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Source: *Journal of the North American Benthological Society*, Vol. 12, No. 2 (Jun., 1993), pp. 112-125
Published by: The University of Chicago Press on behalf of the Society for Freshwater Science
Stable URL: http://www.jstor.org/stable/1467341
Accessed: 01-07-2015 17:53 UTC

J. N. Am. Benthol. Soc., 1993, 12(2):112-125

Dynamics of inorganic particles in headwater streams: linkages with invertebrates

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Abstract. Export of particulate inorganic matter (PIM) from three headwater streams was studied from 1985 to 1991 at Coweeta Hydrologic Laboratory. The study encompassed years of extreme high and low precipitation. During three years of the study, the stream draining Catchment 54 (C 54) received seasonal treatments of an insecticide. This treatment greatly reduced abundance biomass and secondary production of most invertebrate taxa. Streams draining Catchments 53 and 55 (C 53 and C 55) served as reference streams. During treatment, concentration of PIM in C 54 decreased significantly from pretreatment levels for both instantaneous (grab) and continuous samples, while those of reference streams either increased or did not exhibit significant change. Maximum PIM concentrations, measured during rising hydrographs of storms, were over 2× greater in the reference streams than in C 54. During treatment of C 54, export of PIM per unit maximum discharge (L/s) during sampling intervals (~2 wks) decreased significantly compared with that of reference streams. Annual PIM export in reference streams displayed a strong ($p < 0.002$) exponential relationship with annual discharge, whereas that of the treated stream did not ($p > 0.05$). High discharges during post-treatment years (1989-1991) resulted in increased concentration and export of PIM in all streams. However, PIM concentrations in C 54 remained lower than those of the two reference streams.

Invertebrate manipulation apparently reduced PIM export from C 54 by at least two mechanisms. First, the rate of particle generation by feeding activities was reduced. Second, invertebrate manipulation reduced rates of leaf litter processing, which resulted in increased storage of leaf litter and enhanced retention of particles. Comparisons of predicted versus measured export suggest that invertebrate manipulation in C 54 reduced PIM export by ~76%, or 550 (relative to C 53R) to >1000 kg (relative to C 55) over the 6-yr treatment and post-treatment period. These comparisons exceed those made previously for the impact of invertebrate manipulation on FPOM export and provide another example of the link between animal communities and ecosystem processes. This study also provides evidence that stored leaf material, like that of woody debris, augments retention of inorganic particles in small headwater streams.

Key words: seston, inorganic particles, export, flow, discharge, storms, streams, long-term studies.

In the last decade, numerous studies have documented impacts of animals on stream ecosystem processes. Examples include all trophic levels. Predators can influence both algal standing crops (Power et al. 1985, Power 1990) and rates of leaf litter processing (Oberndorfer et al. 1984) by reducing abundances of herbivores and detritivores. Invertebrate grazers can affect periphyton biomass (Mulholland et al. 1983, Lamberti et al. 1989, Hill et al., 1992). Shredding detritivores increase the rate at which coarse particulate organic matter (CPOM) is converted to fine particulate organic matter (FPOM) in laboratory (Petersen and Cummins 1974) and natural streams (Wallace et al. 1982, Cuffney et al. 1990). Grazers enhance transport of FPOM to downstream reaches (Mulholland et al. 1983, Lamberti et al. 1989), and so do detritivores (Wallace et al. 1982, Cuffney et al. 1990, Wallace et al. 1991b). Detritivores have been shown to affect release rates of nutrients (Grimm 1988) and dissolved organic carbon (DOC) (Meyer and O'Hop 1983). These studies have focused on the influence of consumers on biotic processes. With the exception of beaver, whose dam building activities increase retention of organic and in-

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organic particles in streams (e.g. Naiman et al. 1988), few studies have considered the impact of consumers on the dynamics of inorganic particles in streams.

It has been suggested that woody debris may play a major role in retention within headwater streams (Swanson et al. 1982, Molles 1982, Triska and Cromack 1982). Wood removal can influence ecosystem structure and retention (Bilby and Likens 1980, Smock et al. 1989, Trotter 1990). Non-woody organic debris, including leaf litter accumulations (Bormann et al. 1969, Golladay et al. 1987, Webster et al. 1987a), may also contribute to particle retention. However, little study has been devoted to the role of non-woody debris, other than to its importance as the major energy base (Cummins 1974, Anderson and Sedell 1979).

At Coweeta Hydrologic Laboratory, an experimental manipulation of invertebrate populations (insecticide treatment) in one of three streams altered invertebrate community structure (Lugthart and Wallace 1992) and reduced rates of leaf litter processing, without reducing microbial respiration or abundances (Cuffney et al. 1990, Suberkropp and Wallace 1992). By the end of three years of treatment, standing crop of leaf litter in the channel of the treated stream was $>2\times$ greater than that of untreated streams (Wallace et al. 1991a). Treatment also reduced FPOM concentrations and export (Cuffney et al. 1990), lowered FPOM export per unit maximum discharge during storms (Cuffney and Wallace 1989) and altered seasonal responses to storms (Wallace et al. 1991b). Treatment did not alter inputs or physically affect the stream channel; however, the manipulation may have indirectly enhanced physical retention through increased storage of leaf litter.

The objectives of this paper are: to report on the dynamics of particulate inorganic matter (PIM) in headwater streams, as sampled with continuous and instantaneous methods, to examine the influence of storms and drought on export, and to assess the influence of invertebrate manipulation on PIM concentrations and export. Linkages between leaf litter accumulations and inorganic particle export may be much stronger than previously expected. Many studies have addressed the impact of inorganic sediments on invertebrates; however, to our knowledge the seemingly improbable question, "What is the impact of invertebrates on inorganic sediment dynamics?" has not been asked or studied.

