J. N. Am. Benthol. Soc., 1990, 9(2):120–140

Effects of forest disturbance on particulate organic matter budgets of small streams

J. R. WEBSTER, S. W. GOLLADAY[1], E. F. BENFIELD, D. J. D'ANGELO, AND G. T. PETERS[2]

Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061 USA

Abstract. Organic matter dynamics were studied in five streams at Coweeta Hydrologic Laboratory. Three of these streams drained logged watersheds, and two drained reference deciduous forest watersheds. Litter inputs to the streams draining disturbed watersheds were significantly lower than to reference streams. Additionally, while undisturbed litterfall consisted primarily of relatively refractory leaf species, litterfall in the disturbed watersheds was composed of more labile leaf material. Non-woody benthic organic material was generally lower in disturbed streams than in reference streams, and woody benthic material was substantially lower in disturbed streams. Particulate organic matter transport was measured intensively during storms. These data were used in a computer model to estimate annual particulate organic matter transport. The model was driven by empirical equations relating particulate concentration to the rate of increase in flow during storms, time since peak storm discharge, and average baseflow concentation. Results showed that disturbed streams exported significantly more particulate organic matter and that most of this transport occurred during storms. In order to place our results in perspective, the model was also used to estimate transport over a 47-year period. Transport during our study was not significantly different from the long-term average.

Organic matter budgets were calculated from input, standing crop, and export data. This synthesis showed that forest disturbance has increased export, has accelerated turnover of benthic particulate organic matter, and is depleting benthic material. These changes are related primarily to the decline of woody debris dams in the disturbed streams.

Key words: stream, logging, organic matter budgets, litterfall, benthic organic matter, wood, debris dams, seston, model.

Most studies of disturbances to streams have addressed effects of direct impacts such as point discharges of sewage, toxic chemical spills, spates, channelization, or damming. Recently, there have also been extensive studies of nonpoint disturbances such as nutrient runoff from agricultural or urban areas. In both types of study, the disturbance has directly altered the structure and function of streams. Because of the close ties between streams and their watersheds, disturbances to terrestrial ecosystems also may have an impact on streams though the effects are indirect. Watershed disturbances include logging, insect defoliation, invasion or introduction of exotic species, vegetation changes (e.g., forest to agriculture or hardwood forest to coniferous forest), volcanic eruption, fire, disease (e.g., chestnut blight), and overgrazing.

Logging has been extensive throughout the United States, and effects of logging on streams have been widely studied. In eastern U.S. few streams drain forests that have never been logged, and many areas have been logged two or more times. In western U.S. many streams still drain undisturbed forests, but the number is declining rapidly. Effects of logging on streams in the southern Appalachians were recently summarized by Swank and Crossley (1988), and Salo and Cundy (1987) discussed extensively interactions between forestry and fisheries in the Pacific Northwest. In both areas the major effects include:

1. Reduced leaf litter inputs accompanied by increased light reaching the stream. The increase in solar radiation elevates temperatures and may increase autotrophic production by attached algae. These changes are relatively short term (i.e., <10 years).

[1] Present address: Biology Department, Clarkson University, Potsdam, New York 13676 USA.

[2] Present address: Wildlife International, Easton, Maryland 21601 USA.

2. A long-term change in allochthonous input quality resulting from the change of vegetation from mature to successional species.
3. A long-term decrease in input of large woody debris, resulting in a decline in the number of woody debris dams, a decrease in streambed stability and channel complexity, and reduced particulate retention.
4. Elevated dissolved nutrient concentrations, especially nitrate, which along with light and temperature increases may stimulate algal production.
5. High sediment inputs from logging roads and skid trails, or from landslides which are frequently associated with roads. Sediment movement in affected stream channels may continue for many years after logging and may be further increased by the reduction in the number of debris dams in the channel.

All these effects of logging are associated with various organic matter processes in streams, and determination of an organic matter budget should be a useful way to summarize changes caused by logging. Energy or organic matter budgets have been used extensively to summarize and understand functional processes in ecosystems. Although some of the earliest ecological studies of budgets concerned flowing water systems (Odum 1957, Teal 1957, Tilley 1968), recent considerations of stream budgets reveal several problems that may limit their utility (Cummins et al. 1983, Cummins 1988). The primary objective of this study was to measure inputs, outputs, and storage of organic matter in reference streams and in streams draining logged watersheds. Secondarily, we used these data to calculate organic matter budgets for the streams and to quantify logging effects from this perspective. As part of this second objective, we examined the problems and limitations of stream organic matter budgets discussed by Cummins et al. (1983) and Cummins (1988).

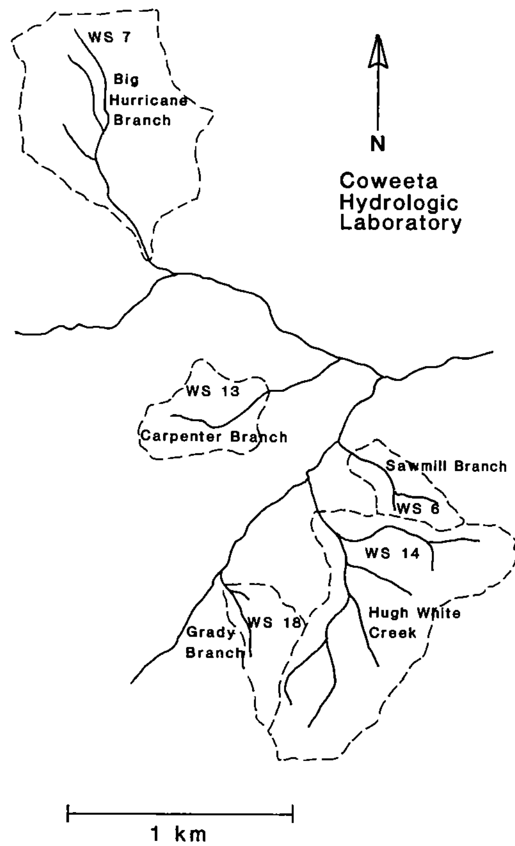

FIG. 1. Map of study area showing the streams, their watersheds, and their proximity to each other.

Study Site

This work was conducted in the southern Appalachian Mountains at Coweeta Hydrologic Laboratory, Macon County, North Carolina, USA. Five sites were selected for study, three streams draining disturbed watersheds and two streams draining reference watersheds (Fig. 1, Table 1). Big Hurricane Branch drains Watershed 7 (WS7), a 58.7-ha watershed, which was clear-cut in 1977. Regrowth is dominated by hardwood sprouts, herbs, vines, and seedlings (Boring et al. 1981). Carpenter Branch drains WS13 (16.1 ha), which was originally mixed hardwoods, but all trees and shrubs were cut in 1939–1940 and again in 1962 (Swank and Douglass 1977). WS13 is presently covered by an intermediate successional hardwood forest dominated by yellow poplar (*Liriodendron tulipifera*) at lower elevations and mixed oaks (*Quercus* spp.) at higher elevations (Leopold and Parker 1985). Sawmill Branch drains WS6 (8.9 ha), which has had a complex history of disturbance that does not typify logging practices in the area. In 1942 all riparian vegetation on WS6 was removed (12% of watershed area); and in 1958 all marketable timber was removed and the slash was burned. The watershed was fertilized, limed, and seeded with grass in 1959; herbicides

TABLE 1. Physical characteristics of the streams of Coweeta Hydrologic Laboratory.

	Grady Branch (WS18)	Hugh White Creek (WS14)	Sawmill Branch (WS6)	Big Hurricane Branch (WS7)	Carpenter Branch (WS13)
Disturbance history	Reference	Reference	Clearcut 1958, regrowth since 1968	Clearcut 1977	Clearcut 1940, 1962
Watershed area (ha)	12.5	61.1	8.9	58.7	16.1
Total channel length (m)	568	3365	450	2445	699
Gradient (m/m)	0.20	0.15	0.24	0.19	0.19
Streambed area (m^2)	1116	8085	277	3274	1330
Average annual discharge (L/sec)	4.1	19.4	2.6	18.5	5.4

were applied from 1960--1965 to inhibit the growth of broadleaf vegetation. WS6 was fertilized again in 1965, and from 1966 to 1968 all vegetation was killed by herbicide treatment (Johnson and Swank 1973). In 1968 the watershed was permitted to begin natural succession and today it is an old-field, with primarily black locust (*Robinia pseudoacacia*) at the lower elevations and yellow poplar at higher elevation sites. Hugh White Creek drains WS14 (61.1 ha) and Grady Branch drains WS18 (12.5 ha). Watersheds 14 and 18 are mixed hardwood forests and are long-term reference watersheds at Coweeta (Swank and Douglass 1977). Both sites were selectively logged before 1925 and, except for the chestnut blight, have been undisturbed for 60 years. The streams are all high gradient and first and second order. Substrate is primarily sand and cobble. Primary production is very low, and stream communities depend largely on allochthonous energy (e.g., Wallace 1988). All five streams are gaged by the Forest Service. These streams have been the subject of many ecological studies, which were recently summarized by Meyer et al. (1988), Wallace (1988), and Webster et al. (1988).

Methods

Litterfall and blow-in

Litterfall was collected in 0.25-m^2 rectangular traps with screen bottoms (mesh opening ca. 2 mm). Ten traps were placed over or adjacent to Sawmill Branch and Grady Branch, and 20 traps were located on Big Hurricane Branch and Hugh White Creek. Equal numbers of blow-in traps were placed on each stream bank. Blow-in traps were 40 cm wide and oriented to catch material moving laterally down the banks into the streams. Litterfall and blow-in traps were placed in pairs at uniform distances along each stream in September 1983. Material accumulating in the traps was collected 10 times during the following 12 mo. The material was dried (50°C), sorted into wood and leaves, and whole leaves were sorted by species. Fruits, nuts, and berries were included with leaves. All material was weighed and subsampled, and subsamples were ashed (500°C) to determine the percent of organic material.

