Internat. Rev. Hydrobiol.	86	2001	4–5	417–427
III. Methods in Litter Breakdown				

J. R. WEBSTER[1], E. F. BENFIELD[1], J. J. HUTCHENS[2], J. L. TANK[3], S. W. GOLLADAY[4], and J. C. ADAMS[5]

[1]Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061, U.S.A.
[2]U.S. Environmental Agency, 26W Martin Luther King Dr., Cincinnati, OH 45268, U.S.A.
[3]Department of Biological Sciences, University of Notre Dame, Notre Dame, IN 46556, U.S.A.
[4]J. W. Jones Ecological Research Center, Route 2, Box 2324, Newton, Georgia 31770, U.S.A.
[5]PO Box 2, DAW Park, SA 5041, Australia

Do Leaf Breakdown Rates Actually Measure Leaf Disappearance from Streams?

key words: stream, leaves, breakdown, leaffall, decomposition

Abstract

We measured leaf input, leaf breakdown, and benthic leaf standing stock in Hugh White Creek, a second-order, Appalachian Mountain stream in North Carolina, U. S. A. Leaf input and leaf breakdown data were used in a computer model to predict standing stocks. Predicted standing stocks were then compared with measured values. Once the model was modified to include leaves in four breakdown rate categories, leaf blow-in, and temperature effects on leaf breakdown, agreement between model prediction and measurement was quite good.

1. Introduction

The earliest measurements of leaf breakdown rates in streams (e.g., MATHEWS and KOWALCZEWSKI, 1969; WITKAMP and FRANK, 1969; THOMAS, 1970; KAUSHIK and HYNES, 1971) followed techniques developed in terrestrial studies (e.g., FALCONER *et al.*, 1933; LUNT, 1935; JENNY *et al.*, 1949; SHANKS and OLSON, 1961). With various modifications such as using leaf packs rather than bags (PETERSON and CUMMINS, 1974), measurement of leaf breakdown rates has become a valuable and extensively used tool of stream ecologists. Breakdown rates can be used to provide three types of information. First, they can be used to study mechanisms of leaf breakdown. Second, breakdown rates provide a metric to compare streams or to evaluate a stream response to some modified conditions (e.g., BENFIELD *et al.* this issue). Third, breakdown rates can be used to estimate a component of the organic matter dynamics of streams, i.e., how fast natural leaves in the stream break down. This rate cannot be directly measured by quantifying the change in standing stock of leaves in the stream through time because leaf inputs are continuous. So mass loss from known quantities of leaves that are somehow confined, tied together, or otherwise identifiable is used as a surrogate for natural leaves in the stream. Our objective in this paper is to evaluate the adequacy of leaf breakdown rate as a measure of what is occurring naturally in the stream. We have done this by measuring inputs and breakdown of leaves and using them in a computer simulation model. Results of this simulation are then compared with measurements of leaf standing stock in the stream.

2. Methods

2.1. Site Description

This study was conducted in Hugh White Creek, a 2nd-order stream at Coweeta Hydrologic Laboratory, North Carolina, USA. Hugh White Creek drains 61.1-ha Catchment 14, which is a reference catchment that has been undisturbed since logging in the early 1900's and death of chestnut (*Castanea dentata* (MARSH.) BORKH.) in the 1930's. The forest is dominated by oaks (*Quercus* spp.), red maple (*Acer rubrum* L.), hickories (*Carya* spp.), and yellow poplar (*Liriodendron tulipifera* L.). Streamside vegetation consists of many hemlocks (*Tsuga canadensis* (L.) CARR), birch (*Betula* spp.), and an often dense sub-canopy of rhododendron (*Rhododendron maximum* L.). Instream primary production is extremely low (MULHOLLAND *et al.*, 1997), and the benthic community is dominated by leaf shredding and collector-gathering insects (GURTZ and WALLACE, 1984). The main channel of Hugh White Creek is 1125 m long and averages 3.69 m wide. However, much of the channel is normally very shallow or dry. Average gradient is 0.15 m/m, and average annual discharge at the weir is 19 L/s. This stream has been extensively studied, and further description of the stream and references to earlier studies were published by WEBSTER *et al.* (1997).