Study Sites

The three study streams are all 1st-order and drain Catchments (C) 53, 54, and 55 at the U.S. Forest Service Coweeta Hydrologic Laboratory (CHL), Macon County, North Carolina, USA. The catchments are forested, and dominant trees include: tulip poplar (*Liriodendron tulipifera*, L.), white oak (*Quercus alba*, L.), red oak (*Quercus rubra*, L.), red maple (*Acer rubrum*, L.), and dogwood (*Cornus florida*, L.). Rhododendron (*Rhododendron maxima*, L.) forms a dense riparian understory, shading the streams throughout the year. Catchment size, elevation, gradient, discharge, and thermal regime are presented in Table 1. Concentrations of most ions are low (<1 mg/L) and pH ranges from 6.6 to 6.8, similar to other streams in the Coweeta Basin (Swank and Waide 1987).

The catchments studied have been relatively undisturbed since the mid 1930s. Streams draining C 53 and C 54 were used in an earlier (1980–1982) study investigating the influence of invertebrate manipulation on leaf litter processing and FPOM concentrations (Wallace et al. 1982, Cuffney et al. 1984, Wallace et al. 1986). In 1980, C 53 was treated with methoxychlor and C 54 served as a reference. During the current study (1985–1991), C 54 was treated seasonally with an insecticide from December 1985 to October 1988. Treatment of C 54 followed a year (1985) of pretreatment studies on C 53, C 54, and C 55. In 1985, C 53 was in its fifth year of recovery from an insecticide treatment. C 55 has never received any experimental manipulation. There are no fish in these streams and salamanders are the only vertebrates present.

The 7-yr study encompassed extreme wet and dry years. During 1986, annual precipitation at Coweeta was only 124 cm (68.8% of the long-term average of 180.1 cm), the lowest measured for the 57-yr period of record. Precipitation in 1988 was 126.7 cm (70.3% of the long-term average), the 3rd-driest year of record. In contrast, precipitation during 1989 was 234.1 cm which was 30% above the long-term average and the wettest year of record. This was followed by another wet year (1990) with 209.4 cm of precipitation (16.3% above the long-term aver-

TABLE 1. Physical characteristics of reference (R) and treated streams (T). Discharge and temperature data are from mid-December 1984 to mid-December 1991.

	C 53(R)	C 54(T)	C 55(R)
Catchment			
Area (ha)	5.2	5.5	7.5
Elevation (m asl at flume)	820	841	810
Channel			
Gradient (cm/m)	27	33	20
Length (m)	145	282	170
Bankful area (m^2)	327	443	373
Discharge (L/s)			
Average (1985–1991)	0.92	1.35	1.53
1985	0.59	0.92	0.95
1986	0.33	0.56	0.50
1987	0.74	1.28	1.43
1988	0.42	0.73	0.69
1989	1.45	1.97	2.34
1990	1.56	1.99	2.48
1991	1.36	1.98	2.33
Minimum daily (7-yr)	0.14	0.17	0.05
Maximum instantaneous (7-yr)	30.3	35.5	46.9
Temperature			
Maximum (7-yr)	19.5	19.5	19.5
Minimum (7-yr)	0.8	1.1	1.6
Annual degree-days (7-yr avg.)	4534	4443	4517

age). As a result, annual discharge over the 7-yr study was extremely variable.

Methods

Discharge

Stream flow was gaged continuously during non-freezing months (April through November) using FW-1 stage recorders attached to a 30.5 cm H-flume (Agricultural Research Service 1962). Discharge and export relationships were derived for each stream from field measurements of stage and discharge. Discharge relationships between a continuously gaged stream (C 2) and the study streams during the gaged months, as well as instantaneous readings during ungaged winter months, were used to estimate discharge for the study streams during freezing months (December through March).

Export estimates

Concentration of particles suspended in stream water was measured biweekly from December 1984 to June 1991 using instantaneous (grab) samples. On each sampling date, 4–9 replicate samples, each consisting of 2–8 L of stream water, were filtered through pre-ashed and preweighed glass fiber filters (Cuffney and Wallace 1988). In the laboratory, these filters were dried, weighed, ashed and reweighed to obtain PIM and ash-free dry mass (AFDM). Concentration of particles in continuous samples were obtained by dividing the total amount of PIM exported (coarse particle collectors plus Coshocton samplers for fine particles, see below) by the total discharge during a sampling interval.

Particulate export, including materials moving on the streambed, was measured continuously using separate coarse and fine collectors (Cuffney and Wallace 1988). A rectangular cage (~3 m × 2 m × 1 m) lined with galvanized hardware cloth (mesh size = 4 × 4 mm) was used for coarse particle collection. The upstream end of each coarse particle trap was bolted to the base of a rock outcrop. Traps sampled the entire stream flow during all discharges. On most dates, all material in the coarse trap was returned to the laboratory for processing; however, on six dates following large storms it was necessary to subsample the contents of the coarse traps. Total wet weight was measured in the field and a representative wet-weighed subsample was returned to the laboratory for processing. The entire subsample was oven dried (3 d at 60°C), weighed, ashed (1 d at 500°C), and reweighed to obtain AFDM and ash (PIM).

Fine particulate export was measured using an H-flume connected to a Coshocton proportional subsampler (Parsons 1954) about 5 m downstream from the coarse trap. The subsampler delivered 0.6% of stream flow to a series of three 100 L settling barrels which removed a constant percentage (~85%) of fine export (see Cuffney and Wallace (1988). Concentrations of particles in each barrel were measured by stirring and filtering three replicate aliquots through pre-ashed and pre-weighed glass fiber filters. Filters were processed to obtain AFDM and PIM concentrations following the drying, weighing, ashing, and reweighing laboratory sequence described by Cuffney and Wallace (1988). Barrels were sampled and cleaned biweekly until June 1991 and every 3-wks from June 1991 to December 1991. In this study, the 0.45μm–4 mm size range used for fine particles was necessary to accommodate the 4-mm opening slot on the Coshocton sampler. PIM mass from the coarse traps was added to barrel export to estimate total PIM export for each interval.