Benthic organic matter

Benthic organic matter (BOM) was collected quarterly from all five streams in 1985-86 (Golladay et al. 1989). Samples were collected with a 0.071-m^2 circular sampler and sorted into large benthic organic matter (LBOM, >1 mm) and fine benthic organic matter (FBOM, 0.45 μm-1 mm). Samples were dried (50°C) and weighed, and subsamples were ashed (550°C). In addition, estimates of woody debris standing crops were made by collecting or measuring and subsampling all wood in 1-m wide transects along each stream. Woody debris was separated into large (>5 cm diameter) and small (1-5 cm diameter) fractions. Further details of this study were described by Golladay et al. (1989).

Particulate organic matter transport

Samples of particulate organic matter (POM) transport were collected from Hugh White Creek, Grady Branch, Carpenter Branch, and Big Hurricane Branch during baseflows and nine storms in 1984 and 1985 (Golladay et al. 1987). Stream water samples were collected with ISCO Model 2100 automated water samplers with intake hoses placed in riffles just upstream of the gaging stations. While this type of sampler misses large particles, previous studies at Coweeta have shown that large particulate organic material is a small fraction (<5%) of total transport (Gurtz et al. 1980, Wallace et al. 1982, Webster et al. 1988). Sampling frequency varied from one sample every 5 min during intense storms to one sample every several hours during less intense rains and after peak flows. Fifteen to 25 samples were collected from each stream during each storm. Samples were filtered (Gelman A/E glass fiber filters), dried (55°C), weighed, ashed (550°C), and reweighed. Organic particle concentration was determined as mass loss on ashing. Further details of this study were described by Golladay et al. (1987).

Results and Discussion

Litterfall and blow-in

Leaffall, leaf blow-in, total litterfall, and total litter blow-in were generally greater in the reference streams than in the disturbed streams (ANOVA; Table 2). Wood blow-in was not different among streams, but wood fall was lowest in Big Hurricane Branch. Attributing any differences to forest disturbance based on this analysis would clearly be pseudoreplication (Hurlbert 1984). However, *t*-tests comparing means of the two disturbed streams with means of the two reference streams showed that reference streams had significantly higher leaf and total inputs but wood inputs were not different (one-tailed *t*-test, $p < 0.05$).

Litterfall (leaves and wood) rates for the two reference streams were fairly similar to rates that have been reported in other studies. Bray and Gorham (1964) found an average of 613 g/m^2 annual litterfall in warm temperate angiosperm forests. Litterfall inputs to streams in similar forests range from 315 to 638 $g\ m^{-2}\ yr^{-1}$ (Fisher 1971, Hall 1972, Winterbourn 1976, Comiskey et al. 1977, de la Cruz and Post 1977, Post and de la Cruz 1977, Dawson 1980, Mulholland 1981, Hornick et al. 1981). Our leaf input rates were also similar to reported measurements of leaf fall in the forests adjacent to our streams (Cromack and Monk 1975, White 1986).

While results show that litter inputs to streams draining disturbed (logged) forests are significantly lower than in reference forests, the differences are small. However, autumn leaf inputs to Big Hurricane Branch only 2 yr after logging were less than 2% of prelogging levels (Webster and Waide 1982). Subsequent measurements have shown that leaffall returned to near reference levels within about seven years (Webster et al. 1988), but the composition of leaf inputs remained altered (Table 3) and will likely remain altered for many years. Successional forest leaffall is generally composed of relatively labile leaf material (e.g., herbaceous plants, birch, black locust, yellow popular), while undisturbed forest leaffall is dominated by more refractory species such as oaks and rhododendron (Webster et al. 1988).

Most leaffall occurred in autumn (Fig. 2). In the two reference streams, 70–80% of leaves fell between 20 September and 20 November. Leaffall to the disturbed streams was slightly lower during autumn, with a higher percent of leaffall in late summer. Blow-in was also greatest in autumn, though the autumn peak accounted for only 30–40% of the annual input. As with leaffall, the autumn peak of blow-in accounted for a lower percentage of the total in the two disturbed streams.

Wood contributed an average of 9% of blow-in and 14% of litterfall. There were few significant differences among streams, and it is evident that our samples were too small for comparing estimates of wood inputs. Woodfall was highly episodic and localized. For example, 39% of the measured woodfall to Sawmill Branch occurred in one trap on one date.

Litterfall and blow-in estimates were converted to total stream inputs by multiplying litterfall by bankful streambed area and multiplying blow-in by twice the total channel length. Blow-in accounted for 14–23% of total inputs to the streams. This is somewhat smaller than values reported by Conners and Naiman (1984) for a spring brook (45% blow-in) but very similar to the 16–25% that has been reported for other first- and second-order forest streams (Fisher 1971, McDowell and Fisher 1976, Comiskey et al. 1977, Gurtz et al. 1982, Hornick et al. 1981, Conners and Naiman 1984). Blow-in may constitute an even higher fraction of allochthonous inputs in areas of more open terrestrial vegetation (Cushing 1988).

TABLE 2. Annual litter inputs to streams at Cowetta Hydrologic Laboratory.[a] Means and 95% confidence limits (in parentheses) on the left are based on ln(x + 1) transformation. Within a column, values followed by the same letter were not significantly different based on analysis of variance followed by a least significant difference test. Confidence limits of arithmetic means were estimated by calculating confidence limits on transformed data and then using the same factor (untransformed) to calculate confidence limits on the arithmetic means (Elliott 1977, Strayer and Likens 1986).

	Transformed Means			Arithmetic Means		
	Leaf	Wood	Total	Leaf	Wood	Total
Blow-in (g AFDM/m)						
Reference Streams						
Grady Branch	79.4 A (26.2–236.7)	7.0 A (3.0–14.9)	87.0 A (29.0–256.8)	136.5 (46.2–403.6)	10.3 (5.2–20.4)	146.7 (50.1–430.0)
Hugh White Creek	64.6 A (60.4–69.2)	3.4 A (1.6–6.7)	70.2 A (47.3–104.1)	88.8 (77.7–101.5)	9.2 (5.0–16.8)	98.1 (66.4–144.8)
Disturbed Streams						
Sawmill Branch	21.1 B (11.0–39.7)	2.5 A (0.8–5.5)	23.8 B (11.4–44.4)	31.8 (17.3–58.5)	4.1 (2.2–7.7)	35.9 (19.6–65.7)
Big Hurricane Branch	21.0 B (10.3–41.5)	3.3 A (0.9–8.9)	24.9 B (11.8–51.3)	52.5 (27.1–101.6)	24.1 (11.1–52.3)	76.7 (38.0–154.7)
Litterfall (g AFDM/m²)						
Reference Streams						
Grady Branch	470.5 A (399.4–607.0)	123.3 A (58.4–259.3)	669.5 A (485.3–923.5)	482.2 (409.6–567.7)	259.7 (105.6–635.4)	741.9 (528.0–1023.1)
Hugh White Creek	409.3 AB (378.0–443.2)	68.0 A (47.0–98.2)	493.7 AB (444.4–548.5)	415.4 (383.6–449.9)	90.9 (63.1–130.9)	506.3 (455.6–562.6)
Disturbed Streams						
Sawmill Branch	318.3 B (252.4–401.2)	72.1 A (37.5–137.7)	416.4 BC (322.7–537.2)	332.3 (263.8–418.6)	105.6 (55.7–200.3)	437.9 (339.5–564.8)
Big Hurricane Branch	311.9 B (241.5–402.9)	16.7 B (8.3–32.8)	336.7 C (257.8–441.9)	354.2 (274.1–457.7)	33.9 (17.7–64.9)	388.1 (296.3–508.4)

[a] Data from most of the litterfall samples were not normally distributed. Blow-in and woody litterfall were extremely skewed, with many small samples and a few very large samples. Therefore, statistical comparisons were made on ln(x + 1) transformed data, and means and confidence limits were calculated on transformed data. However, derived means (sensu Elliott 1977) calculated from transformed data are not appropriate for some purposes. While derived means are the best estimates of litterfall or blow-in expected in traps the same size as ours, these means are dependent on the size of samplers and are inappropriate for calculating budgets and comparing with samples collected with other size samplers. Because they are independent of sampler size and can be expanded to any areal basis, simple arithmetic means should be used in budget calculations that involve combinations of data collected with different types of samplers.

TABLE 3. Percent composition of leaffall to streams at Coweeta Hydrologic Laboratory. Data for Big Hurricane Branch in 1974–75 are from Webster and Waide (1982). The miscellaneous category includes unidentified leaf fragments and species that contributed <5% to any stream.

	Reference Streams			Disturbed Streams	
	Grady Branch	Hugh White Creek	Big Hurricane Branch (1974–75, before logging)	Big Hurricane Branch (1983–84)	Sawmill Branch
Oaks (*Quercus* spp.)	32.7	17.6	32.4	5.5	2.6
Rhododendron (*Rhododendron maximum*)	13.5	14.2	11.6	11.6	0.0
Hemlock (*Tsuga canadensis*)	10.3	2.4	0.0	0.8	0.0
Ash (*Fraxinus* spp.)	8.6	2.8	0.0	0.5	10.5
Birch (*Betula* spp.)	8.2	27.1	5.1	11.8	1.6
Magnolia (*Magnolia* spp.)	6.8	3.9	0.0	5.0	1.1
Yellow Poplar (*Liriodendron tulipifera*)	5.1	12.6	9.1	2.2	28.1
Red Maple (*Acer rubrum*)	4.4	4.4	4.8	11.0	8.0
Dogwood (*Cornus florida*)	1.0	0.6	1.1	6.5	1.0
Willow (*Salix nigra*)	0.0	0.0	0.0	4.3	5.6
Black Locust (*Robinia pseudoacacia*)	0.0	0.1	0.1	3.1	5.7
Beech (*Fagus grandifolia*)	0.1	0.4	7.9	1.9	0.4
Hickories (*Carya* spp.)	0.0	0.1	11.4	0.0	0.1
Herbaceous	0.3	0.3	0.0	8.3	5.0
Miscellaneous	9.0	13.1	15.5	27.3	30.2

Benthic organic matter

Results of the benthic organic matter study have been published previously (Golladay et al. 1989) and will only be summarized here. Carpenter Branch had the highest levels of FBOM and LBOM (Table 4), probably owing to its somewhat different channel morphology. Carpenter Branch has a long, low-gradient section and a short, steep-gradient section. The low-gradient section is deeply incised and accumulated large amounts of non-woody BOM. If we exclude Carpenter Branch from the analysis, reference streams had significantly more non-woody BOM than disturbed streams (t-test on means, $p < 0.05$). Amounts of woody BOM were large in both reference streams and significantly less in disturbed streams (t-test on means, $p < 0.05$). Wood standing crop was lowest in Carpenter Branch, which was first cut in 1939–40. Most wood in the stream before that cutting, and logging slash that entered during cutting, has decomposed. Wood inputs since 1940, either natural or from the 1962 cutting, have probably been low and apparently decomposed rapidly. Sawmill Branch also had very little wood, in part because the slash was burned after the 1958 cutting. There were few logs and no debris dams in Sawmill Branch (Golladay et al. 1989). Big Hurricane Branch, which drains the most recently cut watershed, contains considerable woody debris, some predating logging and some entering the stream as slash. Since total BOM was dominated by large wood, the total was significantly higher in reference than in disturbed streams (t-test on means, $p < 0.05$).

