

Storage and export of organic matter in a headwater stream: responses to long-term detrital manipulations

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Abstract. Riparian habitats provide organic matter inputs that influence stream biota and ecosystem processes in forested watersheds. Over a 13-yr period, we examined the effects of litter exclusion, small- and large-wood removal, and the addition of leaf species of varying detrital quality on organic matter standing crop and export of organic and inorganic particles in a high-gradient headwater stream. Using eight pretreatment years of export data and two pretreatment years of particulate organic matter (POM) standing crop data, we report on 21 and 15 years of continuous export and POM standing crop results, respectively. Litter exclusion resulted in the elimination of leaf standing crop by the end of year three. Wood and fine benthic organic matter (FBOM) standing crops declined significantly during the exclusion and wood removal periods, but never completely disappeared. Following the introduction of artificial wood structures for retention, the addition of fast, slow, and mixed breakdown leaves in the treatment stream resulted in significantly increased mean annual leaf standing crops. After five years of leaf addition, FBOM standing crop and fine particulate organic matter (FPOM) export remained below pre-treatment levels. The reduction in leaf standing crop in the treatment stream resulted in significant increases in FPOM (2×), fine inorganic particulate (3×), and gravel export (10×). After small wood removal we observed significant increases in export of fine inorganic particulates (2×) and gravel (7×) from the treatment stream. A greater proportion of coarse and FBOM standing crop was exported from the treatment stream during the litter exclusion and small wood removal periods than from the reference stream. Following the addition of slow and mixed leaves this trend was reversed, demonstrating the importance of leaf standing crop in the retention of POM. Our long-term experiment demonstrates that the quantity and type of riparian inputs to forested headwater streams will affect POM standing crop and export of POM and sediments to downstream ecosystems, and that small wood is more critical to retaining sediments and POM in small streams than previously recognized.

Key words: allochthonous; Appalachian (USA) streams; Coweeta Hydrologic Laboratory, North Carolina, USA; detrital complexity; detritus; leaf litter exclusion; organic matter standing crop; organic matter transport; sediment transport; seston; storms; wood.

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INTRODUCTION

Linkages between adjacent ecosystems are ubiquitous and are often extremely important to one or both systems (e.g., Polis et al. 1997). Connectivity among the atmospheric, terrestrial, aquatic, and sub-surface systems crosses a wide range of spatial and temporal scales (e.g., Anderson and Polis 2004, Caraco et al. 2010). This spatial and temporal variability can influence prey availability to consumers across system boundaries (e.g., Power et al. 2004) and result in time lags between production and utilization of resources (Sears et al. 2004). Large and small scale physical processes, landscape topography, ecotonal complexity, and migrations of biota can all regulate the flux of materials across ecosystems (e.g., Cadenasso et al. 2004, Witman et al. 2004). Understanding these linkages and the effects of variation in space and time is crucial for mitigating and predicting future environmental impacts on these linkages (e.g., Freeman et al. 2007, Williamson et al. 2008) and improving management and policy decisions.

Linkages between headwater streams and the forest they drain have been recognized for five decades (e.g., Ross 1963, Hynes 1975, Wipfli et al. 2007). Forests supply particulate organic matter (POM) in the form of leaves, wood, and soil particles (e.g., Wallace et al. 1997a, Elosegi et al. 2007), as well as dissolved organic carbon (DOC) from soil water or decomposing leaves (Meyer et al. 1998). Headwater streams may be viewed as sites of input of POM, storage of coarse benthic organic matter (CBOM) and fine benthic organic matter (FBOM), and transformation of organic matter, as coarse particulate organic matter (CPOM) is converted to fine particulate organic matter (FPOM) and dissolved organic matter (DOM) via leaching, microbial exudates, invertebrate feeding, and physical processing (e.g., Kaushik and Hynes 1971, Webster et al. 1999). While CPOM constitutes the major organic matter input to headwater streams, FPOM (Wallace et al. 1995, 1997a, Webster et al. 1999), DOM (Meyer et al. 1998), and biological respiration account for the bulk of organic matter export from these ecosystems.