For 12 storms occurring during 1986 to 1989, PIM concentrations were sampled at the flume during rising and falling hydrographs of storms. Prestorm (background) samples of 0.8–4 L were collected from each stream. During storms, 0.5 L samples were collected by an ISCO model 2100 automated water sampler with intakes positioned at the flume of each stream. Wetness (rainfall) sensors connected to each ISCO initiated sampling. Stream water was sampled continuously over rising and falling storm hydrographs (see Golladay et al. 1987). Samples were filtered through pre-ashed and pre-weighed Gelman A/E glass fiber filters and processed as described for grab samples.

Methoxychlor treatments

C 54 was treated with the insecticide methoxychlor (1,1,1-tri-chloro-2,2-bis[p-methoxyphenyl]ethane; CAS No. 72-43-5) seasonally during three years of this study (December 1985–October 1988 = 12 treatments). Additional details, including concentrations of methoxychlor in stream water and residues in stream sediments, were given by Wallace et al. (1989). The effects of treatment on benthic animal abundances, biomass and production were given by Lugthart and Wallace (1992).

Discharge versus export relationships

Relationships between maximum discharge and PIM export in sampling intervals were compared to assess the effects of treatment and discharge on export of inorganic particles. Regressions were forced through the origin to meet the a priori requirement that export ceased at zero discharge. Measured export over the study period was compared with that predicted by the pretreatment regressions for each stream. Although the Coshocton samplers are designed to sample proportional to discharge, measurement of PIM export does not involve any measure of discharge (e.g., concentration × discharge = export) as export sampling devices and discharge (stage recorder) are from different devices.

Results

PIM Concentrations

In reference streams, concentrations of PIM were lowest during 1985. PIM concentrations in continuous (barrel + coarse trap) samplers during 1985 ranged from 1.7 to 3.8× greater than values obtained with instantaneous (grab) samples (Fig. 1A) and differences between instantaneous and continuous samplers were increasingly evident during the drought years of 1986 and 1988. Furthermore, as Coshoctons sampled all storms (including bedload transport), percent ash of total particulate export (PIM + POM) was greater in continuous than instantaneous samplers, indicating that during storm flows, PIM increased relative to POM (Fig. 1B).

During treatment of C 54 (1986–1988), PIM concentrations in both instantaneous and continuous samples decreased significantly below C 54 pretreatment values. In contrast, among reference streams, only C 55 instantaneous samples had PIM concentrations that were lower than pretreatment (1985) values (Fig. 1A). PIM concentrations in continuous samples from C