Particulate organic matter transport

Particulate transport in the streams was described in a previously published paper (Golladay et al. 1987). These results are summarized here, and we used these data to estimate annual particulate transport.

Baseflow POM concentrations ranged from 0.1 to 7.0 mg/L, were generally highest in summer, and declined to lowest values in winter. Reference and disturbed streams of similar size did not differ significantly (paired t-test, $p > 0.05$).

A typical pattern of POM concentration during storms is illustrated by data from a storm

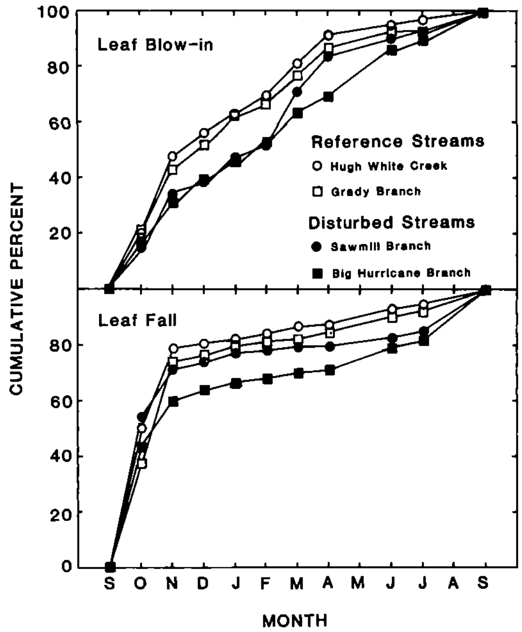

FIG. 2. Cumulative leaf inputs to four streams at Coweeta Hydrologic Laboratory, 1983–84.

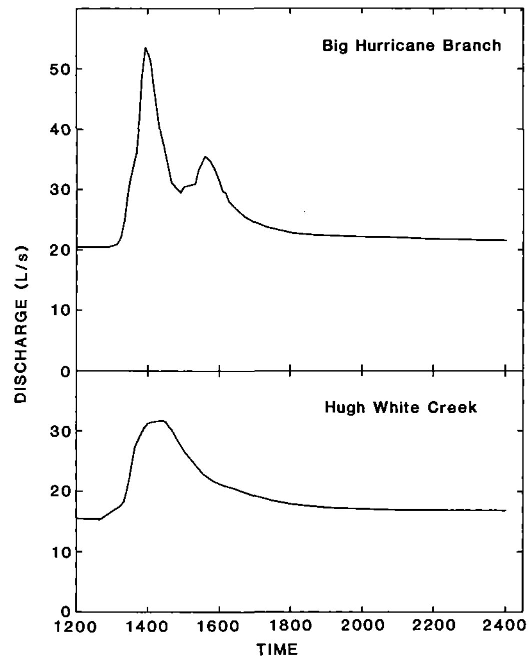

FIG. 3. Discharge in Big Hurricane Branch (disturbed) and Hugh White Creek (reference) during a summer thunderstorm on 20 June 1984.

on 20 June 1984. For consistency, illustrations in this section are limited to Big Hurricane Branch and Hugh White Creek and are all based on data from this one storm. It was a fairly intense summer thunderstorm (1.57 cm rainfall), which approximately doubled discharge in each stream (Fig. 3). POM concentration increased rapidly during the rising hydrograph and peaked at or before peak discharge (Fig. 4). Following peak discharge, POM concentrations decreased rapidly. The second discharge peak in Big Hurricane Branch (Fig. 3) was accompanied by a slight increase in POM concentration (Fig. 4).

POM concentrations during storms were generally higher in disturbed streams than in reference streams. One exception was a brief but intense November storm just after leaffall, when POM export from the two reference streams exceeded export from the paired disturbed streams even though peak POM concentrations were higher in the disturbed streams. Appar-

TABLE 4. Benthic organic matter (g AFDM/m^2) in Coweeta streams. Data are arithmetic means reported by Golladay et al. (1989).

	FBOM (<1 mm)	LBOM[a] (>1 mm)	Small Wood (1-5 cm)	Large Wood (>5 cm)	Total
Reference streams					
Grady Branch	147	244	300	4578	5269
Hugh White Creek	166	213	312	5134	5825
Disturbed streams					
Sawmill Branch	157	129	78	1457	1831
Big Hurricane Branch	113	124	383	2833	3453
Carpenter Branch	387	255	261	232	1135

[a] Includes wood <1 cm diameter.

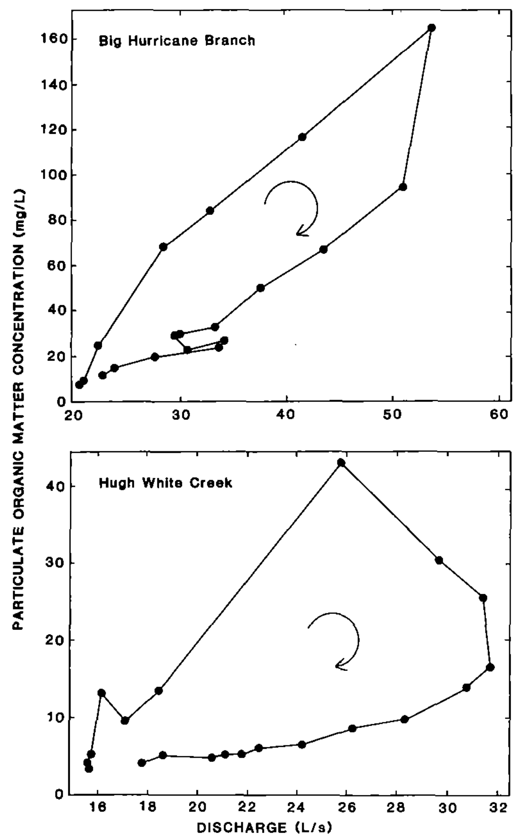

FIG. 4. Particulate organic matter concentration versus discharge in Big Hurricane Branch (disturbed) and Hugh White Creek (reference) during the storm on 20 June 1984 (Fig. 3). The arrows indicate the time sequence of samples. Note the difference in scale on the vertical axis.

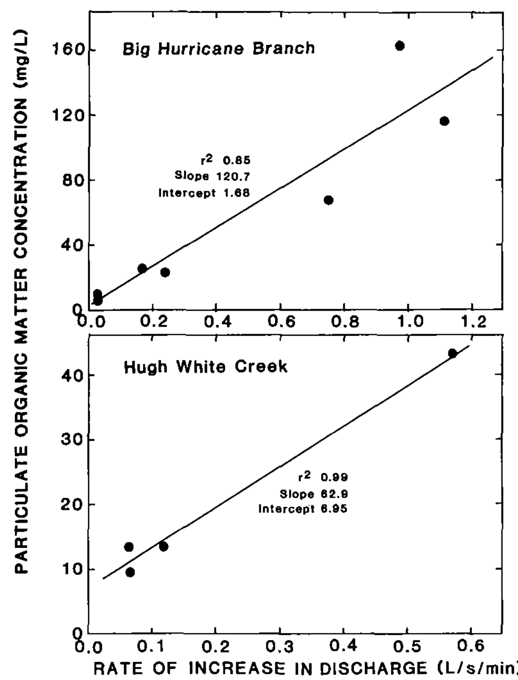

FIG. 5. Particulate organic matter concentrations in Big Hurricane Branch (disturbed) and Hugh White Creek (reference) versus the rate of increase in discharge. Data are from the rising hydrographs of the storm on 20 June 1984 (Figs. 3, 4). Big Hurricane Branch $p = 0.003$; Hugh White Creek $p = 0.006$. For most storms there were more data points than for the storm illustrated in this figure.

ently the disturbed streams were very rapidly flushed of accumulated POM.

Estimating annual transport of particulate organic matter

One of the problems of stream organic matter budgets has been the use of rating curves (i.e., graphs relating POM concentration to discharge) to estimate annual particulate transport (Cummins et al. 1983). When we used rating curves we found they were significant (linear regression, $p \leq 0.05$) for three of the four streams but explained only 19% of the variance at best. Rating curves for individual storms were significant ($p \leq 0.05$) in only 23 of 36 cases (9 storms, 4 streams). The lack of a stronger relationship was due to the hysteretic nature of the relationship (e.g., Fig. 4). Concentrations were higher during rising discharge than at equal discharge when discharge was dropping.