2.2. Leaf Fall

Leaf fall inputs to Hugh White Creek were measured in 1993–94 using 0.1462-m^2 baskets. Five sites were located approximately 200 m apart along the 1125-m main stream channel. At each site, we placed 5 baskets on the stream bank and suspended 5 baskets over the stream. The baskets were put into place on 22 September 1993 and lined with plastic garbage bags with slits in the bottom to prevent water accumulation. Leaves falling in the baskets were collected twice monthly through November and then monthly through the rest of the year. In the laboratory, leaves were separated to species, air dried to constant weight, and weighed. Subsamples were ashed at 500 °C to determine AFDM.

2.3. Leaf Breakdown

Breakdown of red maple, white oak (*Q. alba* L.), and rhododendron leaves was measured in 1994–95 using the mesh bag technique (BENFIELD, 1996). Senescent leaves were picked just prior to abscission. Air dried leaves (6 g maple and oak, 8 g rhododendron) were placed in mesh bags (opening = 5 mm). On 19 November 1994, 21 bags of each species of leaves were placed at each of four sites on Hugh White Creek: 3 sites on headwater tributaries and 1 site on the 2nd-order reach. The bags were anchored to the stream bottom with large nails. Three bags of each species were taken back to the lab to account for weight loss due to handling. Three bags of each species from each site were retrieved after two weeks, one month, and approximately monthly thereafter through May 1995. In the laboratory, leaves were rinsed to remove sediment and debris, air dried to constant weight, and weighed. Subsamples were ashed at 500 °C to determine ash-free dry mass (AFDM). Breakdown rates were determined by regressing natural log of mass remaining versus time (e.g., WEBSTER and BENFIELD, 1986). We also determined breakdown rates by regressing log mass remaining versus cumulative degree days (e.g., MINSHALL *et al.*, 1983). The U. S. Forest Service at Coweeta provided mean daily water temperatures.

2.4. Leaf Standing Stock

Leaf standing stock on the streambed was sampled in 1993–94 using a 0.07-m^2 circular sampler. We divided the 1125-m main stream channel into 5 equal reaches. Within each reach we randomly chose a site and collected 4 samples evenly spaced across the stream channel at 5 transects spaced 5 m apart for a total of 100 samples on each date. Samples were collected in September, November, January, March, May, and July. Coarse particulate organic material was removed by hand and placed in a 1-mm mesh net and rinsed to remove smaller material. In the laboratory, the material was separated into leaves, wood, and other (nuts, flowers, etc.), air dried to constant weight, and weighed. Subsamples were ashed at 500 °C to determine AFDM.

3. Results

3.1. Leaf Fall

Annual leaf fall was 327 g AFDM/m^2. This is somewhat less than the 415 g/m^2/y measured in this stream in 1983–84 (WEBSTER *et al.*, 1990). Birch leaves accounted for nearly a quarter of the annual leaf fall (Table 1), and rhododendron, yellow poplar, oaks, hemlock, hickories, and red maple accounted for most of the rest. Over half of the leaf fall was species with medium breakdown rates (*sensu* PETERSEN and CUMMINS, 1974) though another quarter was species with very slow breakdown (Table 2). Most leaf fall occurred in late October and November, but significant amounts of rhododendron leaf fall began in late July (Fig. 1).

Table 1. Species composition of leaf fall to Hugh White Creek.

Species	Percent of annual leaf fall
Birch (*Betula* spp.)	24.0
Rhododendron (*Rhododendron maximum*)	18.2
Yellow poplar (*Liriodendron tulipifera*)	14.5
White oaks (*Quercus alba*, *Q. prinus*)	9.0
Hemlock (*Tsuga canadensis*)	6.8
Hickory (*Carya* spp.)	6.4
Red maple (*Acer rubrum*)	5.9
Red oak (*Q. rubra*)	4.4
Others	9.3

Table 2. Breakdown rates, leaf fall, and leaf blow-in of the four categories of leaf material used in the simulation model.