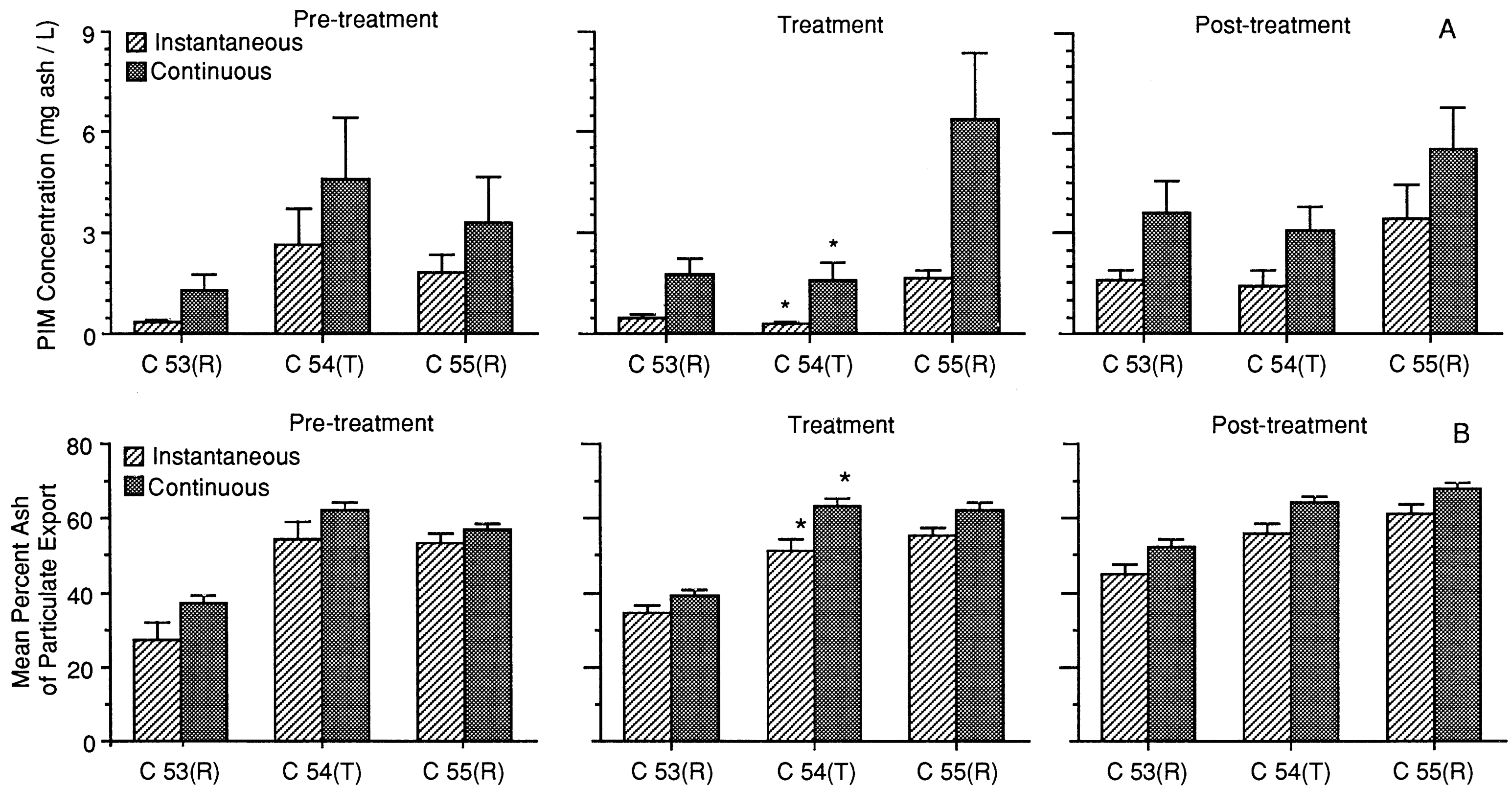

FIG. 1. A (top)—mean PIM concentrations +95% CL of instantaneous and continuous (barrel plus coarse trap) sampling devices in reference (R) and treated (T) streams for pretreatment, treatment, and post-treatment of C 54. B (bottom)—mean percent ash + 95% CL of instantaneous and continuous seston. Asterisks note treatment years of C 54. Pretreatment (autumn 1984 to autumn 1985). Treatment (December 1985 to October 1988). Post-treatment (winter 1988 to autumn 1989).

TABLE 2. Maximum PIM (ash) concentrations (mg/L) from reference (R) and treated (T) streams, measured with automated ISCO samples, and maximum discharge (L/s) during each of twelve storms. The 1986–1988 samples represent the treatment period of C 54.

	Maximum ash concentration			Maximum discharge		
Date	C 53(R)	C 54(T)	C 55(R)	C 53(R)	C 54(T)	C 55(R)
11 Sep 1986	96.5	22.7	488.9	0.30	0.70	0.92
25 Jun 1987	145.0	59.2	78.0	2.18	2.99	5.95
3 Mar 1988	17.0	3.3	33.9	0.73	1.07	1.33
30 Jun 1988	17.8	17.8	63.1	2.94	3.91	4.75
13 Jul 1988	170.8	43.5	634.1	1.28	1.39	0.59
21 Jul 1988	46.0	28.5	175.5	0.62	0.94	0.85
3 Aug 1988	355.1	148.9	314.1	2.94	2.19	1.09
6 Jan 1989	21.6	13.6	29.3	0.81	1.16	1.49
18 Mar 1989	11.3	6.6	16.5	1.03	1.43	1.96
12 Jun 1989	35.9	19.9	65.4	2.40	2.75	2.56
1 Aug 1989	79.3	23.1	30.3	2.93	3.52	4.02
15 Aug 1989	12.5	25.2	43.8	5.05	5.28	10.02
Mean (1986–1988)	121.2	46.3	255.4	1.57	1.88	2.21
Mean (1989)	32.1	17.9	37.1	2.44	2.83	4.01

55 did not increase with greater discharge during the 3-yr post-treatment period, and there were no significant differences between treatment and post-treatment concentrations in this stream.

PIM concentrations measured with automated samplers during rising and falling hydrographs of twelve storms from 1986 to 1989 were much greater than concentrations measured with continuous or instantaneous samples (cf. Table 2 and Fig. 1B). Even small storms during the dry years of 1986 to 1988 produced large increases in PIM concentrations during rising hydrographs. During treatment and first-year recovery of C 54, maximum PIM concentrations in the reference streams during rising hydrographs were higher than C 54 (Table 2), as reported previously for FPOM (Wallace et al. 1991b). During treatment, maximum concentrations in the reference streams averaged 2.6× (C 53) to 5.5× (C 55) higher than C 54. During first-year recovery, maximum concentrations averaged 1.8× (C 53) to 2.1× (C 55) greater than C 54 (Table 2).

Discharge

Although 1989 had the highest precipitation of the 57-yr record at Coweeta, it was preceded by very dry years which depleted groundwater reserves (Fig. 2 and Table 1). Long-term records from C 2 show that total discharge for 1989 ranked only 15th. Total precipitation during 1989 exceeded that of 1990 by 25.5 cm, but discharge during 1990 was the fourth highest on record for C 2. Average discharge rankings for other years were as follows: 1991 = 20th; 1987 = 46th; 1985 = 50th; 1988 = 53rd. The exceptionally dry year (1986) ranked 57th, the lowest on record.

TABLE 3. Number of days during each year with maximum discharges exceeding 2 SD above the mean and minimum discharges more than 1 SD below the mean. Mean and SD of daily discharges are based on daily maximum and minimum flows from late summer 1984 to early winter 1992. R = reference streams, T = treatment stream which received seasonal methoxychlor treatments from December 1985 to October 1988.

	Days with discharge >2 SD			Days with discharge <1 SD		
Year	C 53 (R)	C 54 (T)	C 55 (R)	C 53 (R)	C 54 (T)	C 55 (R)
1985	16	12	15	2	12	21
1986	12	10	10	99	115	111
1987	20	16	19	1	30	20
1988	12	6	12	13	33	35
1989	155	116	136	15	33	32
1990	70	65	67	0	0	0
1991	50	59	52	0	0	0

Total discharge was greatest for all streams during 1990, but 1989 had a greater number of high flow events. Discharge was >2 SD above the 7-yr mean on 116 (C 54) to 155 days (C 53) (Table 3). In contrast, during the extreme drought of 1986 there were ~100 days where discharge fell below 1 SD of the mean, and discharge exceeded 2 SD of the mean on only 10 to 12 days in all streams (Table 3). Minimum discharge never dropped to 2 SD below the mean (= 0 flow) during the 7-yr period. These streams are at or near base flow for most of the year. Discharge increases rapidly during individual storms, but quickly returns to near-base flow conditions (Fig. 3 and Table 3).

Annual inorganic particulate export

Most PIM was exported as fine particles; thus, export collected in Coshocton (barrel) samplers greatly exceeded that of coarse cages. During the 7-yr period, coarse traps accounted for only 2.9% (C 54), 6.3% (C 53), and 9.0% (C 55) of total PIM export. However, during collection intervals with large storms (discharges > 10 L/s), the percentage of total PIM export retained in coarse cages increased (C 54 = 8.2%, C 53 = 13.5%, and C 55 = 18.2%).

