st kilometer upstream of the reach, 77.0% of the riparian corridor was nonforest. Conversely, Greenbriar Branch was 34.2% nonforested when evaluated at the watershed scale, but only 19.2% and 4.3% when the scale of analysis was shifted to the riparian corridor and 1 km subcorridor, respectively.

Physicochemical characterizations

MPS along 50-m reaches ranged from 72.0 mm at Purgatory Tributary to 44.8 mm at Barnhardt Creek, and decreased with the % of nonforested area within the entire riparian corridor and the subcorridors, the strongest relationship occurring with polygons of 1800-m length ($r^2 = 0.80$, $p = 0.003$). Differences in elevation and watershed area among sites contributed to variability in several of the instream physicochemical variables (Table 2). Most of the variability associated with discharge could be attributed to watershed area (*r-l* = 0.76, $p = 0.005$). Specific conductance, hardness, and alkalinity were generally related to elevation at the sample reach ($r^2 = 0.70$, $p = 0.009$; $r^2 = 0.59$, $p = 0.025$; $r^2 = 0.68$, $p = 0.012$, respectively). Mean stream temperature was also related to elevation ($r^2 = 0.77$, $p = 0.004$). Further, when elevation and % nonforested land within the riparian corridor were used in a multiple regression, the explanatory power for mean temperature was much stronger ($R^2 = 0.94$, $p = 0.013$). NH-N and NO,-N concentration (as total inorganic N, TIN) varied among sites (CV = 74.6%) and increased with the % of nonforested area at the watershed scale ($r^2 = 0.54$, $p = 0.036$, not significant after Bonferroni correction). SRI' concentration was not as variable (CV = 50.47%) among sites, and did not correlate to land use at any spatial scale. Neither TIN nor SRP concentration were related to any other physical variables measured in the study.

Leaf breakdown

Leaf breakdown rate was significantly different ($p = 0.0017$) among sites (Table 3), ranging from 0.0051/*d* at Martins Creek to 0.0180/*d* at Powers Branch. Leaf breakdown rate was not related to MPS reach ($r^2 = 0.268$, $p = 0.188$), but was strongly related to MPS site ($r^2 = 0.873$, $p = 0.0007$) (Fig. 3). Variation in leaf breakdown rate was not explained by stream temperature ($r^2 = 0.53$, $p = 0.04$, not significant after Bonferroni correction), TIN ($r^2 = 0.29$, $p = 0.17$), or SRP ($r^2 = 0.0003$, $p = 0.16$) measured in stream water. Finally, breakdown rate was not related to land-cover patterns at the watershed or entire riparian corridor scales ($r^2 = 0.116$, $p = 0.409$; $r^2 = 0.476$, $p = 0.060$, respectively). There was a negative relationship between breakdown rate and % nonforest in riparian subcorridors; however, the strength of this association varied with longitudinal scale. Figure 4 is a plot of r^2 values for the analyses between land cover within subcorridors of variable length and leaf breakdown coefficients (k/d). The data showed that leaf breakdown rate decreased as the % of nonforested land increased within subcorridors of 800 m to 1200 m length.

N accumulation

The initial N concentration in leaf pack material was 13.97 mg TKN /g AFDM, or ~1.4% of the total AFDM. Mass-specific TKN generally increased at all sites with time ($r^2 = 0.55$, $p = 0.0001$). Accordingly, C:N ratios began at 34:1 and declined at all sites throughout the study ($r^2 = 0.57$, $p = 0.0001$). Despite site-specific patterns in TKN accumulation, there was an initial increase during the first 45 d of incubation at all sites (Fig. 5). The magnitude of initial increase was not related to leaf breakdown rate ($r^2 = 0.02$, $p = 0.699$), nor was the mean TKN value obtained for each site over the course of the study ($r^2 = 0.288$, $p = 0.170$). Furthermore, mean N accumulation over the course of the study was unrelated to TIN and SRP in stream water ($r^2 = 0.037$, $p = 0.645$; $r^2 = 0.069$, $p = 0.527$, respectively). The variability in mean N accumulation over the course of the study was best explained by mean stream temperature ($r^2 = 0.71$, $p = 0.009$).