	Characteristic species	Breakdown rate (d^{-1})	Breakdown rate (degree-day^{-1})	Percent of leaf fall	Percent of leaf blow-in
Fast	Dogwood	0.0232	0.00266	2.7	3.9
Medium	Red maple, Yellow poplar, hickories, birches	0.0114	0.00131	57.0	42.9
Slow	Oaks	0.0089	0.00102	15.3	19.9
Very slow	Rhododendron, hemlock	0.0046	0.00054	25.0	33.2

3.2. Leaf Breakdown Rates

Breakdown rates of red maple were the fastest of the three species measured, white oak was intermediate, and rhododendron was slowest (Fig. 2). Breakdown rates were very similar to rates measured for these species in this and other streams at Coweeta, though the red maple and white oak rates were slightly faster than the means of previous measurements (Fig. 3). For white oak and rhododendron, degree-day breakdown rates fit the data slightly better than the simpler model.

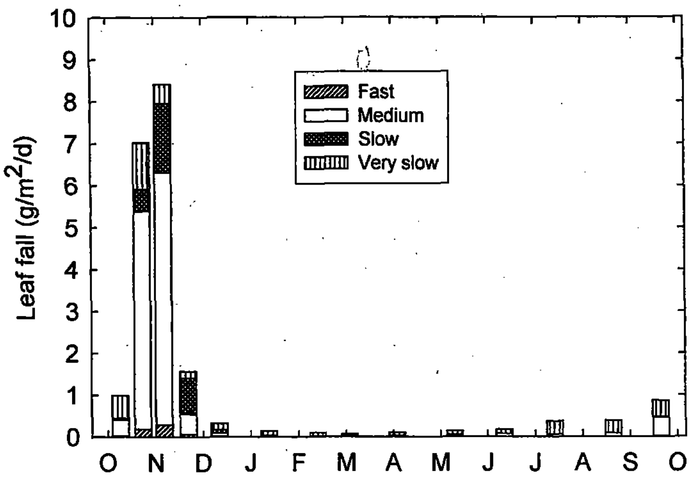

Figure 1. Leaf fall to Hugh White Creek. Leaves were divided into fast, medium, slow, and very slow categories based on breakdown rates (Table 2).

3.3. Leaf Standing Stock

Standing stock of leaves averaged 119.5 g AFDM/m^2, which is very similar to the average of 101.4 g/m^2 measured by STOUT *et al.* (1993). However, our value is considerably less than the 213 g/m^2 reported by GOLLADAY *et al.* (1989), which included wood less than 1 cm diameter. If we add our measurement of small wood, we get 223 g/m^2, which is in close agreement with the average reported by GOLLADAY *et al.* (1989).

With one exception (upstream reach, September), leaves were aggregated at all sites and dates, that is, the variance of the samples was significantly greater than expected for a random distribution (χ^2 test, $\alpha = 0.05$, SOUTHWOOD, 1978). There were no significant trends in the degree of aggregation either through time or along the stream. This high degree of aggregation of leaves in streams has been found in previous studies (e.g., BRETSCHKO, 1990).

The fact that leaves are aggregated suggests that if only a few samples are taken, the mean of these samples will underestimate the standing stock of leaves in a stream. For example, Figure 4 illustrates the highly skewed distribution of leaf samples taken from Hugh White Creek in July 1994. July was chosen for illustration because these data had the most skewed distribution. In July, many of the samples had almost no leaves. The remaining samples fit fairly well to a log-normal distribution (Figure 4B). Total streambed area in Hugh White Creek is 8085 m^2. Thus our 100 0.07-m^2 samples on each date represented less than 0.1% of the streambed area. We used a Monte-Carlo computer simulation to determine if our samples were sufficient to approximate the true leaf standing stock. We generated a set of 115,500 "sample areas" (115,500 = 8085 / 0.07) using the characteristics of the log-transformed July data shown in Figure 4B (27% zeros, mean of remaining log-transformed samples = 0.432, standard deviation of mean = 2.27). We then sampled randomly, either 10 or 100 times, from this set or from a set with a standard deviation twice as great. The sampling was repeated 1000 times, and the data in Table 3 represent the mean and distribution of the 1000 means of the 10 or 100 samples.

In each case, once the sampling scheme was repeated 1000 times, the mean of the means was approximately the same as the true mean obtained by taking the mean of all 115,500 sample areas. However, in all cases the median of the means was less than the true mean.