Annual PIM export decreased in C 54 during treatment (Table 4). Although discharge in C 54 exceeded that of the reference streams during two of the three treatment years, PIM export in C 54 decreased relative to C 53 and C 55 during treatment. Annual PIM export for the 7-yr period was strongly related (exponential regression) to annual discharge in C 53 (r^2 = 0.84, $p < 0.002$) and C 55 ($r^2 = 0.88$, $p < 0.001$)

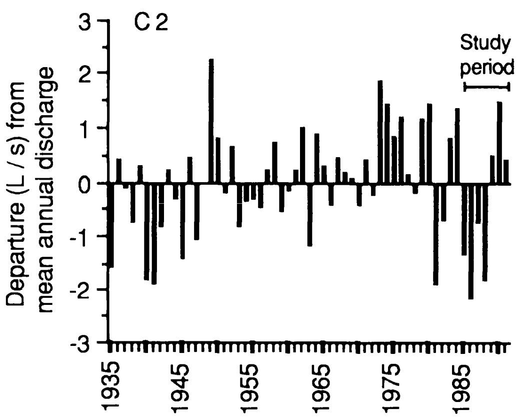

FIG. 2. Annual average departure (L/s) from the long-term mean discharge (L/s = 3.07) for C 2 at Coweeta. Note the years of study included the record low and 4th-highest discharge in the 57-yr record. (Data from U.S. Forest Service, Coweeta Hydrologic Laboratory).

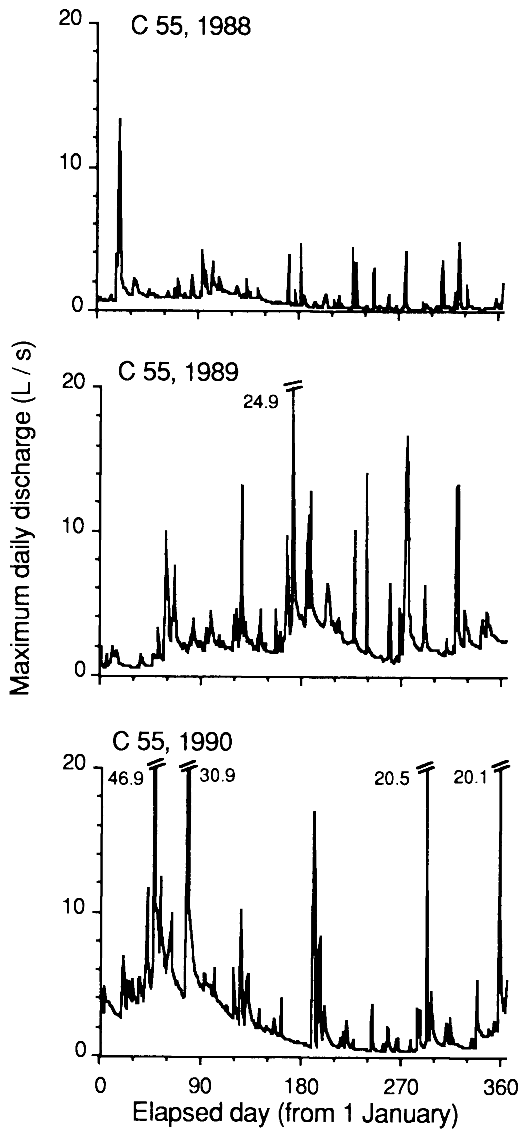

FIG. 3. Maximum daily discharge in C 55, a reference stream, at Coweeta during 1988, 1989, and 1990. Note that large storms were generally absent during 1988, the second-driest year of record, that 1989 had the highest precipitation of record (including the wettest summer), and that discharge during 1990 was the fourth highest on record.

TABLE 4. Annual PIM (ash) export from continuous samplers (barrels + coarse cages) and PIM export per ha of catchment area for reference (R) and treated (T) streams. Asterisks denote C 54 during treatment years.

	Annual PIM export (kg)			Annual PIM export (kg/ha)		
Year	C 53 (R)	C 54 (T)	C 55 (R)	C 53 (R)	C 54 (T)	C 55 (R)
1985	22.4	118.0	86.9	4.3	21.5	11.6
1986	33.6	65.5*	118.5	6.5	11.9*	15.8
1987	24.9	28.5*	150.5	4.8	5.2*	20.1
1988	24.7	29.0*	110.8	4.7	5.3*	14.8
1989	101.3	237.3	374.0	19.5	43.1	49.9
1990	228.8	264.0	539.7	44.0	48.0	72.0
1991	94.1	110.3	304.7	18.1	20.1	40.6

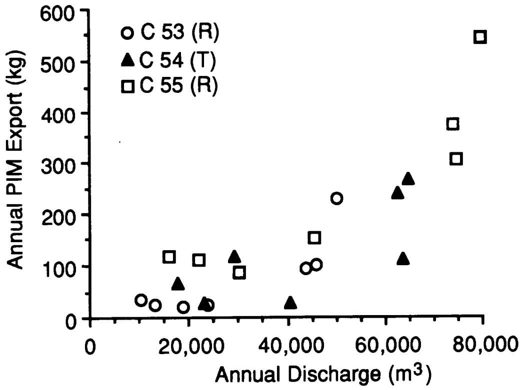

FIG. 4. Annual export of particulate inorganic material (continuous samplers) versus annual discharge for each stream. C 53 and C 54 are best fit by the following exponential regressions: C 53, $y = 11.95 \times 10^{0.000022x}$, $r^2 = 0.84$; C 55, $y = 59.6 \times 10^{0.000011x}$, $r^2 = 0.88$; whereas that of the treated stream (including treatment and non-treatment years of C 54) is best fit by the following simple regression: $y = -28.9 + 0.0035x$, $r^2 = 0.55$. During treatment years of C 54 (three lowest ▲) there was no positive relationship between discharge and PIM export. R = reference and T = treated streams.