Shredders

Shredder density and biomass varied significantly among sites (MANOVA: *Wilk's Lambda* = 0.357, $F_{14,222} = 10.65$, $p < 0.0001$; ANOVA: *density*, $F_{7,12} = 18.5$, $p < 0.0001$; *biomass*, $F_{7,112} = 9.0$, $p < 0.0001$) (Table 4). Mean density (no./g AFDM) ranged over 2 orders of magnitude from 0.08 at Mudlick Creek to 19.50 at Powers Branch. Comparable variation was observed for shredder biomass (mg/g AFDM), with a minimum value of 0.42 at Martins Creek and a maximum value of 50.16 at Powers Branch. Plecopteran taxa dominated shredder assemblages on leaf packs at most sites (e.g., Powers Branch); however, some sites (e.g., Mudlick Creek) had a high % of tipulid larvae (Table 5). Shredder density and biomass were not related to MPS reach; however, they were positively related to MPS

TABLE 2. Physical and chemical conditions in the study streams. Except for watershed area and elevation, values are means (±SE) generated from monthly values for each stream from January to June 1999. * = variables measured once during the study. MPS = mean substrate particle size (mm). LBC = Little Back Creek.

	Powers	Greenbriar	LBC	Purgatory	Barnhardt
Elevation (m)	575.0	381.0	403.0	489.0	332.0
Watershed area (ha)	612.8	248.7	1014.4	27.5	708.1
Discharge (L/s)	47.86	18.03	53.36	17.16	30.49
	(±10.71)	(±3.02)	(±9.42)	(±4.91)	(±6.49)
Temperature (°C)	11.04	13.59	13.77	11.63	13.83
	(±0.07)	(±0.07)	(±0.08)	(±0.06)	(±0.07)
Specific conductance* (µS/cm)	33.9	97.6	64.8	64.5	154.3
Hardness* (ppm)	14.0	32.0	18.0	26.0	78.0
Alkalinity* (ppm)	16.0	36.0	30.0	26.0	80.0
NO_3-N (ppm)	0.394	0.982	0.116	0.115	0.302
	(±0.065)	(±0.151)	(±0.023)	(±0.026)	(±0.034)
NH_4-N (ppm)	0.006	0.014	0.016	0.014	0.012
	(±0.003)	(±0.005)	(±0.002)	(±0.004)	(±0.004)
PO_4-P (ppm)	0.024	0.011	0.015	0.013	0.014
	(±0.004)	(±0.003)	(±0.004)	(±0.002)	(±0.002)
MPS reach* (mm)	66.73	45.84	64.88	72.06	44.81
	(±4.83)	(±3.78)	(±5.17)	(±5.01)	(±4.04)
MPS site* (mm)	89.14	70.18	72.52	59.40	50.33
	(±7.31)	(±6.11)	(±7.09)	(±7.47)	(±4.64)

site ($r^2 = 0.64$, $p = 0.018$, and $r^2 = 0.84$, $p = 0.001$, respectively) (Fig. 6A, 6B). Breakdown rate was strongly related to shredder density ($r^2 = 0.63$, $p = 0.017$) and biomass ($r^2 = 0.76$, $p = 0.005$) (Fig. 7A, 7B) in leaf packs.

Discussion

Leaf breakdown

The mean breakdown rate (0.0096/d) across all sites was within the range previously published for sycamore leaves in streams (Webster and Benfield 1986). However, the range of values in this study includes those indicative of slow, medium, and fast breakdown rates (sensu Petersen and Cummins 1974), depending on site. The disparity among site-specific breakdown rates reflects differences in shredder abundance in leaf packs. At sites with slow breakdown rates (e.g., Martins Creek), shredders were typically limited to low numbers and biomass of winter stoneflies (e.g., *Amphinemoura*). Benfield et al. (1977) found a breakdown rate (0.0057/d) for sycamore leaves in a southern Appalachian pasture stream that was similar to our slowest rate (0.0051 /d at Martins Creek). In that study, Benfield et al. (1977) also found relatively low numbers of shredders in leaf packs, mostly small winter stoneflies, as was the case at some of our sites. Where breakdown rate was more rapid (e.g., Powers Branch), we found shredders in greater density and biomass in leaf packs, including relatively large-bodied species (*e.g., Pteronarcys, Tipula*). Our data support the notion that feeding by shredders can strongly influence leaf breakdown rate (Sedell et al. 1975, Short et al. 1980, Benfield and Webster 1985, Cuffney et al. 1990). Our data also suggest that breakdown rate was influenced by the presence or absence of shredders with large body size. Large shredders (*e.g., Tipula*) feed by removing chunks of leaves, whereas small taxa (e.g., *Tallaperla*) skeletonize leaves (Wallace et al. 1970). This difference in feeding method may influence breakdown rates and make the distribution and abundance of large shredders critical to leaf processing in these streams (Benfield et al. 1977).