Some of our earlier work has suggested that factors other than discharge are useful for predicting POM concentrations during storms (Webster et al. 1983, 1987). POM concentrations during periods of rising discharge are usually correlated with the rate at which discharge is increasing as illustrated in Figure 5. Using the rate of increase in discharge during the 5-min interval prior to each sample, we found that this relationship was significant ($p < 0.05$) for 22 of 29 storms for which we had sufficient data to analyze (Appendix 1). Similarly, during falling discharge, POM concentrations decline exponentially as a function of time since the last peak concentration (Fig. 6). This relationship was significant ($p < 0.05$) for 31 of 33 storms

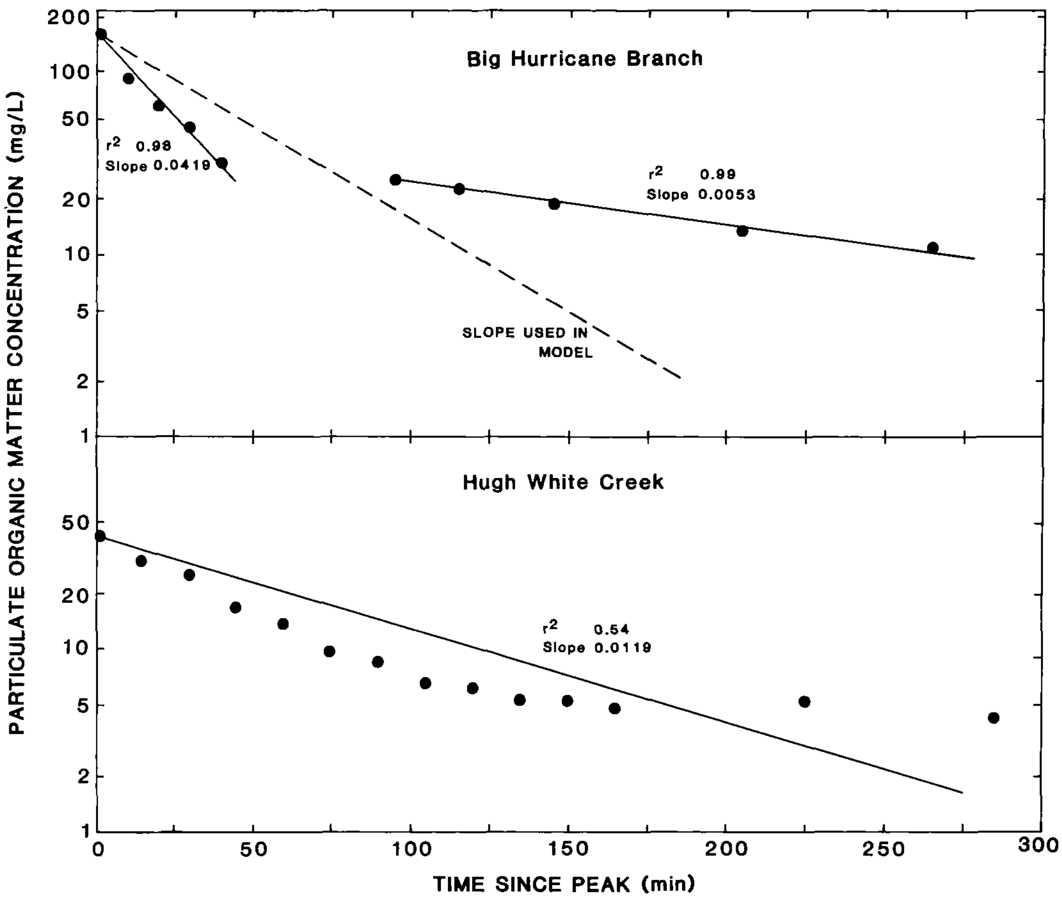

FIG. 6. Particulate organic matter concentrations in Big Hurricane Branch (disturbed) and Hugh White Creek (reference) versus time since peak discharge. Data are from the falling hydrographs of the storm on 20 June 1984 (Figs. 3, 4). Big Hurricane Branch $p = 0.0001$; Hugh White Creek $p = 0.0001$.

(Appendix 1). For several storms it was evident that the rate of decrease in POM concentration changed an hour or so after a peak (Fig. 6). However, this change was not apparent in enough of the data to be incorporated into our model.

Using the relationships between POM concentration and rate of increase in discharge and time since peak (Appendix 1) and hydrologic data supplied by the Forest Service at Coweeta, we developed an empirical computer model to estimate POM concentration for each 5-min interval throughout the year. The first step was to determine if a storm was occurring. Storms were defined using criteria similar to those used by Hewlett and Hibbert (1967). A storm was initiated by a discharge increase of 0.011 L s^{-1} ha^{-1} hr^{-1} or greater, and the storm continued as long as flow remained greater than a line extrapolated from the point of storm initiation with a slope of 0.0055 L s^{-1} ha^{-1} hr^{-1}. Hewlett and Hibbert (1967) used this line to separate quickflow and delayed flow. They also used this slope to define the initiation of a storm, but they eliminated all storms with a total quickflow volume less than 0.254 m^3/ha. We did not delete these small storms, as we measured significant increases in POM concentration even during very small storms.

If a storm was occurring at a particular time, the model then determined if flow was increasing or decreasing, and POM concentration was determined using the appropriate regression equations for that stream at that time of year. If a storm was not in progress, POM concentration was determined from baseflow data. Between days of data collection, model parameters and baseflow concentrations were calculated by linear interpolation between the nearest sample dates.

Model-generated POM concentrations for actual sampling dates were very similar to the calibration data (Fig. 7), though the model overestimated concentrations just after peak discharge and under-estimated them near the end of a storm. Both problems were due to the change in slope mentioned earlier. By summing POM concentration × discharge for various time intervals, we calculated daily, monthly, annual, storm, rising flow, falling flow, and baseflow transport.

One problem quickly became evident. Annual POM transport in Big Hurricane Branch, a disturbed stream, was less than in Hugh White Creek, the reference stream of similar size (Table 5). This was despite the fact that our samples showed generally higher POM concentrations in Big Hurricane Branch. The difference was due to a single thunderstorm on 21 June 1984, which passed over the southern part of the research area (Fig. 1) and was very heavy, especially on WS14 (Hugh White Creek); however, very little rain fell on WS7 (Big Hurricane Branch). This one storm provided 1.1% of the annual discharge in Hugh White Creek and, based on our model, accounted for nearly 50% of annual POM transport. For Big Hurricane Branch the 21 June storm was only 0.2% of annual discharge and 1.8% of annual POM transport. Obviously these differences between streams made it difficult to compare Big Hurricane Branch with Hugh White Creek and to evaluate effects of disturbance on POM transport. As one way of working around this problem, we used Hugh White Creek hydrologic data in the Big Hurricane Branch model to estimate what POM transport would have been if hydrologic regimes of the two streams had been identical. Using the adjusted Big Hurricane Branch data (i.e., based on Hugh White Creek hydrology), it is evident that disturbed streams transport more POM than reference streams (Table 5). The difference was significant on a kg/ha watershed-area basis (paired t-test, $p < 0.05$) but not on a g/m² stream-area basis because the large transport by Big Hurricane Branch caused a very large variance in transport by disturbed streams.

More than 70% of POM transport in all streams occurred during storms, with slightly more transport on the falling side of storm hydrographs than on the rising side (Table 5). Similarly, Cuffney and Wallace (1988) showed that 50–79% of particulate export occurred during storms in other Coweeta streams. Since only 15–17% of annual discharge occurred during storms, and since storms occurred only about 10% of the time, the sampling problem for estimating annual transport is evident. Whether or not our model results represent the actual POM transport that occurred in 1984–85, they do represent a realistic sequence of POM concentrations and can be used to evaluate the effectiveness of various sampling programs (Table 6). Grab samples clearly underestimate total transport. Only with hourly samples, each sample analyzed separately, did the simulations approach the actual

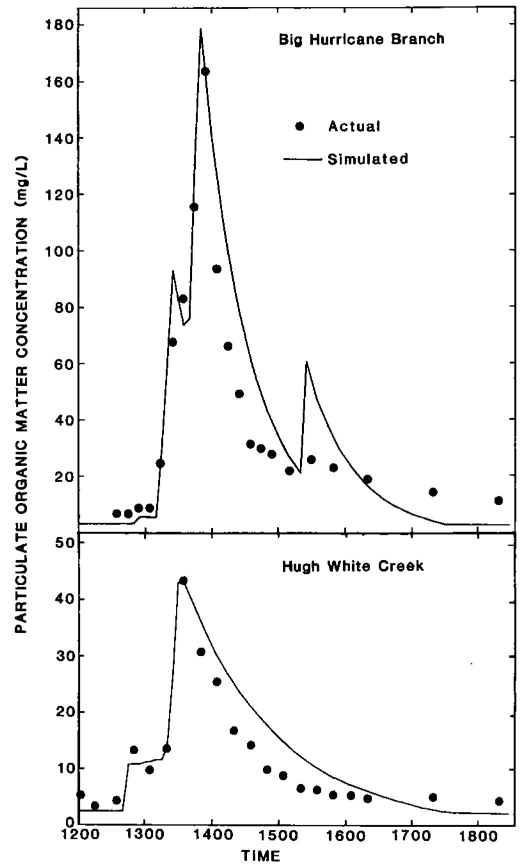

FIG. 7. Simulated versus actual particulate organic matter concentration in Big Hurricane Branch (disturbed) and Hugh White Creek (reference) during the storm on 20 June 1984.

TABLE 5. Discharge and estimates of annual particulate organic matter transport from Coweeta streams. The Big Hurricane Branch* data are based on Hugh White Creek hydrology.

	Reference Streams		Disturbed Streams		
	Grady Branch (WS18)	Hugh White Creek (WS14)	Big Hurricane Branch (WS7)	Big Hurricane Branch* (WS7)	Carpenter Branch (WS13)
Annual discharge					
(m^3)	85,303	432,245	428,049	—	117,758
(m^3/ha)[a]	6824	7074	7292	—	7314
Percent during storms	15.8	17.4	11.7	—	15.5
Percent during rising flows	4.2	5.7	4.3	—	4.4
Percent during falling flows	11.6	11.7	7.4	—	11.1
Annual POM transport					
(kg)	557	4326	2397	6238	1138
(kg/ha)[a]	44.6	70.8	40.8	106.3	70.7
(g/m^2)[b]	499.1	535.1	732.1	1905.3	855.6
Percent during storms	74.6	80.5	47.9	81.8	72.9
Percent during rising flows	31.9	31.6	22.3	36.8	29.6
Percent during falling flows	42.7	48.9	25.6	45.0	43.3

[a] Based on watershed area.
[b] Based on streambed area.

value, i.e., the estimate based on 5-min interval samples. Flow proportional samples (sample frequency proportional to discharge, e.g., Fredricksen 1969, 1970) were much more effective. The range of values for flow proportional sampling resulted from a series of simulations using different sampling frequencies. For example, in one simulation, flows <2 L/s were sampled once every 320 min. With each doubling of flow, sample frequency was doubled up to the maximum rate of one sample every 5 min at flows ≥64 L/s. In this simulation, the maximum number of samples taken per week was 146 and the average was 61. The samples were composited weekly. Annual transport was estimated at 593 kg. The results suggest that when weekly or annual transport is the only information needed, a flow proportional sampling scheme is by far the most efficient.