(Fig. 4). This exponential relationship was not as strong in C 54 ($r^2 = 0.47$, $0.05 < p < 0.10$). A simple linear model ($r^2 = 0.55$, $p < 0.05$) better described discharge–PIM export relationships in C 54 during this study (Fig. 4). During treatment, annual PIM export in C 54 failed to show any positive relationship with discharge.

Maximum discharge–PIM export relationships

PIM export showed a positive relationship with maximum discharge during collection intervals in the pretreatment, treatment, and post-treatment periods in all streams (r^2 range = 0.57 to 0.83, $p < 0.001$, for all streams). Prior to treatment, PIM export per unit maximum discharge (L/s) in collection intervals was significantly greater in C 54 than C 55, which was significantly greater than that of C 53. During treatment, PIM export–maximum discharge slopes for both reference streams were significantly greater than their 1985 values, whereas the slope of C 54 decreased significantly (95% CI slope values for C 55 > C 54 = C 53, Fig. 5). During high flows of the post-treatment period, PIM export–maximum discharge slopes increased markedly in each stream and were significantly different for all streams (C 55 > C 54 > C 53).

In reference streams, percent PIM (% ash) of total exported particles showed much greater increases in collection intervals with high maximum discharges (>10 L/s) than during periods without large storms, e.g., maximum discharge <5 L/s (Fig. 6). Although the % PIM in C 54 increased slightly with maximum discharge during collection intervals, the change was minor compared with that of reference streams and there was little change in percent PIM in C 54 over a wide range of discharges.

Ten storms were responsible for 38% of the PIM export from C 55 and ~41% from C 54 and C 53 over the 7-yr period. Fifty (C 55) to 56% (C 54) of total inorganic export occurred during periods that contained ~25% of the total discharge. In contrast, intervals containing 60% of the total discharge, but few large storms, accounted for 35% of total PIM export in C 53 and C 55, and only 28% in C 54. These data, which emphasize the importance of storms in PIM export, are conservative, as storms occurred over short periods within the 2-wk sampling intervals.

Measured versus predicted inorganic export

PIM export–maximum discharge regressions from the pretreatment year (1985) for each stream were applied to maximum discharge in each collection interval from 1986 to 1991. The value for predicted export based on first-year (1985) regressions was compared with that ac-

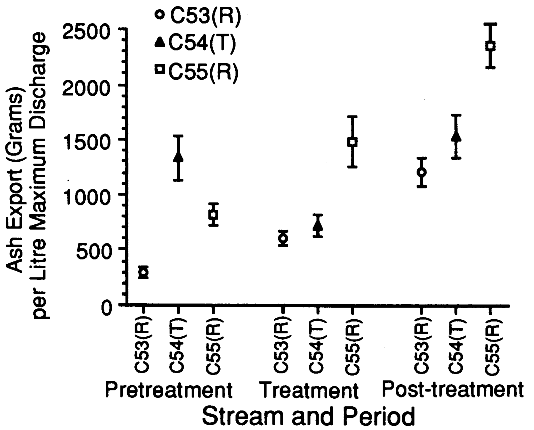

FIG. 5. PIM export from continuous samples (barrel plus coarse trap) as a function of maximum discharge. Data are based on linear regressions through the origin with x = maximum discharge (L/s) and y = g PIM (ash) during each collection interval during pretreatment, treatment, and post-treatment periods of C 54. The 95% CI is for the slope value for each stream and period.

tually measured for each stream. In reference streams, annual departures (measured minus predicted PIM export) were greatest during the last three years of study (1989–1991), and measured PIM export always exceeded that predicted by the first-year regressions (Fig. 7A). In contrast, measured export of PIM in C 54 was below that predicted by the first-year regressions in each of the treatment years and one of the three post-treatment years. Viewed as cumulative departure during the study, measured export of PIM from C 53 and C 55 exceeded the predicted by 331 kg (C 53) and 862 kg (C 55) by the end of 1991. In contrast, C 54 remained 219 kg below that predicted (1072 kg) by pretreatment regressions (Fig. 7B). The average cumulative departure of PIM export between reference and treatment streams was ~815 kg (C 53 and C 54 = 550 kg and C 55 and C 54 = 1081 kg, Table 5). Based on the assumption that C 54 in the absence of treatment would have exhibited a response similar to those of reference streams, expected PIM export in C 54 was reduced by 76% (815.5/1072) during the 3-yr treatment and 3-yr post-treatment period.

Discussion

Our data show large differences in PIM concentrations between instantaneous and continuous sampling devices, and these differences were increasingly evident during the drought years of 1986 and 1988 (=treatment period in Fig. 1A). The greater differences in drought years suggest that most PIM export occurred during storms, especially in drought years, as shown earlier for particulate organic matter (POM) (Cuffney and Wallace 1989, Wallace et al. 1991b). These data demonstrate the importance of storms, rarely sampled with instantaneous methods, in inorganic export.

Manipulation of invertebrate populations probably influenced PIM export through at least two mechanisms. First, reduced abundance and biomass of invertebrates, particularly larger insect taxa (Lugthart and Wallace 1992), reduced the rate of generation of both organic and inorganic particles through feeding activities. Previous studies on these streams have shown that biological activity is responsible for a large portion of the fine particles generated within these streams (Wallace et al. 1982, Cuffney and Wallace 1989, Cuffney et al. 1990, Wallace et al. 1991b). These particles are mixtures of organic and inorganic material (Webster et al. 1987b). Reduced rates of particle generation may account for reduced concentrations of PIM during base flows in C 54 during treatment (instantaneous samples, Fig. 1B).