Nitrogen content in leaves (as mg TKN/g AFDM) increased at all sites over the course of the study, a pattern often attributed to N immobilization and biomass accumulation by microbes (Triska and Buckley 1978, Webster and Benfield 1986, Casas and Gessner 1999). However, TKN accumulation may also result from the formation of complexes between N and oth-

TABLE 2. Extended.

Mudlick	Franklin	Martins
345.0	325.0	448.0
555.3	590.3	415.6
27.13	35.48	17.19
(±5.08)	(-15.75)	(23.37)
14.60	14.40	14.18
(‘-0.10)	(±0.08)	(±0.10)
119.2	199.5	102.6
64.0	108.0	36.0
58.0	98.0	34.0
0.689	0.145	0.594
(±0.103)	(±0.022)	(10.110)
0.016	0.018	0.024
(+ 0.007)	(+ 0.007)	(± 0.007)
0.015	0.020	0.022
(±0.003)	(± 0.009)	(± 0.004)
46.76	46.43	46.71
(±3.73)	(±3.87)	(±3.69)
35.81	45.93	37.69
(±3.01)	(±5.13)	(13.85)

er compounds in leaves (e.g., lignin) (Odum et al. 1978), or reflect differential feeding by invertebrate consumers among sites (Barlöcher 1980, Rossi 1985). Temporal patterns of N accumulation varied among sites, and were not statistically related to leaf breakdown rate. In addition, TKN accumulation was not related to the concentration of inorganic nutrients in streams, despite relatively large differences in TIN among sites. The lack of statistical relationship between TIN in streams and TKN suggests that N was available in excess of that required to support microbial production. Meyer and Johnson (1983) found NO,-N enrichment in an Appalachian headwater stream led to greater microbial biomass (measured both as adenosine triphosphate and TKN) on decomposing leaf litter when

TABLE 3. Mean breakdown rate (k/d) and coefficient of determination (r^2) derived from significant ($p < 0.05$) regressions of sycamore leaf mass and time for each study stream. Breakdown rate was compared using an ANCOVA with site as a dummy variable (Kleinbaum et al. 1988). Values that share superscripts are not significantly different (α = 0.0017, after Bonferroni correction). LBC = Little Back Creek.

Site	kid	r^2
Powers	0.0180"	0.907
Greenbriar	0.0145””	0.979
LBC	0.0107”’	0.959
Purgatory	0.0097^{D}	0.953
Barnhardt	0.0068”	0.938
Mudlick	0.0067^{DI}	0.940
Franklin	0.0053’	0.955
Martins	$0.005\,1^{I}$	0.977

