Am. Midl. Nat. 143:397–404

Effects of Forest Defoliation by the Gypsy Moth on Detritus Processing in Southern Appalachian Streams

J. J. HUTCHENS, JR.[1] AND E. F. BENFIELD
Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg 24061

ABSTRACT.—We investigated whether changes in chestnut oak (*Quercus prinus* L.) leaf quality caused by gypsy moth (*Lymantria dispar* L.) defoliation affected leaf breakdown rates in southern Appalachian streams of differing disturbance history. Breakdown rates of second-flush leaves produced after defoliation were compared to those of natural spring-flush leaves shed in autumn. Second-flush leaves broke down significantly faster than spring-flush leaves in three of the six streams tested. Initial fiber content and the ratio of fiber to protein were significantly higher in spring-flush leaves than in second-flush leaves, showing that initial differences in internal leaf constituents could explain the faster breakdown rates of second-flush leaves. Using changes in leaf toughness through time as a measure of microbial conditioning we found that the faster-decaying second-flush leaves also softened at a faster rate than the spring-flush leaves. In addition, both types of leaves incubated in three streams draining a recovering 14-y-old clear-cut catchment broke down significantly faster than leaves incubated in three streams draining a reference catchment. We attributed this increase in leaf breakdown to significantly higher abundance and density of leaf-shredding insects and greater microbial conditioning in leaf packs in the streams of the recovering clear-cut catchment. Overall, our results show that insect defoliation accelerates detritus processing in southern Appalachian streams and that this acceleration may be especially important in previously disturbed streams in which leaves are already processed faster.

INTRODUCTION

Forested headwater streams in the southern Appalachian Mountains depend on allochthonous organic matter in the form of autumnal leaf fall as their main source of energy (Hornick *et al.*, 1981; Webster *et al.*, 1983; Wallace *et al.*, 1997). Disruption of streamside vegetation by logging can result in internal disruption of energy processing in affected streams (*e.g.*, Webster and Waide, 1982; Benfield *et al.*, 1991). Logging is generally accompanied by physical disturbances in addition to leaf loss, *e.g.*, sedimentation from roads and skid trails (Webster and Waide, 1982) and loss of retention devices (Golladay *et al.*, 1989). Also, changes in primary energy sources can occur resulting in changes in stream communities (Wallace and Gurtz, 1986). Little is known about the effects of massive defoliation of riparian vegetation on stream processes. It is known that nominal herbivory by canopy arthropods can affect potassium, nitrogen and phosphorus cycling in forests (Seastedt and Crossley, 1984) and forest defoliation can increase nitrate-nitrogen in streamwater (Swank *et al.*, 1981; Webb *et al.*, 1995; Eshleman *et al.*, 1998).

Larvae of the gypsy moth (*Lymantria dispar* L., Lepidoptera:Lymantriidae) defoliated about 5.3 million ha of forest in the northeastern U.S. in 1981 (Doane and McManus, 1981). The pest has continued to spread westward and southward and presently threatens southern Appalachian forests (Douce *et al.*, 1994). Larvae hatch in spring from eggs deposited by females the previous year. In heavy infestations local sites suffer total defoliation of preferred tree species (mainly oaks) by late June, and almost any foliage is consumed once the oak leaves disappear. Most trees then produce a second flush of leaves that are

[1] Present address: Institute of Ecology, 711 BioSciences Bldg, University of Georgia, Athens 30602

tougher (Schultz and Baldwin, 1982) and smaller (Grace, 1986) than the natural spring flush. Streams in defoliated areas may also receive significant greenfall, frass and larvae (Grace, 1986). However, it is the fate of the second-flush leaves that enter streams in autumn that is of interest here. We hypothesized that the tougher second-flush leaves would be lower in food quality for detritivores (*e.g.,* Mackay and Kalff, 1973) and would break down slower than spring-flush leaves. In order to test this hypothesis we measured leaf ''toughness'' and fiber and nitrogen content of spring- and second-flush chestnut oak (*Quercus prinus* L.) leaves to characterize their quality. In addition, we measured rates of leaf breakdown in two types of streams. Finally, we enumerated leaf-shredding, aquatic insects (shredders, Merritt and Cummins, 1984) in leaf packs to determine whether the differences in leaf quality influenced detritivores.