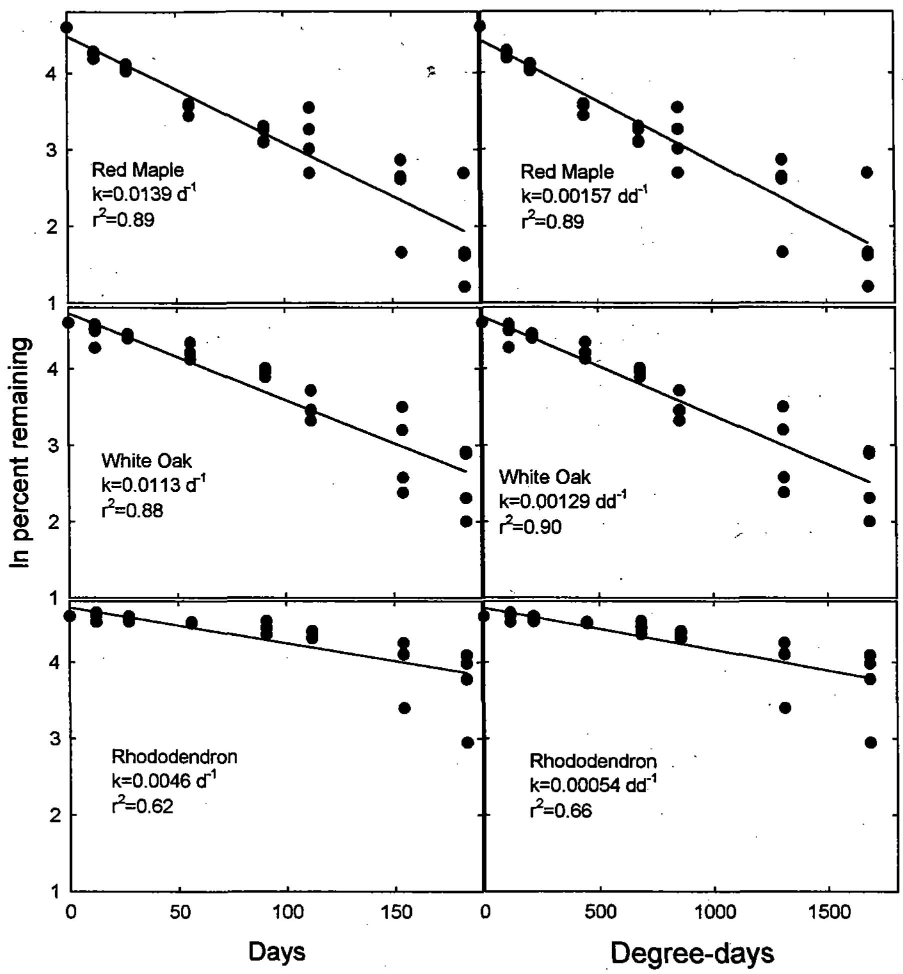

Figure 2. Leaf breakdown rates of red maple, white oak, and rhododendron in Hugh White Creek. Rates in the left column are based on time, and rates in the right column are based on cumulative degree-days. Each dot is the mean of three samples taken from one of the four sites.

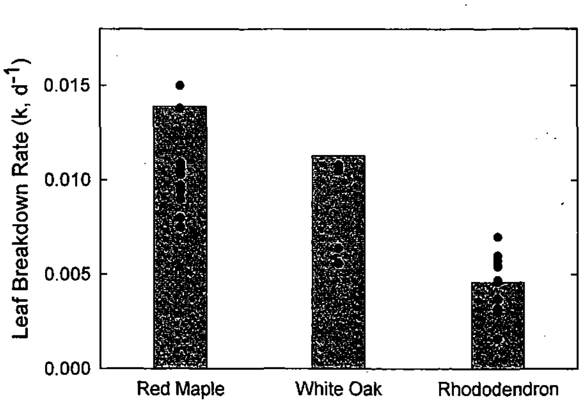

Figure 3. Leaf breakdown rates of red maple, white oak, and rhododendron. The bars represent the rates measured in Hugh White Creek in this study, and the points are other measurements of breakdown rates for these leaf species measured in other reference streams at Coweeta Hydrologic Laboratory (WEBSTER *et al.*, 1999).