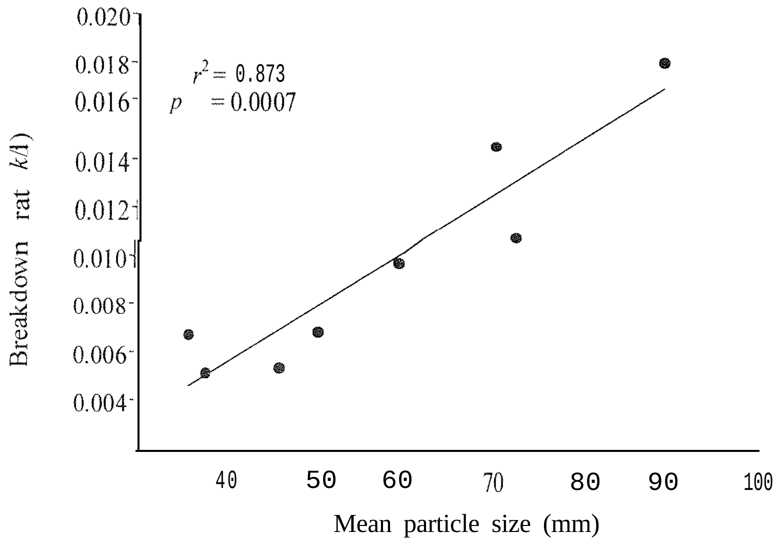

FIG. 3. Relationship between leaf breakdown rate and mean substrate particle size (MI'S) in the 10-m area surrounding the leaf packs (MI'S site).

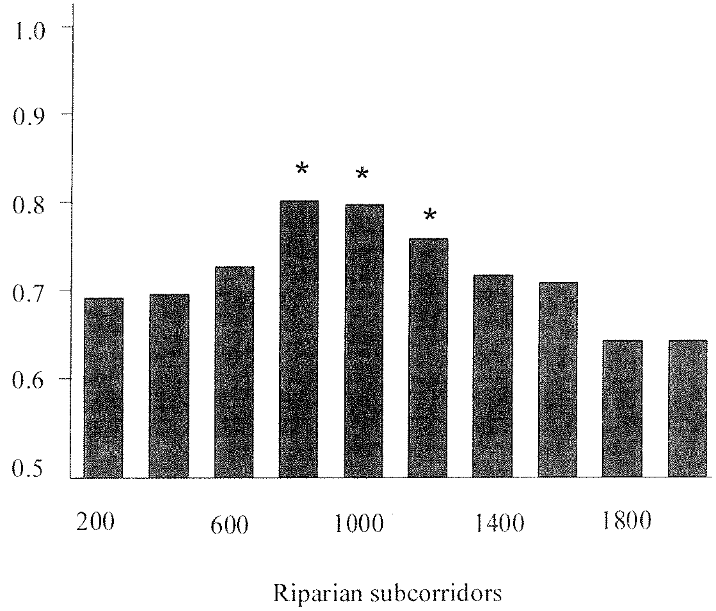

FIG. 4. Coefficients of determination (r^2) derived from bivariate regression analyses between breakdown rate and % nonforest in riparian subcorridors of variable length. * = significant regressions after a sequential Bonferroni correction for multiple comparisons.

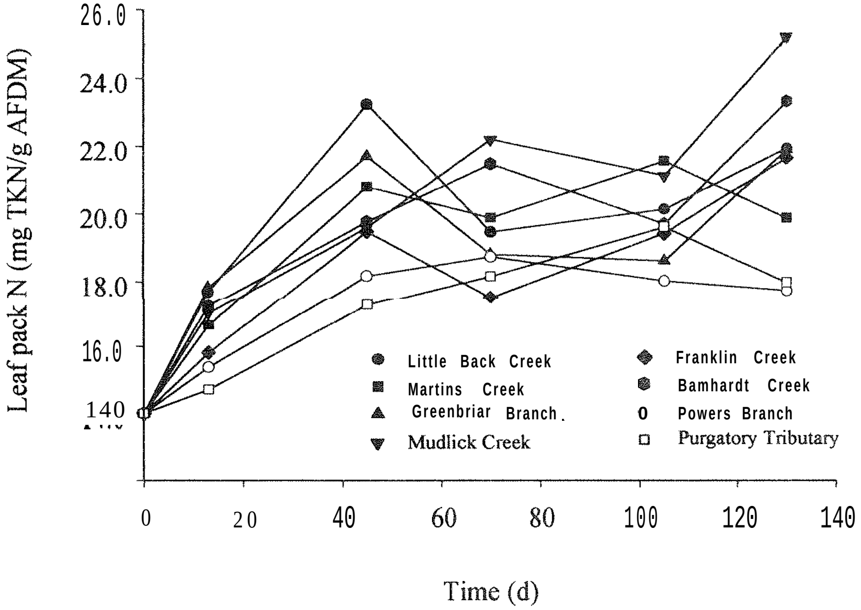

FIG. 5. Patterns of total Kjeldahl N (TKN) accumulation on leaf packs over time for each study site. AFDM = ash-free dry mass.