Our study streams differed in disturbance history: three streams drained a long-term reference catchment and three drained a recovering clear-cut catchment. There is an extensive research history on stream processes in these catchments (*see* review by Webster *et al.*, 1992) that provided a long-term context for our study. Using multiple streams also provided a range of conditions to determine the robustness of our results. We hypothesized that both leaf types would break down faster in the disturbed than in the reference streams because of higher shredder production in the disturbed streams (Stout *et al.*, 1993; Stone and Wallace, 1997).

Our objectives were: (1) to determine whether second-flush leaves had similar breakdown characteristics as spring-flush leaves and (2) to determine whether stream disturbance history affected leaf breakdown patterns.

SITE DESCRIPTION

Our six streams are at the Coweeta Hydrologic Laboratory (CHL), North Carolina in the southern Appalachian Mountains. Three first-order streams drained a 14-y-old, recovering, clear-cut catchment (Catchment 7) and three first-order streams drained a long-term reference catchment (Catchment 14). The two catchments are similar in size, elevation, gradient, discharge and stream temperature (Stout *et al.*, 1993). The reference streams drain mixed hardwood forest dominated by oak (*Quercus* spp.) and hickory (*Carya* spp.). Before clear-cutting, vegetation in the recovering clear-cut catchment was also dominated by oak and hickory. The recovering catchment is now characterized by extensive coppice growth of yellow poplar (*Liriodendron tulipifera* L.), black locust (*Robinia pseudoacacia* L.) and red maple (*Acer rubrum* L.) in stands that were previously cove hardwoods and mixed-oak hardwoods. Former hardwood-pine stands in xeric sites of the catchment are now dominated by chestnut oak, mountain laurel (*Kalmia latifolia* L.) and red maple (Elliott *et al.*, 1997).

METHODS

Leaves picked just before abscission from previously defoliated or undefoliated chestnut oak trees growing in Shenandoah National Park, Virginia were used in leaf breakdown studies. Leaves of two types were collected from about 50 trees: second-flush leaves from trees defoliated by gypsy moths and natural spring-flush leaves. In late November 1990, 25 8-g packs of each leaf type in 5-mm mesh bags were placed in cobble-riffles of each stream. Three replicate leaf packs were retrieved approximately monthly from each stream until $<5\%$ initial leaf mass remained. Leaves were returned to the laboratory, washed of debris and invertebrates, then air dried, weighed and sub-sampled for ash-free dry mass (AFDM) determination. Leaf breakdown rates ($-k$) were computed using an exponential decay model (Petersen and Cummins, 1974) and compared between leaf types and among streams using a general linear model (GLM) with dummy variables, $\alpha = 0.05$ (Kleinbaum *et al.*,

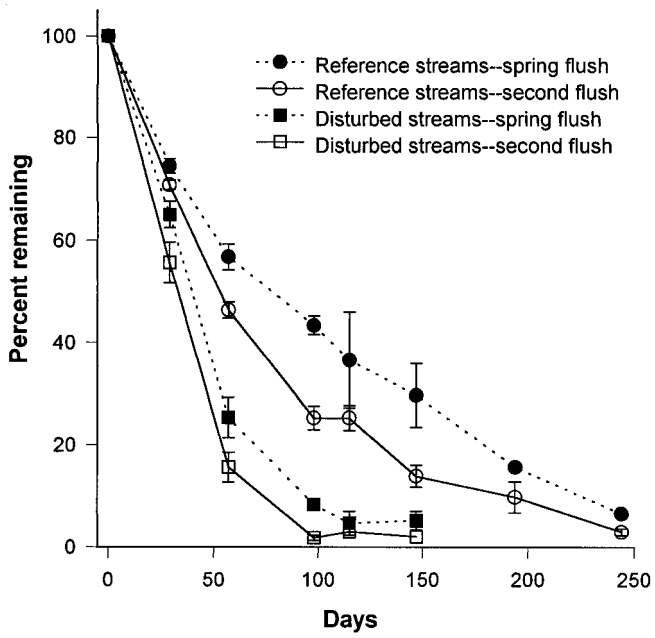

FIG. 1.—Percent remaining values (mean ± SE) for spring- and second-flush chestnut oak leaves incubated in reference and disturbed streams at Coweeta. In some cases the error bars are hidden by symbols

1988). Preserved invertebrates were identified to genus and apportioned into functional feeding groups according to Merritt and Cummins (1984). Shredder abundance (number/bag) and density (number/g AFDM leaf material) were compared between leaf types and between stream types using 2-way analysis of variance (ANOVA, $\alpha = 0.05$).