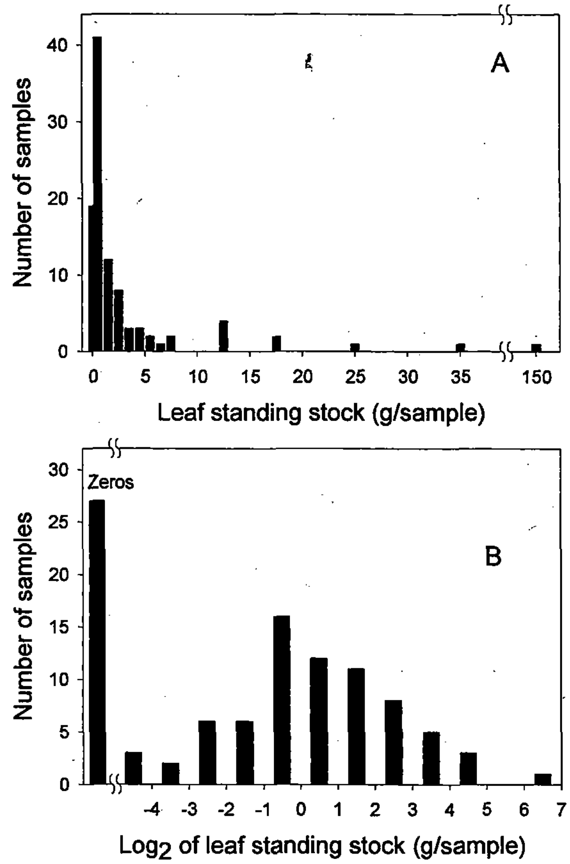

Figure 4. Distribution of leaf standing stock in samples taken from Hugh White Creek in July 1994. Zeros in panel B include all samples with less than 0.02 g/m^2. In both panels the bars are plotted at the midpoints of the standing stock classes. In Panel A the classes are 1 g intervals through 10 g, 10–15, 15–20, 20–30, 30–40, 40–50, 50–100, and 100–200 g. In panel B, the classes are equal intervals based on powers of 2.

Table 3. Results of Monte-Carlo simulation of sampling from an aggregated distribution. The true mean is the mean of the set of 115,500 sample areas taken from the log-normal distribution. Std. Dev. is standard deviation of the mean.

Underlying log-normal distribution		True mean	Number of samples	Results from 1000 replications of sampling		
Mean	Std. Dev.			Mean	Median	Percent of sample means < true mean
0.432	2.27	3.34	100	3.40	3.12	58.0
0.432	2.27	3.34	10	3.50	2.33	66.7
0.432	4.53	116.9	100	111.9	48.3	79.9
0.432	4.53	116.9	10	133.0	13.3	88.6

In the case with an exaggerated standard deviation and only 10 samples, the true mean was underestimated nearly 90% of the time. Nearly 50% of the means were less than 10% of the true mean. Even with 100 samples, nearly 80% of the means were less than the true mean and over 50% of the means were less than one half of the true mean. However, using the actual parameters from the July data, with 100 samples we have probably not underestimated the true mean, at least not by a large amount. In other words, 100 samples is sufficient for sampling benthic leaves in Hugh White Creek.

4. Synthesis

Using the leaf input and breakdown rates reported above, we developed a computer model to predict leaf standing stocks, which we then compared against measured values. The initial model had the following form:

$$\frac{dX}{dt} = I(t) - kX$$

where X is leaf standing stock, t is time, $I(t)$ is leaf fall, and k is the exponential breakdown rate. Daily leaf fall rates were calculated by linear interpolation from data collected in this study (Fig. 1). We used a single breakdown rate based on the average of leaves with fast, medium, slow, and very slow breakdown rates weighted according to their composition in leaf fall. The leaf species in each category and their annual inputs and breakdown rates are shown in Table 2. The breakdown rates are averages of all rates previously measured at Coweeta in reference streams (WEBSTER *et al.*, 1999) plus those measured this study. We did not include loss via transport in this model. Previous studies at Coweeta have shown that streams of this size are highly retentive, leaves break down very close to where they enter the stream, and leaf export is a small fraction of the total leaf input (e.g., WEBSTER *et al.*, 1999). The model was solved numerically using Runge-Kutta integration with a Fortran computer program.