Along with serving as an energy source to streams, organic matter reduces erodibility of sediments in forested streams. This role has been

attributed primarily to wood accumulations in streams (e.g., Swanson et al. 1982, Triska and Cromack 1984). Many studies of large wood (>10 cm diameter) have shown how critical large wood is for physical retention of sediments in streams (e.g., Nakamura and Swanson 1993, Thompson 1995). Less attention has been focused on the role of non-woody inputs such as leaf litter and small wood (<10 cm diameter) in organic and inorganic particle export from forested headwater streams.

Measuring organic matter storage and export in lotic ecosystems is difficult because of temporal variability in inputs, storage, and export (Cummins et al. 1983). Export is often estimated as the product of instantaneous measures of POM concentration and discharge over a given interval using rating curves (e.g., Webster et al. 1990, Karlsson et al. 2005). However, discharge and POM concentrations are generally poorly related (e.g., Bilby and Likens 1979, Cummins et al. 1983). Cummins et al. (1983) pointed out both the paucity of and the necessity for long-term studies relating to organic matter export from streams. Cuffney and Wallace (1988, 1989) used a continuous sampling device and compared instantaneous vs. continuous estimates of export. They showed that continuous estimates of total FPOM export were strongly related to maximum discharge during individual two week intervals during a two year drought. However, a later study showed that this relationship exhibited seasonal and wet and dry year variability (Wallace et al. 1991).

In 1992 we started an ecosystem-scale study in the southern Appalachian Mountains, USA to assess the linkages between forest inputs, stream biota, and ecosystem processes by excluding new organic matter inputs for a 13-yr period (Wallace et al. 1997b). Here we report on the effects of this long-term manipulation on organic matter standing crop and export as compared with that of a nearby reference stream. We compare these effects for periods of only litter exclusion (three years); small (<10 cm in diameter) and large wood removal (two years each); addition of artificial retention structures (polyvinyl chloride (PVC) pipe addition for one year); two years of adding rapidly decaying (“fast”) leaves, two years of adding slowly decaying (“slow”) leaves, and one year of mixed leaf addition (Fig. 1A, B).