TABLE 4. Invertebrate abundance on artificial leaf packs. Shredder density and biomass are mean (±SE) derived from 5 collection dates per site. Mean biomass and density were compared using a MANOVA followed by univariate ANOVAs with Tukey's Studentized Range Test (HSD) for multiple comparisons. Values that share superscripts are not significantly different. LBC = Little Back Creek. AFDM = ash-free dry mass.

Study sites	Powers	Greenbriar	LBC	Purgatory	Barnhardt	Mudlick	Franklin	Martins
Density	19.50^{A}	11.11^{A}	1.11^{BC}	2.32^{B}	1.75^{BC}	0.08^{C}	0.36^{BC}	1.42^{BC}
(no./g AFDM)	(±5.42)	(±2.94)	(±0.28)	(±0.73)	(±0.49)	(±0.04)	(±0.12)	(±0.41)
Biomass	50.16^{A}	11.50^{ABC}	15.96^{AB}	3.64^{BCD}	1.84^{CD}	1.87^{CD}	4.92^{CD}	0.416^{D}
(mg/g AFDM)	(±23.27)	(±4.88)	(±9.10)	(±1.07)	(±1.30)	(±1.16)	(±3.31)	(±0.28)

compared to leaves in a low NO,-N reference stream. However, the difference in microbial biomass resulted from an increase in stream NO,-N of 2 orders of magnitude (0.006 vs 0.6 ppm). In our study, NO,-N concentrations at most sites were similar to the enriched values reported by Meyer and Johnson (1983). Average TKN on leaves was highest at sites with elevated mean temperatures, suggesting that N immobilization and microbial biomass accumulation was greater in warmer streams (e.g., Paul et al. 1978, Irons et al. 1994). In our study, biomass accumulation and the potential influence of microbial activity on breakdown rate may be masked by other, more important factors, namely feeding by shredders (e.g., Short et al. 1980, Irons et al. 1994).

Watershed-scale effects

Variability in leaf breakdown rates among streams in the URRB was closely related to land-cover patterns within watersheds, provided the appropriate spatial scale was used for analysis. Of watershed-scale features, elevation was related to several instream physical and chemical variables. For example, alkalinity, hardness, and specific conductance were strongly related to elevation, reflecting changes from noncarbonate to carbonate geology as streams reached lower elevation in the Roanoke Valley (Wailer 1976). Also, elevation and land cover in riparian corridors interacted to influence mean stream temperature. In contrast to many studies (e.g., Suberkropp et al. 1975, Paul et al. 1983), breakdown rate did not increase with stream temperature. Because land cover in riparian corridors and mean stream temperature were also related, we contend that the lack of relationship between leaf breakdown and temperature reflects the negative influence of land-cover patterns on leaf breakdown through other processes (e.g., sedimentation). Finally, there was a

TABLE 5. Distribution of shredders throughout study sites. Values are percentages of the total number represented by each genus. LBC = Little Back Creek.

Taxa	Powers	Greenbriar	LBC	Purgatory	Barnhardt	Mudlick	Franklin	Martins
Plecoptera								
Pteronarcys sp.	35.5		21.2	30.9				3.1
Tallaperla sp.	11.0		23.1	20.2			4.7	
Peltoperla sp.	0.2 I							
Oomopteryx sp.	13.3		1.9	3.2			4.7	
Taeniopteryx sp.	0.2		21.2					
Amphinemoura sp	17.0	87.3		32.2	90.0		38.0	78.4
Shipsa sp.	I x.7		7.7		1.0	20.0	4.7	6.2
Allocapnia sp.	3.1	0.02	3.x		3.0		9.5	1.0
Leuctra sp.		1.0		5.3			4.7	1.0
Trichoptera								
Pycnopsyche sp	0.6			1.1				
Diptera								
Tipula sp.	0.4	11.2	21.2	2.1	6.0	x0.0	33.3	10.3
Total number	382	365	52	94	101	5	21	97