In addition, indirect linkages between invertebrates, leaf litter storage, and retention were important mechanisms for reduction of PIM export. Biomass and production of shredder taxa

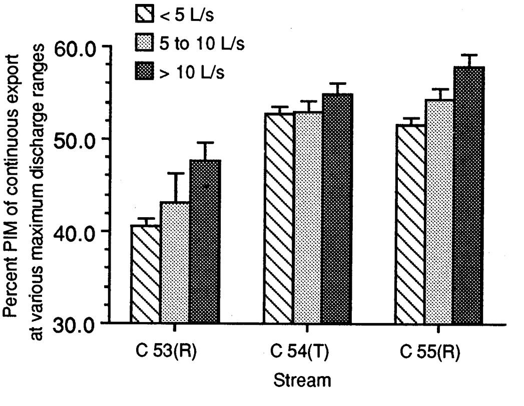

FIG. 6. Percent PIM +95% CL of total particulate export in continuous export (barrel) samples at various ranges of maximum discharge during sampling intervals for reference (R) and treated (T) streams. Means and confidence limits were calculated on arcsine transformed data.

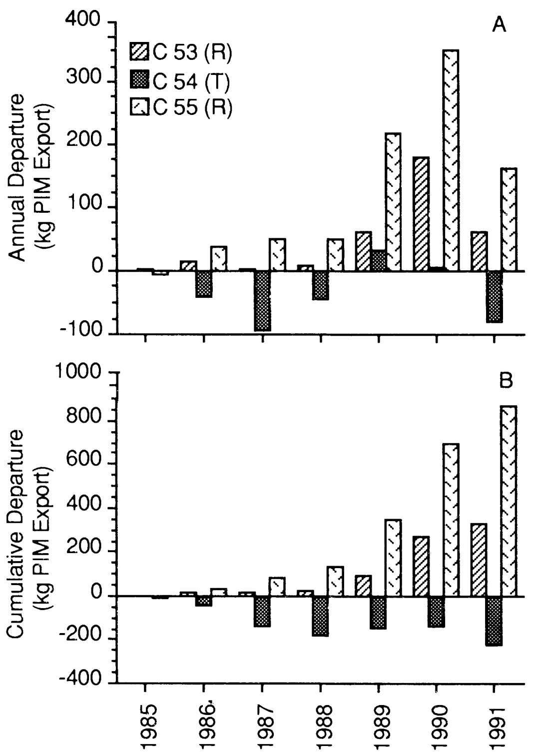

FIG. 7. A.—Annual departure (measured PIM export minus predicted PIM export) during each year of the study. Predicted PIM export was based on first-year PIM export–maximum discharge regressions applied to maximum discharge during each sampling interval for the period of 1986 to 1991. B.—Cumulative departure (measured PIM export minus predicted PIM export) during the study. R = reference and T = treated streams. C 54 received seasonal methoxychlor treatments from December 1985 to October 1988.

were reduced by 90 and 88%, respectively, in C 54 during the treatment period (Lugthart and Wallace 1992). This reduction resulted in much lower rates of leaf litter processing (Cuffney et al. 1990) and large increases in leaf litter standing crops by the third summer of treatment (Wallace et al. 1991a). Amassed leaf litter within the wetted channel of C 54 during treatment undoubtedly enhanced retention of PIM and probably accounted for the following: (1) reduced PIM concentrations in both instantaneous and continuous samplers (Fig. 1A); (2) lower PIM concentrations during rising hydrographs of individual storms (Table 2); (3) a significant reduction in PIM export per unit maximum discharge during storms (Fig. 5); and (4) the absence of significant differences in % PIM of particle export during intervals with high (>10 L/s) and low, (<5 L/s) maximum discharges, which indicates little increase in % PIM during storms in C 54 (Fig. 6). All of the above suggest that inorganic particles were less susceptible to transport in C 54 during treatment years. These differences cannot be attributed to discharge, as discharge was greatest in C 54 during two of the three treatment years (Table 1). Webster et al. (1987a) showed experimentally that the addition of leaf packs to channels reduced particle entrainment and particle concentrations during "artificial" storms. Retention of particles by accumulations of leaf litter, especially during storms, is the most logical explanation for reduced inorganic export in C 54 during treatment.

Although large storms during 1989 and 1990 removed most accumulated leaf litter from the surface of the stream bed in C 54, only a small portion was exported as CPOM. The large litter accumulations during treatment of C 54 were redistributed along the margin of the channel or formed accumulations with sediments during these storms (personal observations). Only 1% (C 53) to about 3% (C 54 and C 55) of CPOM inputs (leaves, woody debris, seeds, etc.) during the 7-yr period were exported as CPOM, and values for leaves alone are slightly lower (Wallace, unpublished data). During post-treatment, PIM export increased dramatically in all streams (Table 4). Although invertebrate recovery was well underway by 1989 (Whiles and Wallace 1992) and leaf litter processing rates were restored by 1990 (Chung 1992), there is ample evidence of lingering treatment effects on PIM

TABLE 5. Measured and predicted export (kg ash) of PIM for the 7-yr period from each stream. Predicted export was calculated from regressions of PIM export vs. maximum discharge during sample interval for 1985 (pretreatment year of C 54), which were applied to maximum discharge during each sampling interval from 1986 to 1991. R = reference streams, T = treated stream.

	C 53 (R)	C 54 (T)	C 55 (R)
Measured export	530	853	1685
Predicted export	199	1072	823
Difference (measured − predicted)	+331	−219	+862
Net difference with C 54	+550		+1081

export in C 54 during the post-treatment period. First, C 54 had the lowest average PIM concentrations among the three streams during treatment and post-treatment, despite having had the highest concentration before treatment (Fig. 1B). Second, C 54 was the only stream that did not show a significant increase in percent PIM for both instantaneous and continuous particle samples during the 3-yr post-treatment period of high discharge (Fig. 1B). Thirdly, although PIM export per unit maximum discharge in C 54 during post-treatment surpassed C 53, that of C 54 remained well below C 55, which is in sharp contrast to pretreatment (Fig. 5). Larger amounts of accumulated litter at the periphery of the wetted stream area in C 54 may have retarded transport of PIM.