Two parameters used in the computer model were selected somewhat arbitrarily: the rate of increase in discharge used to define the beginning of a storm and the flow separation slope used to define the end of a storm. Their effects on our estimates of annual transport were evaluated by running the model with different parameter values. Results of this analysis indicated very little sensitivity to these parameter values. During most storms the initial rate of increase in discharge was well above the parameter value we used. Also, after a storm peak, the POM concentration usually dropped to near baseflow values well before the storm ended, i.e., before the model defined the end of the storm. Therefore it was not surprising that these

TABLE 6. Estimates of annual POM transport from Grady Branch based on simulations of various sampling programs.

	Annual POM Transport (kg)
"Actual" (samples every 5 min)	557
Hourly samples	
Each sample analyzed	513
Composited daily	313
Composited weekly	266
Daily samples (9:00 AM)	219
Weekly samples	
Average	241
Wednesday samples	393
Sunday samples	182
Flow proportional samples (composited weekly)	525–605

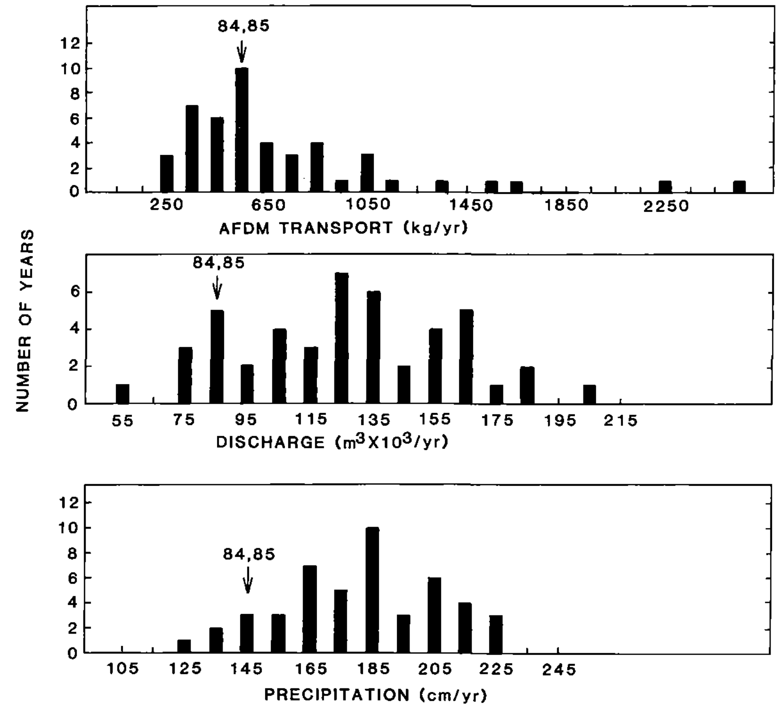

FIG. 8. Frequency histogram for annual particulate organic matter (AFDM) transport, discharge, and precipitation in Grady Branch (WS18). Discharge and precipitation data are from Forest Service records at Coweeta Hydrologic Laboratory. Particulate transport is from our simulation. 84, 85 indicates the year of our study. Data are for 1938 through 1985 and are based on May–April water years.

two parameters had little effect on annual transport estimates or on the percent of transport occurring during storms.

A frequent criticism of ecological studies is that they are short-term and can't be placed in a long-term perspective. Using our model we were able to compare our results with long-term averages and trends. While we don't know how transport-discharge relationships have changed over the last 47 years, we can look at how export might have varied in response to different annual discharge patterns if transport-discharge relationships were the same. Simulations of transport in Grady Branch for 47 yr (1938–84) showed that while the year of our study (1984–85) was extremely dry based on precipitation and discharge, POM transport was about average (Fig. 8). Annual transport in 1984–85 was below the 95% confidence limits for the 47-yr mean (Table 7), but the distribution was highly skewed by a few years of very high transport. Two years in particular, 1973–74 and 1976–77, were characterized by very high discharge and high transport. When the annual transport data were ln transformed, the 1984–85 value was within the 95% confidence limits.

A number of correlations were apparent in the 47-yr data set (Table 8); however, the correlations between transport and discharge are questionable since the same factor, discharge, is a component of both variables. Average concentration (annual transport/annual discharge) is probably a more meaningful variable in this analysis. POM concentration was significantly correlated with several discharge-related variables, but the highest correlation was with annual stormflow.

Based on the 47-yr data, monthly discharge was high in winter and low throughout the summer, reaching lowest values in early fall (Swift et al. 1988, Fig. 9). Stormflow followed the same pattern but was a lower fraction of total flow during the growing season than during winter. POM transport, after a peak follow-

TABLE 7. Forty-seven year average compared with data from the year we sampled (1984–85). Long-term averages are based on May through April water years. Discharge, POM transport, and POM concentration are for Grady Branch (WS18). Precipitation is for the main climate station at Coweeta, staff gage 19.

	47-yr data			
	Mean (95% CL)	Minimum	Maximum	1984–85
Annual discharge (m^3/yr)				
Total	127,600 (117,600–137,500)	59,100	200,100	85,300
Storm	34,800 (30,700–38,900)	11,300	65,400	13,500
Storm as percent of total	25.4 (24.9–27.9)	15.6	37.4	15.8
Rising flow	8500 (7700–9400)	3500	14,600	3600
Falling flow	26,300 (22,900–29,600)	7200	51,800	9900
Annual precipitation (cm/yr)	182.0 (174.6–189.4)	124.4	224.7	150.0
Annual POM transport (kg/yr)				
Total	745 (600–891)	228	2555	557
Storm	584 (445–722)	127	2342	416
Storm as percent of total	73.2 (70.5–75.9)	52.0	91.6	74.8
Rising flow	234 (189–280)	69	686	178
Falling flow	349 (254–445)	58	1655	238
POM concentration (mg/L)	5.52 (4.80–6.24)			6.53

ing autumn leaffall, was lowest in early to mid winter and peaked in spring. Transport remained fairly high through the summer. This pattern has been generally observed in other Coweeta studies (Webster 1983, Webster and Golladay 1984). 1984–85 fit the pattern fairly well except for the very high transport in June and the low transport in winter resulting from low discharge.

Synthesis

Organic matter budget calculations

We estimated POM budgets for the five streams using the data reported above (Table 9). For Carpenter Branch where we had limited litter-input data, we used several averages based on the other streams (detailed in footnotes to Table 9). Also, for Sawmill Branch where we did not have storm POM concentrations, we estimated minimum annual export from baseflow concentrations. One criticism of the budgets is that inputs, standing crops, and export were measured in different years—1983–84, 1985–86, and 1984–85, respectively. We doubt there were large changes in inputs over this period, but, as discussed previously, year-to-year differences in export are a major problem of organic budgets. Quarterly standing crop measurements did not show major long-term (i.e., greater than annual) changes (Golladay et al. 1989). Even major differences in standing crops (±50%) would not modify our conclusions concerning differences between disturbed and reference streams.

Inputs were lowest to disturbed streams (Table 9), reflecting the somewhat lower leaffall of successional forests. If wood was included, BOM standing crops were much greater in the reference streams, but if wood was excluded, Carpenter Branch stood out because of anomalously high LBOM and FBOM standing crops. Export was greatest from the disturbed streams, especially from Big Hurricane Branch and Sawmill Branch. Turnover rates and other budget parameters are dependent on stream size, so ratios in Table 9 need to be paired by stream size for comparison, i.e., Grady Branch can be compared with Sawmill Branch and Carpenter Branch, and Hugh White Creek is comparable to Big Hurricane Branch. When compared in this way, the ratios of inputs to standing crop were smaller in the reference streams than in the disturbed streams. This difference was primarily due to the large amount of wood stored in the reference streams. If small and large wood were not included in this calculation, all the ratios would be fairly similar. The annual input was about

TABLE 8. Relationships between annual POM transport, average annual POM concentration, and various flow related parameters. These results are based on 47 yr of data for Grady Branch.

Dependent Variable	Independent Variable	r^2	p
Annual POM transport	Annual flow	0.53	0.0001
	Annual storm flow	0.54	0.0001
	Percent storm flow	0.28	0.0001
	Total rainfall	0.40	0.0001
	Rainfall during dormant season	0.20	0.0014
	Rainfall during growing season	0.16	0.0054
Average POM concentration	Annual flow	0.26	0.0003
	Annual storm flow	0.28	0.0001
	Percent storm flow	0.15	0.0076
	Total rainfall	0.17	0.0040
	Rainfall during dormant season	0.08	0.0526
	Rainfall during growing season	0.07	0.0722

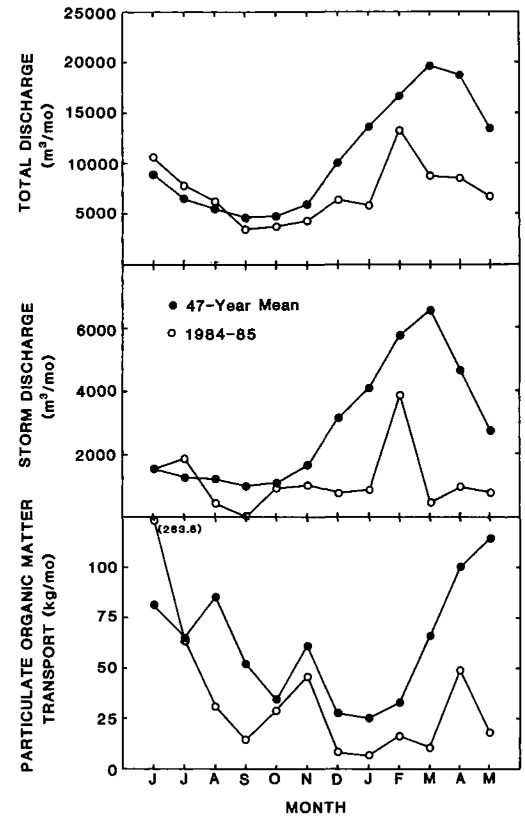

FIG. 9. Monthly means of total discharge, storm discharge, and particulate organic matter transport for 1938 through 1984 and 1984-85 in Grady Branch (WS18). Discharge data are from Forest Service records at Coweeta Hydrologic Laboratory. Particulate transport data are from our simulations.

equal to or perhaps slightly larger than the standing crop.