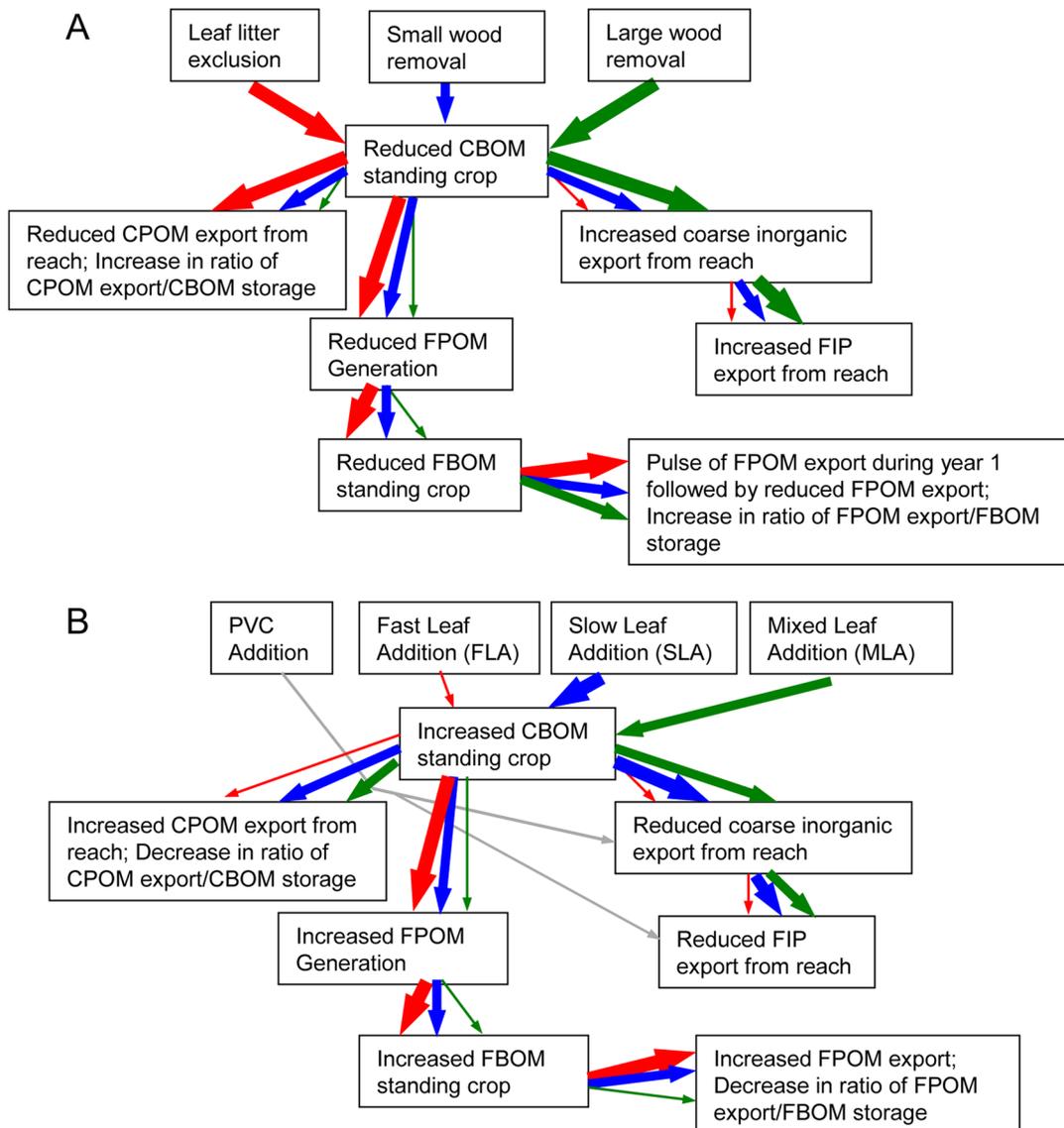


Fig. 1. Conceptual framework of predicted effects of reduction of (A) leaf litter (red), small wood (blue), and large wood (green); and (B) PVC addition (gray) and fast breakdown (red), slow breakdown (blue), and mixed breakdown (green) leaf additions in a high-gradient, forested headwater stream. Width of arrow is proportional to expected magnitude of effect. CBOM = coarse benthic organic matter, CPOM = coarse particulate organic matter, FBOM = fine benthic organic matter, FPOM = fine particulate organic matter, FIP = fine inorganic particle.

We conducted the wood removal in two stages to investigate differences in the structural role of small vs. large wood in particulate storage and transport (Fig. 1A) and added leaves of different functional characteristics (fast, slow, and mixtures of various breakdown rates) in three stages to examine the consequences of detrital quality

and complexity on ecosystem function (Fig. 1B).

During the manipulations we maintained 13 years of continuous measurements of POM and inorganic export. Combined with eight additional years of continuous pretreatment measurements of export, the 21 years of export measurements we present here represent one of

the longest continuous records of POM export from headwater streams. We made six predictions for responses to these manipulations. First, we predicted that leaf litter exclusion and large wood removal, more so than small wood removal, would have the greatest negative effect on CBOM standing crop (Fig. 1A) and the addition of slow breakdown leaves and to a lesser extent mixed leaf species would result in the greatest increase in CBOM standing crops (Fig. 1B). Second, we hypothesized that FBOM standing crop would decrease the most during the leaf litter exclusion period due to a decline in FPOM generation from leaf breakdown and the loss of retention by leaves (Fig. 1A) and increase the most during the addition of fast breakdown leaves (Fig. 1B). Third, we predicted that CPOM and FPOM export would decline as CBOM standing crop declined during exclusion and wood removal periods (Fig. 1A) and increase with each successive year of leaf addition (Fig. 1B). Fourth, we hypothesized that inorganic export would increase as a result of the litter exclusion and wood removal with a much greater increase following large wood removal (Fig. 1A), and subsequently decrease during the leaf addition periods (Fig. 1B). Fifth, we predicted that ratios of coarse and fine organic matter export/storage would increase during the organic matter reduction years which would vary in magnitude by organic matter type (Fig. 1A). Sixth, we hypothesized that the export to storage ratio would decline during the leaf addition years which would vary by leaf breakdown type (Fig. 1B). Finally, we used our long-term data set to compare the relationship between maximum discharge and export during each manipulation period.