Results of the initial simulation agreed fairly well with measured leaf standing stock but underestimated standing stock throughout winter and spring (Fig. 5). To improve the model,

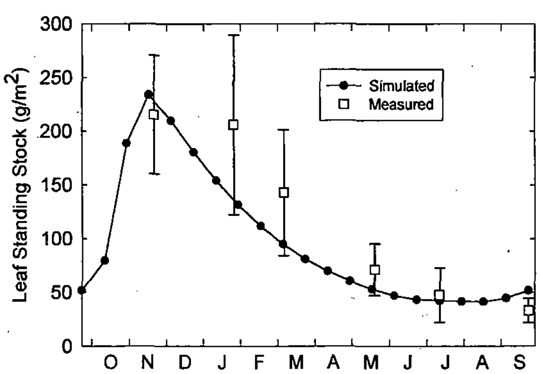

Figure 5. Simulation of leaf standing stock compared to measured data. The error bars of the measured data are 95% confidence limits using the means of the four samples from each cross section as replicates (N = 25). The simulation is based on a single compartment model using a weighted average breakdown rate.

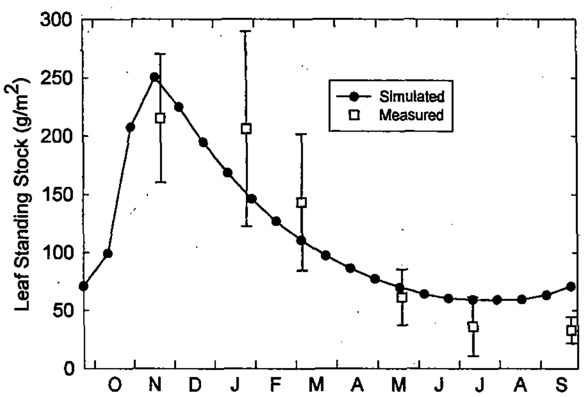

Figure 6. Simulation of leaf standing stock compared to measured data. Error bars as in Figure 5. The simulation is based on a four compartment model using breakdown rates determined for each compartment.

we divided the single compartment into four, representing the four categories of leaf breakdown rates. This modification resulted in a small improvement, but in general the simulated leaf standing stock peaked earlier than the measured standing stock (Fig. 6). A possible reason for this difference is that we did not include blow-in, the lateral movement of leaves into the stream. Blow-in inputs peak after direct leaf fall (WEBSTER *et al.*, 1990) and could account for the later peak of measured standing stock. We did not measure blow-in in the current study, but blow-in was measured in an earlier study in Hugh White Creek (WEBSTER *et al.*, 1990). Blow-in was 18% of direct leaf fall in that study. Blow-in data from that study were included in the model to produce the simulation shown in Figure 7. This addition to the model resulted in a higher autumnal peak and somewhat higher standing stocks through the winter.

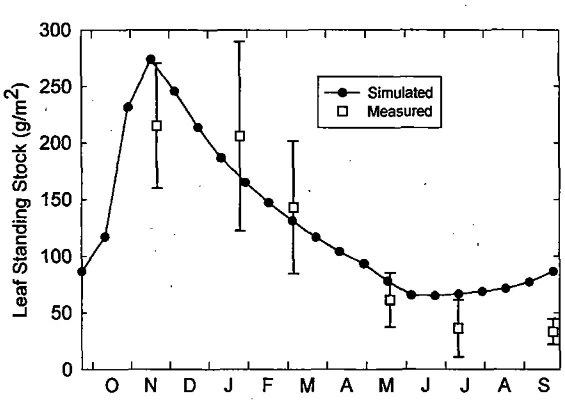

Figure 7. Simulation of leaf standing stock compared to measured data. Error bars as in Figure 5. The simulation is based on a four compartment model using breakdown rates determined for each compartment. This simulation includes blowin of leaves.

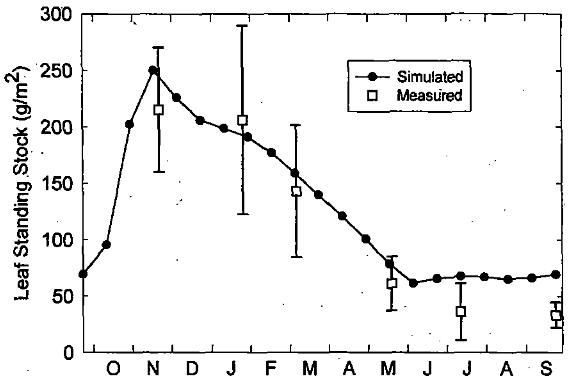

Figure 8. Simulation of leaf standing stock compared to measured data. Error bars as in Figure 5. The simulation is based on a four compartment model using degree-day breakdown rates determined for each compartment. This simulation includes blowin of leaves.