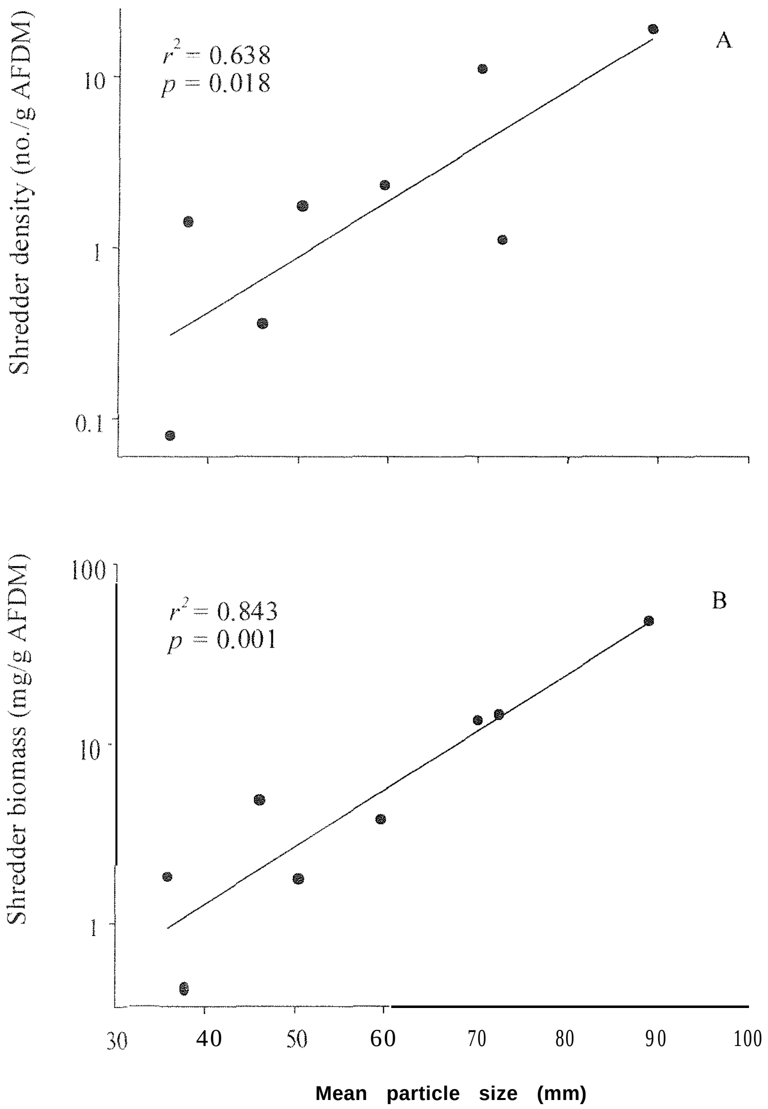

FIG. 6. Relationship between shredder density (A), biomass (B) and mean substrate particle size (MPS) in the 10-m area surrounding the leaf packs (MPS site). AFDM = ash-free dry mass.

trend (non-significant) of higher TIN concentration with increased % of nonforested land at the watershed scale. This relationship is similar to that observed in many studies that have shown watershed-scale characteristics to be generally good predictors for dissolved nutrients, particularly NO_3-N (Omernick 1977, Close and Davies-Colley 1990, Johnson et al. 1997). Differences in the concentration of inorganic nutrients among streams were not closely coupled to leaf breakdown in our study (but see Meyer and Johnson 1983).

Ripurian corridor effects

The impact of land-cover patterns on leaf breakdown rate in our streams appeared minimal when analyzed at the watershed and entire riparian corridor scale. However, breakdown rate did show a strong inverse relationship with