Looking at turnover rates using export/standing crop, we see an even greater distinction between reference and disturbed streams. Only about 10% of the standing crop POM was exported each year from reference streams, whereas 50 to over 100% was exported from disturbed streams. Calculating these ratios independent of wood was not possible because we don't know what fraction of export was wood-derived.

The lack of steady state was clearly evident from the ratios of export to input. Input exceeded export for both reference streams. However, these export values do not include leaching and biotic conversion of organic matter to CO_2, i.e., respiration. Using respiration rates reported by Cuffney et al. (1990) for benthic material in small Coweeta streams, we estimated respiration losses of 728 and 770 g m^{-2} yr^{-1} for Grady Branch and Hugh White Creek, respectively. These are probably large over-estimates, because the interior mass of large wood does not respire at rates similar to the small pieces of wood used in the respiration measurements; however, these calculations do suggest that leaching and respiration could account for the difference between input and export in the reference streams and that these reference streams may be near steady state most years. Petersen et al. (1989) reached a similar conclusion for a stream in Michigan. However, export greatly exceeds input in some years. If we assume that input to Grady Branch has been constant, export would have exceeded input 11 times between 1938 and 1984 (Fig. 8) and in three of those years was 2–3× input. Thus during most years there must be a small but consistent aggradation of organic matter. Alternatively, input may not be constant, and infrequent years of very high input, e.g., when a large tree falls into the stream, may balance years of high export.

In the three disturbed streams, there was clear degradation of stored organic matter—export

TABLE 9. Particulate organic matter budgets for streams at Coweeta Hydrologic Laboratory.

	Input ($g\ m^{-2}\ yr^{-2}$)	Standing Crop (g/m^2)	Export ($g\ m^{-2}\ yr^{-1}$)	Input ÷ Standing Crop	Export ÷ Standing Crop	Export ÷ Input
All particulate organic matter						
Reference streams						
Grady Branch	891	5269	499	0.17	0.10	0.56
Hugh White Creek	588	5825	535	0.10	0.09	0.91
Disturbed streams						
Sawmill Branch	556	1822	2174[a]	0.30	1.19	3.91
Big Hurricane Branch	503	3453	1905	0.15	0.55	3.79
Carpenter Branch	433[b]	1135	856	0.55	0.75	1.36
Not including wood >1 cm						
Reference streams						
Grady Branch	621	391	—	1.59	—	—
Hugh White Creek	489	379	—	1.29	—	—
Disturbed streams						
Sawmill Branch	437	286	—	1.53	—	—
Big Hurricane Branch	433	237	—	1.83	—	—
Carpenter Branch	400[b]	642	—	0.78	—	—

[a] We estimated a minimum export for Sawmill Branch by assuming an average annual POM concentration 2× the baseflow concentration (Webster and Golladay 1984). For the other streams, average annual concentrations ranged from 2.7 to 5.7 baseflow concentrations.

[b] Carpenter Branch leaffall was measured by Risley (1987). Total input was estimated by assuming wood blow-in of 18.6% of total wood input (the average for the other streams) and wood fall of 21.4% of total litter fall (the average for the other streams). Leaf blow-in was estimated as 23.5% of total leaf input (the average for the other streams).

substantially exceeded input (Table 9). In fact, our estimates of export were so much greater than inputs, that all standing crop organic matter should be lost from Sawmill Branch in less than two years and from Big Hurricane Branch and Carpenter Branch in less than three years if our turnover rates are accurate. These very high turnover rates were determined for a year that apparently had average or below-average transport, and they do not include leaching or respiration. However, our data for Big Hurricane Branch indicate that standing crop organic matter is not actually declining as rapidly as indicated by the turnover rate in Table 9. Transport from Big Hurricane Branch has been high ever since it was logged in 1977 (Gurtz et al. 1980, Webster et al. 1983). Because the standing crop in this stream before disturbance was not abnormally high (Webster et al. 1983), we need to consider possible explanations of these high turnover rates—either additional inputs, unmeasured stored material, or over-estimated export.

Dissolved organic matter (DOM) is an input that we didn't include in our calculations. Biotic uptake of DOM is an important pathway of energy flow in Coweeta streams (Meyer et al. 1988); however, Meyer and Tate (1983) showed that DOM export exceeded DOM input in both Hugh White Creek and Big Hurricane Branch. Cuffney et al. (1990) showed similar instream generation of DOM in other small Coweeta streams. Therefore, loss of DOM by leaching must exceed biotic uptake, DOM flocculation, and abiotic DOM uptake.

The most likely explanation of our high turnover rates is deep storage of BOM. We sampled only to a depth of 10 cm, but BOM is at much greater depths in many places in the stream channel. Channel cutting and headwater erosion is evident in Sawmill Branch. Also, the deeply incised channel on WS13 (Carpenter Branch) may be the result of the long history of disturbance to that watershed. Channel erosion is not yet evident in WS7 (Big Hurricane Branch), but we expect it to occur as debris dams within the channel decay and break up.

It is certainly possible that we have overestimated export for the disturbed streams, though for Sawmill Branch, with the fastest turnover, our export estimate is very conservative. For Big Hurricane Branch and Carpenter Branch, our export simulations match actual measurements for sampled storms (Fig. 7). However, our model may be giving us over-estimates during storms where we had no actual measurements, especially the 21 June storm.

Even if our turnover estimates are substantially higher than rates actually occurring, it is clear from our results that forest disturbance has increased export, accelerated turnover of BOM, and is depleting BOM. Accelerated turnover and depletion of BOM can partially be attributed to faster decomposition of both leaves (Benfield et al., in press) and wood (Golladay and Webster 1988) in disturbed streams. However, these changes are primarily associated with the effect of forest disturbance on woody debris dams in the streams. Studies at various sites throughout the U.S. have shown the connection between forest disturbance and the frequency of debris dams (Swanson and Lienkaemper 1978, Likens and Bilby 1982, Molles 1982, Webster and Golladay 1984, Hedin et al. 1988, Golladay et al. 1989). The general pattern is that, during forest succession, large logs are not added to streams and old debris dams gradually decay and break up. Consequently, the frequency of debris dams declines until trees start dying and forming new dams. The importance of debris dams to maintaining channel stability has been demonstrated in experimental studies (Bilby and Likens 1980, Bilby 1981, 1984, Trotter 1990). Thus once the debris dams break up, stored organic and inorganic particulate material is released and exported, principally during storms (Bilby 1981, 1984).

Hedin et al. (1988) suggested that at Hubbard Brook the period of accelerated particle loss may last about 25 yr. After that time, debris dams begin to reform and act as net sinks for particulate materials. Following forest fire in western U.S., accelerated runoff from denuded slopes may cause a large loss of channel debris, but this material begins to reaccumulate within a very few years (Minshall et al. 1989). At Coweeta the period of accelerated particle transport prior to debris dam reformation may be considerably longer. Death of successional vegetation may contribute a small pulse of wood to streams during the first 25–50 years after disturbance (Likens and Bilby 1982, Triska et al. 1982), but this material is generally small, decays rapidly (Golladay and Webster 1988), and does not form stable debris dams. Therefore, for a period of perhaps 100 yr or more, the time necessary for trees to mature and senesce, the abundance of woody debris dams in disturbed Coweeta streams remains low, streambed stability is low, and relatively rapid downcutting and headwater erosion occur in stream channels.

There are several reasons why this long-term degradation of stream channels has not yet been observed. Up until the last several decades, most logging was selective. The time for uncut trees to mature and die may have been sufficiently short to maintain fairly high debris dam densities in streams. Also, death of chestnut in the 1930s added considerable wood to streams throughout the eastern deciduous forest (Likens and Bilby 1982). In Big Hurricane Branch, many of the existing debris dams are old chestnut logs (Webster, personal observation). Finally, most of the accelerated transport occurs during large storms; samples collected during base flows or even at regular intervals of more than a few hours may fail to show high levels of particle export.

Problems of stream organic matter budgets

Many of the problems and limitations of stream organic matter budgets discussed by Cummins et al. (1983) and Cummins (1988) do not apply to our study. However, some of their concerns and other problems should be considered in interpreting our results.

Long-term responses to major storms and other disturbances necessitate long-term data to calculate and use budgets for comparisons among streams.— We assumed that the five neighboring streams had similar climatic histories. This allowed us to use short-term budgets to evaluate effects of different anthropogenic watershed disturbances imposed on the streams. The problem with this assumption was illustrated by the local storm on 21 June 1984, which we estimated accounted for nearly 50% of the annual transport in Hugh White Creek (WS 14) but less than 2% in Big Hurricane Branch (WS 7). So, despite the proximity of the streams, climatic variables may not have been identical. In order to evaluate effects of anthropogenic disturbance on export with our data we used our model to simulate similar hydrologic conditions for these two streams.

Detrital storage is seldom adequately determined.—To overcome the patchy distribution of benthic detritus, our benthic detritus means were based on 120–240 samples per stream, and we demonstrated several statistically significant differences among streams. However, we probably did not adequately sample deep storage in some areas.

The history of past events has not been adequately considered in many short-term studies.—In contrast to most studies, ours was part of a long-term investigation of forest hydrology and ecology going back to the 1930s with stream studies continuous since the 1960s (Woodall and Wallace 1972). Additionally, using hydrologic data going back to 1938 and transport relationships measured in this study, we were able to examine how our estimates of annual particulate export might have varied if the hydrologic conditions had been different (Fig. 8).