METHODS

Study sites

Catchments 53 (reference stream) and 55 (treatment stream) are located within the 1625-ha drainage basin at the US Forest Service's Coweeta Hydrologic Laboratory in the Blue Ridge Province of the southern Appalachian Mountains (Macon County, North Carolina, USA; Swank and Crossley 1988). Our first-order study streams included entire stream reaches from the headwater seep to a weir. Both

catchments have similar physical characteristics (Table 1). The overall roughness of the streambed topography results in high retention, with abundant accumulations of leaves and wood. Catchment vegetation consists of mixed hardwoods and dense growths of understory rhododendron (*Rhododendron maxima*), resulting in heavy shading of the streams with allochthonous inputs of detritus providing >90% of the organic matter available for consumer production (Wallace et al. 1997a).

Organic matter standing crop

Seven benthic samples, four from mixed substrates and three from bedrock outcrops were collected monthly from both streams during September 1985–August 1986 and September 1992–August 2006 using the methods of Wallace et al. (1999). Benthic samples were not collected from 1987 to 1991 due to funding constraints. Coarse and fine particulate organic matter in samples was elutriated from the inorganic substrate, separated, dried, ashed, and reweighed to obtain ash-free dry mass (AFDM; see Wallace et al. 1999). All organic matter masses were standardized by the area sampled and expressed as g AFDM/m².

Discharge

During nonfreezing months of 1985 to 1993, stream water level was measured with a FW-1 (Belfort Instruments, Baltimore, Maryland, USA) stage recorder connected to a 1-ft H-flume at the bottom of each catchment. During freezing periods in 1985 to 1993, daily average, maximum, and minimum discharge for each stream was estimated from regressions with Catchment 2, which was gauged continuously by the US Forest Service. After March 1993 discharge in both streams was measured with an ISCO 4230 Bubbler Flow Meter (ISCO Inc., Lincoln, Nebraska, USA).

Export measurements

FPOM and CPOM export was measured continuously using separate collectors in each stream from 1985 to 2006 following methods of Cuffney and Wallace (1988). A Coshocton proportional subsampler (Parsons 1954) connected to an H-flume shunted 0.6% of all discharge to a series of three 125-L settling barrels that were

Table 1. Physical characteristics of reference and treatment streams.

Physical characteristic	Reference stream	Treatment stream
Catchment		
Area (ha)	5.2	7.5
Elevation (m asl at flume)	820	810
Channel		
Gradient (cm/m)	27	20
Length (m)	135	170
Wetted area (m ²)	207	247
Substrate		
Bedrock (% of streambed)	27	14
Mixed substrate (cobble/pebble) (%)	73	86
Mean discharge (max) (L/s)		
1985–1993 pre-treatment, 9 yr	0.63 (26.63)	1.32 (49.49)
1994 litter exclusion, yr 1	0.83 (23.36)	1.62 (41.00)
1995 litter exclusion, yr 2	0.82 (19.06)	1.41 (34.33)
1996 litter exclusion, yr 3	1.04 (24.84)	1.87 (39.71)
1997 small wood removal, yr 1	1.26 (15.82)	2.01 (33.56)
1998 small wood removal, yr 2	1.21 (32.13)	1.74 (71.45)
1999 large wood removal, yr 1	0.40 (11.07)	0.64 (20.15)
2000 large wood removal, yr 2	0.30 (13.19)	0.45 (16.15)
2001 PVC addition, yr 1	0.22 (13.37)	0.37 (40.11)
2002 fast leaf addition, yr 1	0.52 (7.68)	0.75 (12.64)
2003 fast leaf addition, yr 2	1.44 (15.93)	2.16 (27.23)
2004 slow leaf addition, yr 1	0.75 (19.82)	1.19 (42.85)
2005 slow leaf addition, yr 2	1.59 (20.77)	2.19 (58.94)
2006 mixed leaf addition, yr 1	0.73 (11.30)	1.02 (15.33)
1985–2006 grand mean \pm 1 SE	0.76 \pm 0.01	1.32 \pm 0.02
Temperature (°C)		
1985–1993 pre-treatment, 9 yr		
Mean	12.4	12.3
Maximum/minimum	19.8/0.8	19.5/1.6
1994–2006 post-treatment, 13 yr		
Mean	12.1	12.0
Maximum/minimum	20.5/0.0	20.1/–0.5