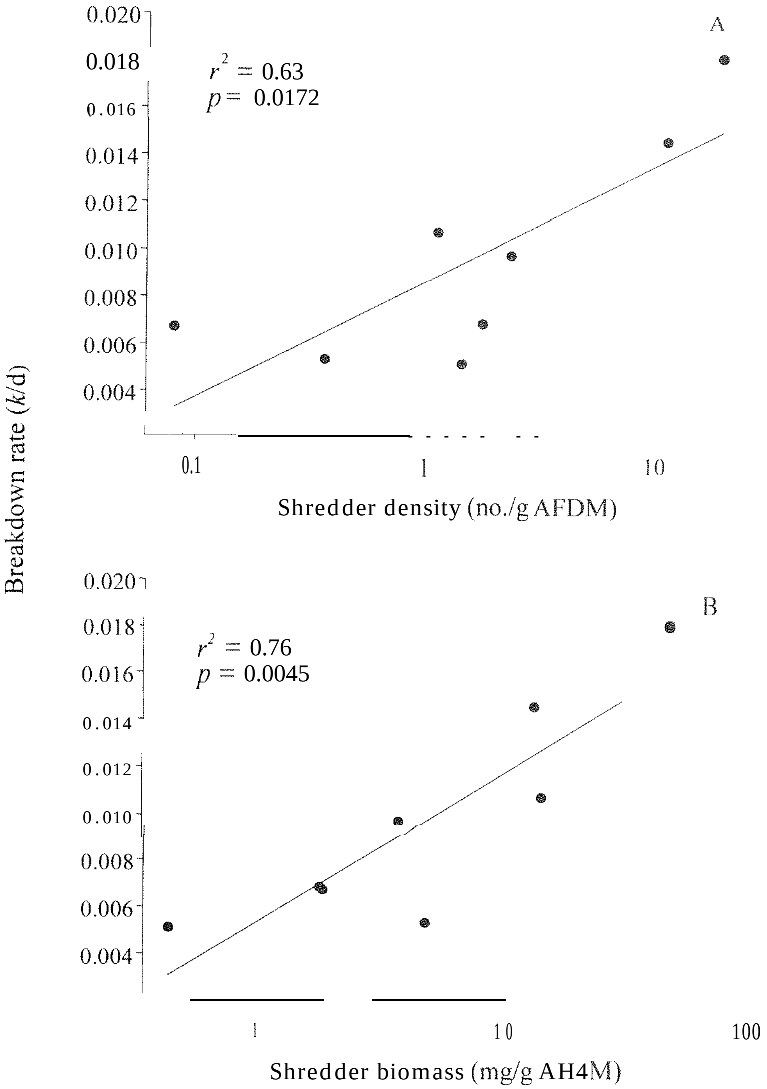

FIG. 7. Relationship between leaf breakdown rate and shredder density (A) and biomass (B). AFDM = ash-free dry mass.

land cover in riparian subcorridors. Furthermore, the strength of this relationship depended on where development existed upstream of sampling reaches. Our results suggest that land-cover patterns within riparian subcorridors of ~1 km in length have the most influence on leaf breakdown rate. The importance of this longitudinal distance is most likely related to the spatial characteristics of upstream development. Development in many of these watersheds is concentrated in low-gradient areas adjacent to riparian corridors, whereas the high-gradient, upland areas are generally forested. This spatial pattern is an apparent aspect of development documented for many Appalachian watersheds (Wear and Bolstad 1998). In our study, the 1 km distance may maximize the % of developed land per unit of longitudinal distance. Evaluating the influence of riparian land cover over short longitudinal distances (e.g., 200-m subcorridors) may not include enough of the upstream landscape to generate predictive relationships between land-cover variables and instream processes. In addition, functional redundancy among taxa that are differentially tolerant to environmental stress (e.g., *Pteronarcys* vs *Tipula*) may create a situation where local land-use disturbances do not effectively reduce the influence of shredder feeding on leaf breakdown rate. Alternatively, evaluating riparian land cover over long longitudinal distances (e.g., entire riparian corridor) often includes high-gradient upland areas, which are generally forested. Therefore, the % of nonforested land quantified at large spatial scales is reduced, and analyses between land cover at these scales and instream variables are often less explanatory.