Because of long-term changes caused by disturbances, steady state cannot be assumed.—All budget parameters used in our study were either measured or estimated from measured data. No parameters were estimated by difference, i.e., by assuming steady state. Our results clearly illustrate the lack of steady state in disturbed streams.

Methods of measuring and calculating POM transport are often inadequate.—Daily and even hourly samples may be inadequate for estimates of annual transport (Table 6). To minimize problems associated with other sampling regimes, we collected samples on an event basis, with samples taken as frequently as every 5 min during heavy rains. We developed empirical models to estimate annual transport using relationships determined from experimental studies (Webster et al. 1987). These models worked considerably better than rating curves.

Budgets are dependent on stream size.—We paired our comparisons by watershed size, and in most comparisons we used streambed area to normalize budget parameters.

Viewed with appropriate caution, we believe organic matter budgets are useful for studying stream ecosystems. Budgets have been used for understanding and comparing various processes in streams (e.g., Fisher and Likens 1972, 1973, Fisher 1977, Iversen et al. 1982, Triska et al. 1982, Petersen et al. 1989) and for comparing different streams (e.g., Minshall 1978, Cushing and Wolf 1982, Cummins et al. 1983, Naiman et al. 1986). However, organic matter budgets have not been widely used as a means of evaluating effects of disturbance to streams, though Fisher and Grimm (1985) looked at short-term budgets to evaluate the effects of storms on desert streams, and Cuffney et al. (1990) reported changes in many organic matter processes resulting from insecticide treatment of a small stream. Cummins (1969) pointed out the potential of energy (organic matter) budgets for ecosystem management. In our studies of forest management practices at Coweeta Hydrologic Laboratory, we have used organic matter budgets as a tool for studying the effects of these disturbances on streams. Our results point particularly to the long-term response to disturbance and to the problems of estimating annual particulate export in a system with a highly variable hydrologic regime.

Acknowledgements

This research was supported by grants from the National Science Foundation: BSR 8012093, BSR8316000, and BSR 8514328. We appreciate the help of Bill Perry, Rich Kazmierczak, Lee Reynolds, and Kitti Reynolds in the field and laboratory data collection. Wayne Swank and Bryant Cunningham provided the hydrologic data. Bruce Wallace commented on an early draft of the manuscript. We especially appreciate Rosemary Mackay's willingness to temporarily interrupt her sabbatical leave and resume her role as managing editor for this paper.

Literature Cited

BENFIELD, E. F., J. R. WEBSTER, S. W. GOLLADAY, G. T. PETERS, AND B. M. STOUT. Effects of forest disturbance on leaf breakdown in streams. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie. In press.

BILBY, R. E. 1981. Role of organic debris dams in regulating the export of dissolved and particulate matter from a forested watershed. Ecology 62: 1234–1243.

BILBY, R. E. 1984. Removal of woody debris may affect stream channel stability. Journal of Forestry 82:609–613.

BILBY, R. E., AND G. E. LIKENS. 1980. Importance of organic debris dams in the structure and function of stream ecosystems. Ecology 61:1107–1113.

BORING, L. R., C. D. MONK, AND W. T. SWANK. 1981.

Early regenerating of a clear-cut southern Appalachian forest. Ecology 62:1244–1253.

BRAY, J. R., AND E. GORHAM. 1964. Litter production in forests of the world. Advances in Ecological Research 2:101–157.

COMISKEY, C. E., G. S. HENDERSON, R. H. GARDNER, AND F. W. WOODS. 1977. Patterns of organic matter transport on Walker Branch Watershed. Pages 439–469 *in* D. L. Correll (editor). Watershed research in eastern North America. Smithsonian Institution, Washington, D.C.

CONNERS, M. E., AND R. J. NAIMAN. 1984. Particulate allochthonous inputs: relationships with stream size in an undisturbed watershed. Canadian Journal of Fisheries and Aquatic Sciences 41:1473–1484.

CROMACK, K., AND C. D. MONK. 1975. Litter production, decomposition, and nutrient cycling in a mixed hardwood watershed and a white pine watershed. Pages 609–624 *in* F. G. Howell, J. B. Gentry, and M. H. Smith (editors). Mineral cycling in Southeastern ecosystems. ERDA Symposium Series (CONF 740513), National Technical Information Service, Springfield, Virginia.

CUFFNEY, T. F., AND J. B. WALLACE. 1988. Particulate organic matter export from three headwater streams: discrete versus continuous measurements. Canadian Journal of Fisheries and Aquatic Sciences 45:2010–2016.

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 Biology 23. In press.

CUMMINS, K. W. 1969. Energy budgets. *In* The stream ecosystem. Technical Report number 7. Institute of Water Research, Michigan State University, East Lansing, Michigan.

CUMMINS, K. W. 1988. The study of stream ecosystems: a functional view. Pages 247–262 *in* L. R. Pomeroy and J. J. Alberts (editors). Concepts of ecosystem ecology. Springer-Verlag, New York.

CUMMINS, K. W., J. R. SEDELL, F. J. SWANSON, G. W. MINSHALL, S. G. FISHER, C. E. CUSHING, R. C. PETERSEN, AND R. L. VANNOTE. 1983. Organic matter budgets for stream ecosystems: problems in their evaluation. Pages 299–353 *in* J. R. Barnes and G. W. Minshall (editors). Stream ecology. Plenum Press, New York.

CUSHING, C. E. 1988. Allochthonous detritus input to a small, cold desert spring-stream. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 23: 1107–1113.

CUSHING, C. E., AND E. G. WOLF. 1982. Organic energy budget of Rattlesnake Springs, Washington. American Midland Naturalist 107:404–407.

DAWSON, F. H. 1980. The origin, composition and downstream transport of plant material in a small chalk stream. Freshwater Biology 10:419–435.

DE LA CRUZ, A. A., AND H. A. POST. 1977. Production and transport of organic matter in a woodland stream. Archiv für Hydrobiologie 80:227–238.

ELLIOTT, J. M. 1977. Some methods for the statistical analysis of samples of benthic invertebrates. Freshwater Biological Association, Ambleside, England.

FISHER, S. G. 1971. Annual energy budget for a small forest stream ecosystem, Bear Brook, West Thornton, New Hampshire. Ph.D. Dissertation, Dartmouth College, Hanover, New Hampshire.

FISHER, S. G. 1977. Organic matter processing by a stream-segment ecosystem: Fort River, Massachusetts, U.S.A. Internationale Revue der gesamten Hydrobiologie 62:701–727.

FISHER, S. G., AND N. B. GRIMM. 1985. Hydrologic and material budgets for a small Sonoran Desert watershed during three consecutive cloudburst floods. Journal of Arid Environments 9:105–118.

FISHER, S. G., AND G. E. LIKENS. 1972. Stream ecosystem: organic energy budget. BioScience 22:33–35.

FISHER, S. G., AND G. E. LIKENS. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecological Monographs 43:421–439.

FREDRIKSEN, R. L. 1969. A battery powered proportional stream water sampler. Water Resources Research 5:1410–1413.

FREDRIKSEN, R. L. 1970. Erosion and sedimentation following road construction and timber harvest on unstable soil in three small western Oregon watersheds. USDA Forest Service Research Paper PNW-104, Portland, Oregon.

GOLLADAY, S. W., AND J. R. WEBSTER. 1988. Effects of clearcut logging on wood breakdown in Appalachian mountain streams. American Midland Naturalist 119:143–155.

GOLLADAY, S. W., J. R. WEBSTER, AND E. F. BENFIELD. 1987. Changes in stream morphology and storm transport of organic matter following watershed disturbance. Journal of the North American Benthological Society 6:1–11.

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

GURTZ, M. E., G. R. MARZOLF, K. T. KILLINGBECK, D. L. SMITH, AND J. V. MCARTHUR. 1982. Organic matter loading and processing in a pristine stream draining a tallgrass prairie/riparian forest watershed. Kansas Water Resources Institute Contribution No. 230. Manhattan, Kansas.

GURTZ, M. E., J. R. WEBSTER, AND J. B. WALLACE. 1980. Seston dynamics in southern Appalachian streams: effects of clear-cutting. Canadian Journal of Fisheries and Aquatic Sciences 37:624–631.

HALL, C. A. S. 1972. Migration and metabolism in a temperate stream ecosystem. Ecology 53:585–604.

HEDIN, L. O., M. S. MAYER, AND G. E. LIKENS. 1988. The effect of deforestation on organic debris dams. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 23:1135–1141.

HEWLETT, J. D., AND A. R. HIBBERT. 1967. Factors affecting the response of small watersheds to precipitation in humid areas. Pages 275–290 *in* W. E. Sopper and H. W. Lull (editors). Forest hydrology. Pergamon Press, Oxford.

HORNICK, L. E., J. R. WEBSTER, AND E. F. BENFIELD. 1981. Periphyton production in an Appalachian Mountain trout stream. American Midland Naturalist 106:22–36.

HURLBERT, S. H. 1984. Psuedoreplication and the design of ecological field experiments. Ecological Monographs 54:187–211.

IVERSEN, T. M., J. THORUP, AND J. SKRIVER. 1982. Inputs and transformation of allochthonous particulate organic matter in a headwater stream. Holarctic Ecology 5:10–19.

JOHNSON, P. L., AND W. T. SWANK. 1973. Studies of cation budgets in the southern Appalachians on four experimental watersheds with contrasting vegetation. Ecology 54:70–80.

LEOPOLD, D. J., AND G. R. PARKER. 1985. Vegetation patterns on a southern Appalachian watershed after successive clearcuts. Castanea 50:164–186.

LIKENS, G. E., AND R. E. BILBY. 1982. Development, maintenance and role of organic detris dams in New England streams. Pages 122–128 *in* F. J. Swanson, R. J. Janda, T. Dunne, and D. N. Swanston (editors). Sediment budgets and routing in forested drainage basins. USDA Forest Service Technical Report PNW-141, Portland, Oregon.