Temperature was monitored in each stream with max-min thermometers. Sub-samples of leaves before and 2 mo after placement in each stream were ground to a fine powder and assayed for percent fiber (Goering and Van Soest, 1970) and percent protein (total Kjeldahl nitrogen × 6.25). Changes in leaf toughness due to microbial conditioning were measured by penetrance after Feeny (1970). Penetrance data for leaf packs were ln transformed, regressed against time, and compared using a GLM with dummy variables.

RESULTS

Mean temperature in the six streams was nearly identical throughout the study (mean for reference streams = 9.5 C, range: 3–16.5 C; mean for disturbed streams = 9.9 C, range: 2–15.5 C). The disturbed streams were slightly warmer in spring, but this was after most of the breakdown had already occurred.

The proportion of initial leaf mass remaining for both leaf types declined rapidly in the streams draining the recovering clear-cut catchment—less than 5% leaf mass remained after 5 mo (Fig. 1). In contrast, 8 mo were required to reach a similar level in the reference streams. Second-flush leaves broke down faster in five of six streams though only three of the comparisons were statistically significant (Table 1). Between-stream comparisions show that both leaf types broke down significantly faster in the disturbed streams than in the reference streams (Table 1).

TABLE 1.—Leaf breakdown rates (−k) for spring- and second-flush chestnut oak leaves in reference (REF) and disturbed (DIST) streams at Coweeta. Asterisks indicate a significant ($P < 0.05$) difference between leaf types within streams; values with the same letter were not significantly different among streams

Stream	Spring-flush (−k)	Second-flush (−k)
REF1	0.0112^{A}	0.0144^{A}
REF2	0.0113^{A}*	0.0168^{A}
REF3	0.0107^{A}*	0.0142^{A}
DIST1	0.0293^{B}	0.0457^{B}
DIST2	0.0226^{B}*	$0.0320^{B,C}$
DIST3	0.0391^{B}	0.0300^{C}

We measured percent fiber and percent protein in dried leaf material before and after 2 mo of incubation in the streams. Preincubation spring- and second-flush leaves did not differ significantly in percent protein, but percent fiber and the ratio of fiber to protein were significantly lower in the second-flush leaves (Table 2). After 2 mo incubation in the streams initial differences between leaf types disappeared and percent fiber and protein content increased over time.

Leaf toughness (penetrance) declined for both leaf types in all streams over the study. Slopes ($-k \pm SE$) of regression lines for leaf toughness were significantly steeper for second-flush (mean = 0.0200 ± 0.0013) than for spring-flush (mean = 0.0132 ± 0.0017) leaves, and in disturbed (mean = 0.0253 ± 0.0032) than in reference (mean = 0.0164 ± 0.0012) streams.

Shredders present in leaf packs in the streams included the caddisflies *Pycnopsyche* spp. and *Lepidostoma* spp., the stoneflies *Tallaperla* spp. and *Taeniopteryx* spp. and the dipteran *Tipula* spp. There were no significant differences between leaf types for either shredder number per bag or density ($P > 0.05$; Table 3). However, there were significantly higher shredder numbers ($P < 0.01$) and density per bag ($P < 0.01$) in disturbed than in reference stream leaf packs.

DISCUSSION

Effects of leaf type on leaf breakdown.—Contrary to our prediction, second-flush leaves generally broke down faster than spring-flush leaves. We attribute the faster breakdown by

TABLE 2.—Mean percent fiber, protein and fiber : protein in spring-flush (SPRING) and second-flush (SECOND) chestnut oak leaves before (Initial) and 2 mo after placement in reference (REF) and disturbed (DIST) streams at Coweeta. Asterisks indicate a significant ($P < 0.05$) difference between leaf types. Values with the same letter were not significantly different between initial and incubated leaves

	Percent fiber		Percent protein		Fiber : protein	
	Spring	Second	Spring	Second	Spring	Second
Initial	45.6^{A}*	37.9^{A}	6.0^{A}	6.5^{A}	7.6^{A}*	5.8^{A}
Incubated						
REF	61.2^{B}	62.1^{B}	7.5^{B}	7.5^{B}	8.3^{A}	8.3^{B}
DIST	60.4^{B}	59.4^{B}	7.6^{B}	8.4^{B}	7.9^{A}	7.1^{B}