Notes: Mean/maximum discharge and temperature calculated to coincide with start and end of treatment periods (e.g., 1 September of previous year to 31 August of year listed). Maximum discharge in parentheses. SE = standard error.

stirred and sampled biweekly for FPOM. Particle concentrations were measured by filtering replicate aliquots (47 mm, 1.0 μ m Gelman A/E glass fiber filters; Pall Corporation, Ann Arbor, Michigan, USA). Filters were processed in the laboratory to obtain AFDM and the amount of POM in each barrel (Cuffney and Wallace 1988). CPOM was sampled by >4 m³ cages (4-mm mesh) located upstream of the flume. Traps were bolted to the bedrock outcrop and extended from bank to bank to sample the entire stream flow. Each trap was covered with plastic to prevent direct-fall of litter. Total wet weight of all material accumulated in the traps was measured at 2-wk intervals. Subsamples were sorted into leaf, wood, seeds, and gravel (inorganic particles >4 mm) categories, dried, weighed, ashed, and reweighed to obtain AFDM (Cuffney et al. 1990). Organic and inorganic material <4 mm was dried and ashed, and the AFDM added to

FPOM export for the interval. The size range we used for FPOM and fine inorganic particles (FIP) is larger than the typical 0.45- μ m to 1-mm particle size. This adjustment was necessary to match the opening slot (4 mm) on the Coshocton sampler. The larger size fraction has small impact on our results because POM >250 μ m represents a small fraction (1.3%) of total POM transported in Coweeta streams (e.g., Cuffney et al. 1990).

Treatments

Direct-fall litter was excluded from the treatment stream from September 1993 to August 2006 using 1.2-cm mesh gill net canopy erected across the channel, while blow-in litter was excluded using 20-cm high bird netting along the stream sides (Table 2) (Litter Exclusion; LE). Small wood (<10 cm diameter) was manually removed from the exclusion stream in August 1996 (see Wallace et al. 2000) (Small Wood

Table 2. Description of treatments and treatment periods of detrital manipulations in treatment stream (Catchment 55).

Dates	Treatment	Treatment description
9/1/1985–8/31/1993 9/1/1993–8/31/1994	Pre-treatment years (PreTmt-1–8) Litter exclusion yr 1 (LE-1)	Normal detrital inputs to treatment stream Canopy and lateral fence constructed 1–6 September 1993 over 170 m treatment stream to exclude all organic matter inputs (>1.2 cm diameter)
9/1/1994–8/31/1995 9/1/1995–8/31/1996 9/1/1996–8/31/1997 9/1/1997–8/31/1998 9/1/1998–8/31/1999 9/1/1999–8/31/2000 9/1/2000–8/31/2001	Litter exclusion yr 2 (LE-2) Litter exclusion yr 3 (LE-3) Small wood removal yr 1 (SWR-1) Small wood removal yr 2 (SWR-2) Large wood removal yr 1 (LWR-1) Large wood removal yr 2 (LWR-2) PVC pipe addition yr 1 (PVC)	Continued litter exclusion Continued litter exclusion All small wood <10 cm diameter removed Continued small wood removal All large wood >10 cm diameter removed Continued large wood removal PVC pipe and plastic branches added equivalent to number of pieces and surface area of small and large wood removed
9/1/2001–8/31/2002	Fast leaf addition yr 1 (FLA-1)	Fast leaf species added 33.3% by weight of tulip poplar, dogwood, and American sweetgum
9/1/2002–8/31/2003 9/1/2003–8/31/2004	Fast leaf addition yr 2 (FLA-2) Slow leaf addition yr 1 (SLA-1)	Continued fast leaf addition Slow leaf species added 33.3% by weight of rhododendron, white pine, and northern red oak
9/1/2004–8/31/2005 9/1/2005–8/31/2006	Slow leaf addition yr 2 (SLA-2) Mixed leaf addition yr 1 (MLA-1)	Continued slow leaf addition Mixed leaf species added 33.3% by weight of tulip poplar, rhododendron, and red maple

Note: Exclusion of natural litter inputs continued during all treatment periods.