MCDOWELL, W. H., AND S. G. FISHER. 1976. Autumnal processing of dissolved organic matter in a small woodland stream ecosystem. Ecology 57:561–569.

MEYER, J. L., AND C. M. TATE. 1983. The effects of watershed disturbance on dissolved organic carbon dynamics of a stream. Ecology 64:33–44.

MEYER, J. L., C. M. TATE, R. T. EDWARDS, AND M. T. CROCKER. 1988. The trophic significance of dissolved organic carbon in streams. Pages 269–278 *in* W. T. Swank and D. A. Crossley (editors). Forest hydrology and ecology at Coweeta. Springer-Verlag, New York.

MINSHALL, G. W. 1978. Autotrophy in stream ecosystems. BioScience 28:767–771.

MINSHALL, G. W., J. T. BROCK, AND J. D. VARLEY. 1989. Wildfires and Yellowstone's stream ecosystems. BioScience 39:707–715.

MOLLES, M. C. 1982. Trichopteran communities of streams associated with aspen and conifer forests: long-term structural change. Ecology 63:1–6.

MULHOLLAND, P. J. 1981. Organic carbon flow in a swamp-stream ecosystem. Ecological Monographs 51:307–322.

NAIMAN, R. J., J. M. MELILLO, AND J. E. HOBBIE. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). Ecology 67:1254–1269.

ODUM, H. T. 1957. Trophic structure and productivity of Silver Springs, Florida. Ecological Monographs 27:55–112.

PETERSEN, R. C., K. W. CUMMINS, AND G. M. WARD. 1989. Microbial and animal processing of detritus in a woodland stream. Ecological Monographs 59:21–39.

POST, H. A., AND A. A. DE LA CRUZ. 1977. Litterfall, litter decomposition, and flux of particulate organic material in a coastal plain stream. Hydrobiologia 55:201–207.

RISLEY, L. S. 1987. Acceleration of seasonal leaffall by herbivores in the southern Appalachians. Ph.D. Dissertation, University of Georgia, Athens, Georgia.

SALO, E. O., AND T. W. CUNDY (editors). 1987. Streamside management: forestry and fisheries interactions. College of Forestry Resources, University of Washington, Seattle, Washington.

STRAYER, D., AND G. E. LIKENS. 1986. An energy budget for the zoobenthos of Mirror Lake, New Hampshire. Ecology 67:303–313.

SWANK, W. T., AND D. A. CROSSLEY (editors). 1988. Forest hydrology and ecology at Coweeta. Springer-Verlag, New York.

SWANK, W. T., AND J. E. DOUGLASS. 1977. Nutrient budgets for undisturbed and manipulated hardwood forest ecosystems in the mountains of North Carolina. Pages 343–362 *in* D. L. Correll (editor). Watershed research in eastern North America. Smithsonian Institution, Washington, D.C.

SWANSON, F. J., AND G. W. LIENKAEMPER. 1978. Physical consequences of large organic debris in Pacific Northwest streams. USDA Forest Service Technical Report PNW-69, Portland, Oregon.

SWIFT, L. W., G. B. CUNNINGHAM, AND J. E. DOUGLASS. 1988. Climatology and hydrology. Pages 35–55 *in* W. T. Swank and D. A. Crossley (editors). Forest ecology and hydrology at Coweeta. Springer-Verlag, New York.

TEAL, J. M. 1957. Community metabolosm in a temperate cold spring. Ecological Monographs 27: 283–302.

TILLY, L. J. 1968. The structure and dynamics of Cone Spring. Ecological Monographs 38:169–197.

TRISKA, F. J., J. R. SEDELL, AND S. V. GREGORY. 1982. Coniferous forest streams. Pages 292–332 *in* R. L. Edmonds (editor). Analysis of coniferous forest ecosystems in the western United States. Hutchinson Ross, Stroudsburg, Pennsylvania.

TROTTER, E. H. 1990. The impact of forest succession on stream ecosystems through the addition of wood. Journal of the North American Benthological Society 9:141–156.

WALLACE, J. B. 1988. Aquatic invertebrate research. Pages 257–268 *in* W. T. Swank and D. A. Crossley (editors). Forest hydrology and ecology at Coweeta. Springer-Verlag, New York.

WALLACE, J. B., D. H. ROSS, AND J. L. MEYER. 1982. Seston and dissolved organic carbon dynamics in a southern Appalachian stream. Ecology 63:824–858.

WEBSTER. J. R. 1983. The role of benthic macroinvertebrates in detritus dynamics of streams: a computer simulation. Ecological Monographs 53: 383–404.

WEBSTER, J. R., E. F. BENFIELD, S. W. GOLLADAY, B. H. HILL, L. E. HORNICK, R. F. KAZMIERCZAK, AND W. B. PERRY. 1987. Experimental studies of physical factors affecting seston transport in streams. Limnology and Oceanography 32:848–863.

WEBSTER, J. R., E. F. BENFIELD, S. W. GOLLADAY, R. F. KAZMIERCZAK, W. B. PERRY, AND G. T. PETERS. 1988. Effects of watershed disturbance on stream seston characteristics. Pages 279–294 *in* W. T. Swank and D. A. Crossley (editors). Forest ecology and hydrology at Coweeta. Springer-Verlag, New York.

WEBSTER, J. R., AND S. W. GOLLADAY. 1984. Seston transport in streams at Coweeta Hydrologic Laboratory, North Carolina, U.S.A. Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie 22:1911–1919.

WEBSTER, J. R., M. E. GURTZ, J. J. HAINS, J. L. MEYER, W. T. SWANK, J. B. WAIDE, AND J. B. WALLACE. 1983. Stability of stream ecosystems. Pages 355–395 *in* J. R. Barnes and G. W. Minshall (editors). Stream ecology. Plenum Press, New York.

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

WHITE, D. L. 1986. Litter production, decomposition, and nitrogen dynamics in black locust and pine-hardwood stands of the southern Appalachians. M.S. thesis, University of Georgia, Athens, Georgia.

WINTERBOURN, M. J. 1976. Fluxes of litter falling into a small beech forest stream. New Zealand Journal of Marine and Freshwater Research 10:399–416.

WOODALL, W. R., AND J. B. WALLACE. 1972. The benthic fauna of four small southern Appalachian streams. American Midland Naturalist 88:393–407.

Received: 2 November 1989
Accepted: 26 February 1990

APPENDIX 1. Regression equations used in POM transport model. For rising flows the equation was $C = aDQ5 + b$; where C was POM concentration (mg AFDW/L), DQ5 was the rate of increase in discharge during the 5-min interval preceding the sample (L sec^{-1} min^{-1}), a = slope, and b = intercept. For falling flows we used the equation $C = C_p e^{-kt}$; where C_p was peak POM concentration for the storm, t was time (min) since the peak concentration occurred, k = the rate of exponential decline in POM concentration.

Dates of Data Collection	Rising Flow				Falling Flow		
	Intercept	Slope	p	n	Exponent	p	n
Grady Branch							
15–16 Jun 84	—[a]	—	—	—	0.0154	0.0004	5
20 Jun 84	11.6	233.9	0.008	7	0.0102	0.0001	14
28 Aug 84	—[a]	—	—	—	0.0258	0.0001	9
10–11 Nov 84	12.1	254.3	0.11	11	0.0125	0.001	7
4–6 Dec 84	2.1	158.9	0.0003	6	0.0063	0.0001	7
11–13 Feb 85	3.1	42.6	0.02	7	0.0072	0.0006	7
21–23 Mar 85	3.5	102.0	0.07	5	0.0062	0.002	6
1–2 May 85	—[a]	—	—	—	0.0023	0.03	4
7–10 May 85	3.7	181.1	0.05	6	0.0039	0.002	3
Hugh White Creek							
15–16 Jun 84	—[a]	—	—	—	—[a]	—	—
20 Jun 84	6.9	62.9	0.006	4	0.0119	0.0001	14
28 Aug 84	8.3	68.4	0.01	3	0.0214	0.0001	7
10–11 Nov 84	21.1	73.2	0.001	15	0.0086	0.0002	6
4–6 Dec 84	1.9	25.7	0.02	11	0.0037	0.003	6
11–13 Feb 85	2.5	13.9	0.01	9	0.0055	0.0001	9
21–23 Mar 85	0.9	61.7	0.001	8	0.0065	0.002	4
1–2 May 85	2.7	130.4	0.08	5	0.0029	0.10	3
7–10 May 85	3.0	64.4	0.0004	17	0.0030	0.0004	4
Big Hurricane Branch							
15–16 Jun 84	9.7	110.6	0.11	3	0.0052	0.007	4
20 Jun 84	1.7	120.7	0.003	7	0.0236	0.0001	10
28 Aug 84	—[a]	—	—	—	0.0191	0.0001	6
10–11 Nov 84	14.4	140.4	0.01	10	0.0127	0.0001	8
4–6 Dec 84	3.0	124.9	0.004	13	0.0064	0.0003	6
11–13 Feb 85	8.3	42.6	0.005	9	0.0038	0.0002	9
21–23 Mar 85	—[b]	—	0.33	11	—[b]	0.18	3
1–2 May 85	—[a]	—	—	—	—[a]	—	—
7–10 May 85	6.0	93.0	0.02	5	0.0023	0.04	3
Carpenter Branch							
15–16 Jun 84	12.0	751.3	0.10	5	0.0159	0.0002	4
20 Jun 84	5.4	593.9	0.0001	7	0.0204	0.0001	13
28 Aug 84	5.8	433.6	0.13	4	0.0168	0.0005	7
10–11 Nov 84	9.5	312.8	0.0004	9	0.0052	0.0001	11
4–6 Dec 84	1.3	165.5	0.0008	9	0.0031	0.0001	10
11–13 Feb 85	4.5	101.0	0.0008	7	0.0027	0.0001	12
21–23 Mar 85	4.0	376.6	0.03	6	0.0082	0.002	5
1–2 May 85	—[a]	—	—	—	—[a]	—	—
7–10 May 85	6.1	328.6	0.008	7	0.0037	0.02	6

[a] Insufficient data for analysis.
[b] Highly insignificant relationship; not used in model.

Webster_1991_Effects