TABLE 3.—Mean ± 1 SE shredder abundance (number/bag) and density (number/g AFDM leaf material) in chestnut oak leaf packs incubated in reference (REF) and disturbed (DIST) streams at Coweeta. Values with the same letter were not significantly ($P \geq 0.05$) different between streams

	Abundance		Density	
Stream	Spring-flush	Second-flush	Spring-flush	Second-flush
REF	11.9 ± 2.5^{A}	12.3 ± 2.4^{A}	10.9 ± 5.5^{A}	9.0 ± 5.1^{A}
DIST	19.0 ± 2.2^{B}	17.8 ± 2.4^{B}	52.2 ± 24.4^{B}	50.5 ± 18.3^{B}

second-flush leaves, at least partly, to differences in intial fiber content between leaf types. Leaf breakdown rates in freshwater are negatively correlated with initial fiber content (Webster and Benfield, 1986; Ostrofsky, 1997) and spring-flush leaves were significantly higher in initial fiber than second-flush leaves. However, the initial difference in fiber between leaf types disappeared after 2 mo in the streams and percent fiber increased in both leaf types as the less refractory material was removed by decomposition.

Our prediction that second-flush leaves would be tougher than spring-flush leaves was only true before they were placed in the streams. After entering the streams second-flush leaves actually softened at a faster rate than spring-flush leaves. Change in leaf toughness through time is used as an index of microbial conditioning (Suberkropp and Klug, 1981); hence, second-flush leaves were more conditioned than spring-flush leaves. This leaf processing by fungi and bacteria undoubtedly contributed to the faster breakdown rates of second-flush leaves.

In a study similar to ours, Irons *et al.* (1991) examined breakdown rates of birch leaves from trees that had been previously browsed by moose. They found that second-flush birch leaves broke down faster than spring-flush leaves as a result of higher initial concentrations of nitrogen and rapid leaching of tannin in second-flush leaves. Taken together, both studies show that terrestrial herbivory by vertebrates or invertebrates can accelerate stream ecosystem processes through changes in leaf quality.

Effects of disturbance history on leaf breakdown.—Previous studies in the streams affected by clear-cutting have shown slower leaf breakdown during logging, but faster breakdown 1 y (Webster and Waide, 1982) and 9 y after logging (Benfield *et al.*, 1991). In our study 14 y after logging, both spring- and second-flush leaves broke down significantly faster in the streams in the recovering clear-cut catchment than in the reference streams. We attribute these faster breakdown rates to higher numbers of shredders and greater microbial conditioning in leaf packs in the disturbed streams. The importance of shredders to detritus processing in streams was demonstrated when elimination of shredders by insecticide application reduced leaf breakdown rates by 25–28% compared to a reference stream (Cuffney *et al.*, 1990). The higher microbial conditioning in the disturbed streams, however, was unexpected. Although the importance of microbes, expecially fungi, to the decomposition and palatability of leaves in streams is well known (Kaushik and Hynes, 1971; Webster and Benfield, 1986; Boulton and Boon, 1991), there have been no studies comparing microbial processes on leaves in our study streams. Our results show that microbial activity needs to be addressed to better understand the long-term higher rates of detritus processing associated with logging disturbance to the surrounding catchment.

The combined effects of rapid microbial conditioning and increased shredder feeding activity in the recovering clear-cut catchment resulted in remarkably fast breakdown rates ($-k$) for both types of chestnut oak leaves (overall mean ± SE = 0.0331 ± 0.0033). This value is much higher than the rates reported for four species of oak [range: 0.0021–0.0169;

mean (SE) = 0.0076 (0.0009), n = 21] in a review of leaf breakdown rates in eastern U.S. streams (Webster *et al.*, 1995). Although oaks are considered a slow-decomposing species (*i.e.*, $-k < 0.005$; Petersen and Cummins, 1974), the breakdown rates seen in the disturbed streams would classify chestnut oak as fast ($-k > 0.01$).