Our measurements of PIM export are generally within the range of values reported in the literature. Annual PIM export from our streams averaged 14.6 (C 53), 22.2 (C 54), and 32.1 (C 55) kg ha^{-1} yr^{-1}. Coefficients of variation (CV) among the 7 years were high, i.e., 70.9% (C 53), 77.9% (C 54), and 99.8% (C 55). Our average values are similar to the 29–32 kg ha^{-1} yr^{-1} reported by Monk (1975) for a 2-yr study of C 18, which drains a mature 12.5 ha forest at Coweeta. Annual discharge during both years of Monk's study was close to the long-term average at Coweeta and no comparisons can be made based on extreme discharge. Our average inorganic export is also in the same range as the 22.2 kg ha^{-1} yr^{-1} reported by Likens et al. (1977) for Watershed 6 at Hubbard Brook. Over an 8-yr period, which also included extreme dry and wet years at Hubbard Brook, Likens et al. (1977) found annual PIM export range from 3 to 91 kg ha^{-1} yr^{-1} (CV = 134%) and exceeded the range we observed at Coweeta. Swanson et al. (1982) measured 130 kg ha^{-1} yr^{-1} of PIM export from a clearcut catchment in the Cascade Range of Oregon and noted that inclusion of high-magnitude low-frequency events such as debris torrents would result in much greater losses.

Although PIM losses from our catchments range from >22 to >500 kg/yr (Table 4), most inorganic losses from our catchments occur as dissolved material. Estimates of dissolved inorganic export based on biweekly to monthly concentrations × discharge (Wallace and W.T. Swank, Coweeta Hydrologic Laboratory, unpublished data) indicate that dissolved losses from the three study catchments exceeded particulate export by 2.9 (C 55) to 5.3 (C 53) fold. As a percent of total inorganic export (particulate/[dissolved + particulate]), particulate inorganic export from individual catchments during the period of 1988–1991 ranged from 13.2 to 28.5% (avg. = 18.8%) for C 53, 11.1 to 28.5% (avg. = 20.5%) for C 54, and 30.1 to 40.7% (avg. = 34.2%) for C 55. The highest percentages for particulate export were during the year of maximum discharge (1990) for each stream. In contrast, during years of lower discharge (1988 and 1991), a greater proportion of inorganic export occurred as dissolved losses. This trend is similar to that reported by Likens et al. (1977) at Hubbard Brook. The particulate export from C 53 and C 54, 18.8–20.5% of dissolved, is almost identical to the 20% reported by Likens et al. (1977) for WS 6 at Hubbard Brook, while that of C 55, 34.2% of dissolved, is more similar to that (30.2%) reported by Swanson et al. (1982) for WS 10 at H. J. Andrews in Oregon. We suspect that, in part, the disparity between dissolved and particulate inorganic export from C 53 and C 54 versus that of C 55 is that in the latter there is evidence of the remains of a large debris avalanche. Landslides and debris avalanches contribute to enhanced PIM losses (e.g., Swanson et al. 1982).

Velbel (1987) calculated that the "normal" erosional losses from Coweeta catchments by stream flow are much less than the 600 kg ha^{-1} yr^{-1} required to maintain long-term dynamic equilibrium (steady state with respect to chemical weathering). Thus, in addition to "normal" streamflow losses, long-term equilibrium is maintained by high-magnitude, low-frequency events that include landslides and debris avalanches associated with severe storms (Velbel 1987, Grant 1987). Over the long-term, i.e. centuries, such low-frequency, high magnitude events probably overwhelm our measurements of inorganic export. However, our results suggest that biota influence "normal" erosional losses.

Based on differences between measured and predicted PIM export, the impact of invertebrate manipulation on PIM export was slightly greater (as % reduction) than the impact reported previously for FPOM export (Wallace et al. 1991b). For example, following three years of treatment and 1-yr of recovery, FPOM export in C 54 was reduced by 56% (Wallace et al.

1991b), whereas during this same period PIM export was reduced by ~59%. In terms of absolute mass, the reduction was much greater for PIM than FPOM. During the 3-yr treatment and first year recovery, the average difference in measured and predicted export of FPOM between C 54 and reference streams was 179.2 kg AFDM (Wallace et al. 1991b) versus 366 kg for PIM during the same period.

In summary, insecticide treatment reduced benthic abundances, biomass, and production in C 54 relative to reference streams (Lugthart and Wallace 1992). This reduction in benthic fauna decreased the rate of fine particle generation. It also decreased leaf litter processing rates (Cuffney et al. 1990) in C 54, resulting in a 2× increase in standing crop of leaf litter in C 54 over a 3-yr period (Wallace et al. 1991a). This accumulated leaf litter probably enhanced retention of particles. Based on habitat-weighted production (Lugthart and Wallace 1992), treatment of C 54 reduced macrofaunal production in the entire stream from about 2.3 to 0.9 kg AFDM/yr. Considering only mass, the impact of treatment on export of PIM was several orders of magnitude greater than the impact on invertebrate production. Thus, despite having relatively low levels of secondary production as well as representing a small portion of total catchment biomass, benthic animal communities can have large impacts on ecosystem processes. When we initiated this study, the impact of invertebrate manipulation on PIM export was not a consideration. We did not anticipate the exceptional abilities of these small streams to retain unprocessed leaf litter and thereby enhance retention of inorganic particles. This is another example of indirect effects of animal communities on ecosystem processes.

Acknowledgements

We thank J. Hutchens, A. Lingle, G. A. Schurr, S. Stroud, P. Vila, and Drs. F. L. Smith-Cuffney, A. D. Huryn, D. Imm, S. W. Golladay, and D. J. D'Angelo for assistance with field and laboratory work. We thank Dr. Wayne T. Swank, G. B. Cunningham, and other personnel of the Coweeta Hydrologic Laboratory for providing discharge data and assistance with various aspects of the project. Drs. J. M. Culp and R. J. Mackay and two anonymous referees provided useful criticism on the manuscript. This research was supported by grants from the National Science Foundation.

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Received: 16 July 1992
Accepted: 22 February 1993