We contend that development within the riparian corridors influences leaf breakdown by altering sediment inputs. This notion is supported by the strong negative relationship between the % of nonforested land in the riparian corridor (and many subcorridors) and MPS reach. A reduction in the mean particle size of course substrate reflects an increased abundance of particles in small size classes (e.g., sand, silt). In headwater streams, decreased particle size often results from sediment inputs from near-stream development (Lemly 1982, Lenat and Crawford 1994, Waters 1995). Sedimentation can directly slow the rate of detritus processing by burying leaf packs (Herbst 1980, Webster and Waide 1982, Rounick and Winterbourn 1983). Burial may reduce breakdown rates by decreasing the amount of exposed surface area available for microbial activity, minimizing physical abrasion, or creating anoxic conditions (Herbst 1980, but also see Boulton and Foster 1998). Leaf packs taken from watersheds with extensive agricultural and residential development (e.g., Martins Creek) were frequently filled with fine sediment and silt and often were blackened and smelled of H_2S, indicating anoxic conditions. Sedimentation may also indirectly affect leaf breakdown by influencing the distribution and availability of shredders in streams. The strong relationship between shredder density and leaf breakdown rate, and shredder density and MPS site supports this view. Reice (1974) suggested that reduced habitat stability and subsequent changes in community structure that correspond to the local distribution of fine sediments can lead to low shredder density and slow leaf breakdown rates. A reduction in substrate particle size, through sedimentation, may also limit the accumulation and retention of leaf material in streams and thus prevent the development and maintenance of local shredder populations (Rounick and Winterbourn 1983).

Conversion of riparian forests to pastures or suburban neighborhoods may also influence the distribution of shredders by decreasing both the total amount and diversity of leaf species entering streams (Benfield et al. 1977, Campbell et al. 1992). Wallace et al. (1997) demonstrated that a reduction in the amount of leaf inputs to streams could reduce shredder biomass and production. However, in our study, many of the pixels in riparian corridors that were classified as nonforest actually had thin riparian strips (often <1 m wide). As a result, all streams seemed to receive substantial inputs of leaf-fall, most of which was sycamore or black walnut (R. Sponseller, unpublished observation). However, a reduction in riparian diversity associated with agricultural or residential development could result in a break in the *leaf-processing continuum* (Petersen and Cummins 1974), where leaf species with inherently different processing rates attain a state of optimal conditioning along a temporal continuum and thus meet annual resource needs for detritivores. Eliminating diversity in leaf inputs may, therefore, prevent the long-term establishment of shredder populations in some streams (Renfield et al. 1977, Golladay et al. 1983). This result could explain why the presence of riparian forest patches located upstream of sample reaches often corresponded to high breakdown rates. For example, Greenbriar Branch, which had a high % of nonforested land (mostly agriculture) at the watershed scale, had several hundred meters of intact riparian forest upstream of the study reach. This stream also had the 2nd highest shredder density and 2nd fastest leaf breakdown rate of the 8 sites. Johnson and Covich (1997) found that upstream riparian cover (500- and 1000-m segments) was closely related to the amount of leaf material in transport in Oklahoma streams. Therefore, upstream riparian forest patches may be influencing local shredder assemblages and breakdown rate by contributing leaf species required to complete the processing continuum.

Microhabitat effects

Despite the strong relationship between land-cover patterns in the riparian corridor and substrate particle size at large spatial scales (MPS reach), shredder abundance could only be predicted from substrate characteristics at small scales (MPS site). This result may be because leaf packs were sometimes placed in riffles with substrata not representative of the entire 50-m reach. This patchy distribution of habitat type was particularly evident at Greenbriar Branch, where the substrate in the riffle habitat used for study represented ≤10% of the entire 50-m reach. In this case, the riffle area may have acted as an important processing patch, where in situ organic matter was retained on the surface and served as a source of invertebrate shredders for the artificial leaf packs. Reice (1974) suggested that variability in leaf pack processing may be attributed to patch-specific community dynamics that are governed by the relative distribution of sediment particles of different sizes and the resources associated with them. Therefore, a decline in forested land cover in the riparian corridor may result in reduced particle sizes over larger spatial scales (e.g., MPS reach), but patches where detritus processing occurs may still persist within these systems. Land-cover patterns are not longitudinally homogeneous, so streams in developed watersheds may have patches where inputs of coarse particulate organic matter and the distribution of appropriate substrate would support detritus processing rates more representative of streams not affected by residential or agricultural development. Moreover, continued human development may reduce the distribution and abundance of such patches and, ultimately, the retention and processing of organic matter in headwater streams draining developing watersheds may decline.

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