An unanticipated outcome of the rapid breakdown associated with catchment disturbance was that it hindered our ability to detect differences in breakdown rates between spring- and second-flush leaves in the disturbed streams. Only one of the streams in the disturbed catchment had significant differences between leaf types, whereas significant differences were found in two of the three reference streams (Table 1). Our ability to detect significant differences (*i.e.*, statistical power) decreased because fewer collections (*i.e.*, a lower sample size) were required in the disturbed than in the reference streams until <5% initial leaf mass remained. As a result, differences reported in breakdown rates between spring- and second-flush leaves in the disturbed streams are probably conservative.

Overall, our findings indicate that effects of gypsy moth defoliation on leaf quality result in accelerated detritus processing in southern Appalachian streams. Faster breakdown of typically slow-processing leaves such as oak results in a contraction of the leaf processing continuum (Petersen and Cummins, 1974), and create food deficits for shredders during spring when slow-processing leaves are normally the only available leaf resource (Richardson, 1991). Furthermore, our data show that detritus processing pathways in streams previously disturbed by clear-cutting are particularly vulnerable to the consequences of defoliation because leaves are already processed faster in these streams.

Acknowledgments.—We thank Keith Watson of the National Park Service who helped us locate defoliated sites and the study streams in SNP. Robert Brent, Robert Cook and Dr. Jennifer Tank provided laboratory assistance. We also thank the Forage Fiber Lab at Virginia Tech for conducting the fiber and protein analyses. Jon Benstead, Sue Eggert, Dr. Mark Hunter, Brent Johnson, Alonso Ramirez, Kate Schofield and two anonymous reviewers provided valuable comments that improved this paper. This research was supported by Coweeta Hydrologic Laboratory and grant BSR90-11611 from the National Science Foundation.

LITERATURE CITED

BENFIELD, E. F., J. R. WEBSTER, S. W. GOLLADAY, G. T. PETERS AND B. M. STOUT. 1991. Effects of forest disturbance on leaf breakdown in southern Appalachian streams. *Verh. Int. Ver. Limnol.*, **24**: 1687–1690.

BOULTON, A. J. AND P. I. BOON. 1991. A review of methodology used to measure leaf litter decomposition in lotic environments: time to turn over an old leaf? *Aust. J. Mar. Freshwater Res.*, **42**:1–43.

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

DOANE, C. C. AND M. L. MCMANUS (EDS.). 1981. The gypsy moth: research toward integrated pest management. *USDA Forest Service Technical Bulletin,* 1584, 757 p.

DOUCE, G. K., R. D. HAMILTON AND G. L. CLEMENT. 1994. 1992 gypsy moth programs in the southeast. *J. Entomol. Sci.*, **29**:381–397.

ELLIOTT, K. J., L. R. BORING, W. T. SWANK AND B. R. HAINES. 1997. Successional changes in plant species diversity and composition after clearcutting a southern Appalachian watershed. *For. Ecol. Manage.*, **92**:67–85.

ESHLEMAN, K. N., R. P. MORGAN, J. R. WEBB, F. A. DEVINEY AND J. N. GALLOWAY. 1998. Temporal patterns of nitrogen leakage from mid-Appalachian forested watersheds: role of insect defoliation. *Wat. Resour. Res.*, **34**:2005–2116.

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

GOERING, H. K. AND P. J. VAN SOEST. 1970. Forage analyses (apparatus, reagents, procedures, and some applications). *USDA Handbook,* 379, 20 p.

GOLLADAY, S. W., J. R. WEBSTER AND E. F. BENFIELD. 1989. Changes in stream benthic organic matter following watershed disturbance. *Hol. Ecol.*, **12**:96–105.

GRACE, J. R. 1986. The influence of the gypsy moth on the composition and nutrient content of litter fall in a Pennsylvania oak forest. *For. Sci.*, **32**:855–870.

HORNICK, L. E., J. R. WEBSTER AND E. F. BENFIELD. 1981. Periphyton production in an Appalachian Mountain trout stream. *Am. Midl. Nat.*, **106**:22–36.

IRONS, J. G., J. P. BRYANT AND M. W. OSWOOD. 1991. Effects of moose browsing on decomposition rates of birch leaf litter in a subarctic stream. *Can. J. Fish. Aquat. Sci.*, **48**:442–444.

KAUSHIK, N. K. AND H. B. N. HYNES. 1971. The fate of the dead leaves that fall into streams. *Arch. Hydrobiol.*, **68**:465–515.