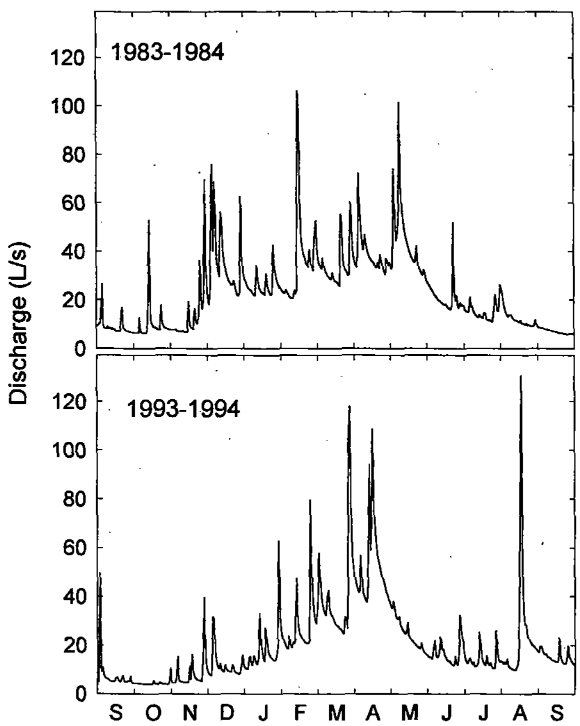

Figure 9. Discharge in Huge White Creek in 1983–1984 and during the present study (1993–1994). Data from U.S. Forest Service, Coweeta Hydrologic Laboratory.

Another aspect of leaf dynamics that we have not as yet considered is the effect of temperature on leaf breakdown rates. To include temperature, we modified the model to use degree-day breakdown rates and mean daily water temperatures. The resulting simulation was greatly improved and provided predictions well within the error bounds of the measured leaf standing stock except in late summer-early fall (Fig. 8). We recorded large leaf fall of rhododendron leaves during this time (Fig. 1), however, we did not find a correspondingly large abundance of these leaves in our September benthic samples. This may simply be an artifact of our random sampling. Benthic data from 1983–84 (GOLLADAY *et al.*, 1989) show CBOM standing stock in July of over 100 g/m^2. Also, the unusual, large storm in August 1994 (Fig. 9) may have caused the large input of leaves and also washed leaves out of the stream, however this does not help explain the lack of correspondence between simulated and measured leaf standing stocks in July.

Results of this study suggest that measured leaf breakdown rates are good estimates of rates at which leaf material is disappearing from streams. To use breakdown rates in this way, two things are required. First, it is essential to account for the differing breakdown rates of different species. The wide range of breakdown rates in streams draining mixed deciduous forests provides a continuum of food availability to benthic leaf-feeding invertebrates (CUMMINS *et al.*, 1989). Second, seasonal temperature variation is a major factor affecting leaf breakdown in temperate zone streams. Also, in streams that are less retentive (e.g., KING *et al.*, 1987; BRETSCHKO, 1990), transport must be taken into account.

5. Acknowledgements

This research was supported by grants from the Long-Term Ecological Research Program of the National Science Foundation for the Coweeta LTER site. Stream flow and temperature data were provided by the U.S. Forest Service at Coweeta. We thank BRIAN WARD, PATRICIA TURNER, and many undergraduate students for their help with the field and laboratory work. We also appreciate the help of Dr. JEFFERY BIRCH, Department of Statistics, Virginia Tech, who provided advice on the statistical analyses. Discussion with Dr. MARK GESSNER also improved this paper.

6. References

BENFIELD, E. F., 1996: Leaf breakdown in stream ecosystems. – *In*: F. R. HAUER and G. A. LAMBERTI (eds.) Methods in stream ecology. – Academic Press. San Diego. pp. 579–589.

BENFIELD, E. F., J. R. WEBSTER, J. L. TANK and J. J. HUTCHENS, 2001: Long-term patterns in leaf breakdown in streams in response to watershed logging. – Internat. Rev. Hydrobiol. **86**: 467–474.