KLEINBAUM, D. G., L. L. KUPPER AND K. E. MULLER. 1988. Applied regression analysis and other multivariable methods. PWS-Kent Publishing Co., Boston, 718 p.

MACKAY, R. J. AND J. KALFF. 1973. Ecology of two related species of caddis fly larvae in the organic substrates of a woodland stream. *Ecology*, **54**:499–511.

MERRITT, R. W. AND K. W. CUMMINS (EDS.). 1984. An introduction to the aquatic insects of North America, 2nd ed. Kendall-Hunt, Dubuque, Iowa, 722 p.

OSTROFSKY, M. L. 1997. Relationship between chemical characteristics of autumn-shed leaves and aquatic processing rates. *J. N. Am. Benthol. Soc.*, **16**:750–759.

PETERSEN, R. C. AND K. W. CUMMINS. 1974. Leaf processing in a woodland stream. *Freshwater Biol.*, **4**: 343–363.

RICHARDSON, J. S. 1991. Seasonal food limitation of detritivores in a montane stream: an experimental test. *Ecology*, **72**:873–887.

SCHULTZ, J. C. AND I. T. BALDWIN. 1982. Oak leaf quality declines in response to defoliation by gypsy moth larvae. *Science*, **217**:149–151.

SEASTEDT, T. R. AND D. A. CROSSLEY. 1984. The influence of arthropods on ecosystems. *BioScience*, **34**: 157–161.

STONE, M. K. AND J. B. WALLACE. 1997. Long-term recovery of a mountain stream from clear-cut logging: the effects of forest succession on benthic invertebrate community structure. *Freshwater Biol.*, **39**:151–169.

STOUT, B. M., E. F. BENFIELD AND J. R. WEBSTER. 1993. Effects of a forest disturbance on shredder production in southern Appalachian headwater streams. *Freshwater Biol.*, **29**:59–69.

SUBERKROPP, K. AND M. J. KLUG. 1981. Degradation of leaf litter by aquatic hyphomycetes, p. 761–776. *In*: D. T. Wicklow and G. C. Carroll (eds.). The fungal community. Marcel Dekker, Inc., New York.

SWANK, W. T., J. B. WAIDE AND D. A. CROSSLEY. 1981. Insect defoliation enhances nitrate export from forest ecosystems. *Oecologia*, **51**:297–312.

WALLACE, J. B., S. L. EGGERT, J. L. MEYER AND J. R. WEBSTER. 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science*, **277**:102–104.

——— AND M. E. GURTZ. 1986. Response of *Baetis* mayflies (Ephemeroptera) to catchment logging. *Am. Midl. Nat.*, **115**:25–41.

WEBB, J. R., B. J. COSBY, F. A. DEVINEY, K. N. ESHLEMAN AND J. N. GALLOWAY. 1995. Change in the acid-base status of an Appalachian mountain catchment following forest defoliation by the gypsy moth. *Wat. Air Soil Pollut.*, **85**:535–540.

WEBSTER, J. R. AND E. F. BENFIELD. 1986. Vascular plant breakdown in freshwater ecosystems. *Annu. Rev. Ecol. Syst.*, **17**:567–594.

———, S. W. GOLLADAY, E. F. BENFIELD, J. L. MEYER, W. T. SWANK AND J. B. WALLACE. 1992. Catchment disturbance and stream response: an overview of stream research at Coweeta Hydrologic Laboratory, p. 231–253. *In*: P. J. Boon, P. Calow, and G. E. Petts (eds.). River conservation and management. John Wiley and Sons, Chichester, England.

———, M. E. GURTZ, J. J. HAINS, J. L. MEYER, W. T. SWANK, J. B. WAIDE AND J. B. WALLACE. 1983.

Stability of stream ecosystems, p. 355–395. *In*: J. R. Barnes and G. W. Minshall (eds.). Stream ecology. Plenum Press, New York.

——— AND J. B. WAIDE. 1982. Effects of forest clearcutting on leaf breakdown in a southern Appalachian stream. *Freshwater Biol.*, **12**:331–344.

———, J. B. WALLACE AND E. F. BENFIELD. 1995. Organic processes in streams of the eastern United States, p. 117–187. *In*: C. E. Cushing, K. W. Cummins, and G. W. Minshall (eds.). River and stream ecosystems. Elsevier, Amsterdam.

SUBMITTED 17 DECEMBER 1998 ACCEPTED 13 AUGUST 1999