BRETSCHKO, G., 1990: The dynamic aspect of coarse particulate organic matter (CPOM) on the sediment surface of a second order stream free of debris dams (RITRODAT-LUNZ study area). – Hydrobiologia **203**: 15–28.

CUMMINS, K. W., M. A. WILZBACH, D. M. GATES, J. B. PERRY and W. B. TALIAFERRO, 1989: Shredders and riparian vegetation. – BioScience **39**: 24–30.

FALCONER, G. J., J. W. WRIGHT and H. W. BEALL, 1933: The decomposition of certain types of fresh litter under field conditions. – Amer. J. Bot. **20**: 196–203.

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.

GURTZ, M. E. and J. B. WALLACE, 1984: Substrate-mediated response of stream invertebrates to disturbance. – Ecology **65**: 1556–1569.

JENNY, H., S. P. GESSEL and F. T. BINGHAM, 1949: Comparative study of decomposition rates of organic matter in temperate and tropical regions. – Soil Sci. **68**: 419–432.

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

KING, J. M., J. A. DAY, B. R. DAVIES and M.-P. HENSHALL-HOWARD, 1987: Particulate organic matter in a mountain stream in the south-western Cape, South Africa. – Hydrobiologia **154**: 165–187.
LUNT, H. A., 1935: Effect of weathering upon dry matter and composition of hardwood leaves. – J. For. **33**: 607–609.
MATHEWS, C. P. and A. KOWALCZEWSKI, 1969: The disappearance of leaf litter and its contribution to production in the River Thames. – J. Ecol. **57**: 543–552.
MINSHALL, G. W., R. C. PETERSEN, K. W. CUMMINS, T. L. BOTT, J. R. SEDELL, C. E. CUSHING, and R. L. VANNOTE, 1983: Interbiome comparison of stream ecosystem dynamics. – Ecol. Monogr. **53**: 1–25.
MULHOLLAND, P. J., E. MARZOLF, J. R. WEBSTER, D. R. HART and S. P. HENDRICKS, 1997: Evidence that hyporheic zones increase heterotrophic metabolism and phosphorous uptake in forest streams. – Limnol. Oceanogr. **42**: 443–451.
PETERSEN, R. C. and K. W. CUMMINS, 1974: Leaf processing in a woodland stream. – Freshwat. Biol **4**: 345–368.
SHANKS, R. E. and J. S. OLSON. 1961. First-year breakdown of leaf litter in southern Appalachian forests. – Science **134**: 194–195.
SOUTHWOOD, T. R. E., 1978: Ecological methods. Chapman and Hall. London.
STOUT, B. M., E. F. BENFIELD and J. R. WEBSTER, 1993: Effects of a forest disturbance on shredder production in southern Appalachian headwater streams. – Freshwat. Biol. **29**: 59–69.
THOMAS, W. A., 1970: Weight and calcium losses from decomposing tree leaves on land and in water. – J. Appl. Ecol. **7**: 237–242.
WEBSTER, J. R. and E. F. BENFIELD, 1986: Vascular plant breakdown in freshwater ecosystems. – Annu. Rev. Ecol. Syst **17**: 567–594.
WEBSTER, J. R., S. W. GOLLADAY, E. F. BENFIELD, D. J. D'ANGELO, and G. T. PETERS, 1990: Effects of forest disturbance on particulate organic matter budgets of small streams. – J. N. Am. Benthol. Soc. **9**: 120–140.
WEBSTER, J. R., J. L. MEYER, J. B. WALLACE and E. F. BENFIELD, 1997: Organic matter dynamics in Hugh White Creek, Coweeta Hydrologic Laboratory, North Carolina, USA. – *In*: J. R. WEBSTER and J. L. MEYER (eds.) Stream organic matter budgets. – J. N. Am. Benthol. Soc. **16**: 74–78.
WEBSTER, J. W., E. F. BENFIELD, T. P. ERHMAN, M. A. SCHAEFFER, J. L. TANK, J. J. HUTCHENS and D. J. D'ANGELO, 1999: What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta. – Freshwat. Biol. **41**: 687–705.
WITKAMP, M. and M. L. FRANK, 1969: Loss of weight, 60Co and 137Cs from tree litter in three subsystems of a watershed. – Environ. Sci. Tech. **3**: 1195–1198.