Removal; SWR) and large wood (>10 cm diameter) was manually removed from the stream in August 1998 (Wallace et al. 2001) (Large Wood Removal; LWR). During August 2000, we added artificial retention structures to provide the physical complexity previously provided by large and small wood, in the form of PVC pipe and plastic tubing equivalent to the numbers, lengths, diameters, and surface area of all wood pieces removed from the stream wetted area (PVC addition; PVC). To examine the importance of functional diversity of leaf litter species for ecosystem structure and function we then added fast decomposing leaf litter for two years, slow decomposing leaves for two years, followed by one year of mixed (slow, fast, and medium) leaves to the treatment stream. A total of 81 kg dry mass (DM) (27 kg of each of three leaf species of various breakdown rates) were evenly distributed (230 g AFDM/m² equivalent to natural inputs of each species) over the treatment stream bottom over a two month period (October and November) each year during each of the three leaf addition periods: Fast Leaf Addition (FLA)—27 kg DM each of dogwood, (*Cornus florida*), tulip poplar (*Liriodendron tulipifera*), and American sweetgum (*Liquidambar styraciflua*) added during autumn of 2001 and 2002; Slow Leaf Addition (SLA)—27 kg DM each of rhodo-

dendron (*Rhododendron maximum*), white pine (*Pinus strobus*), and red oak (*Quercus rubra*) added during autumn 2003 and 2004; Mixed Leaf Addition (MLA)—27 kg DM each of leaf species with fast (tulip poplar), slow (rhododendron), and medium (red maple) breakdown rates added during autumn 2005. Funding constraints prevented a second year of mixed leaf addition. The litter exclusion canopy was maintained throughout all treatment periods.

Statistical analyses

Since this series of manipulations was conducted in unreplicated treatment and reference catchments, Randomized Intervention Analysis (RIA; Carpenter et al. 1989) was used to test null hypotheses of no change in variables of interest in the treatment stream relative to the reference stream following each treatment period when compared to the pre-treatment period (Table 2). The pre-treatment period for each test included the period from 1 September 1985 to 31 August 1993 when no manipulation of detrital inputs occurred in either catchment (Table 2). This experiment was a sequential series of manipulations in the same system. The potential for lags in response means that the treatments lack strict independence. Rejection of the null hypothesis of no change in the relationship between sites

following a manipulation, plus visual inspections of divergent trends in the data set, implies a treatment effect. Exclusion of litter inputs continued during all treatment periods. To examine interactions between treatments and magnitude of FPOM, wood, leaf, and fine sediment export during increases in discharge over a treatment period, we regressed export against maximum water discharge (L/s) for each 2-wk sampling interval for the treatment and reference streams. Data were log transformed to meet assumptions of normality and homogeneity of variance. Relationships between maximum discharge and export were compared between streams and between pre- and post-treatment periods within the treatment stream by comparing differences between slopes (Zar 1984). We do not include detailed export responses based on season or individual storms here, as these are being examined separately.

RESULTS

Benthic organic matter standing crop

During the initial 3-yr litter exclusion period standing crops of CBOM, leaf, and FBOM differed significantly ($P < 0.0001$, $P < 0.0001$, $P < 0.001$, RIA) between the reference and treatment streams, but wood did not (Fig. 2A–D and Appendix A). By the end of year three of litter exclusion, leaf standing crop in the treatment stream had declined to 0 g AFDM/m². Removal of small and large wood resulted in additional significant differences between streams in total CBOM, leaf, wood, and FBOM (Fig. 2A–D). Although total CBOM, leaf, and total wood standing crops approached 0 g AFDM/m² in the treatment stream, FBOM standing crop in the mixed substrates remained ≥ 300 g AFDM/m² (Fig. 2D and Appendix A). FBOM standing crop declined in the last year of LWR in the treatment stream (Appendix A), but leaf addition reversed the trend of declining FBOM standing crop in the treatment stream. During the LE through PVC periods, the treatment stream lost an average of 151 g AFDM/m² of FBOM per wetted stream area per year; whereas, the reference stream gained an average of 114 g AFDM/m² of FBOM. During the 5-yr FLA through MLA period, the treatment stream lost an average of 25 g AFDM/m²

of FBOM compared to losses of 75 g AFDM/m² in the reference stream.

Standing crop of CBOM and leaves increased with fast litter addition (FLA) to the treatment stream (Fig. 2A, B); however, FBOM didn't increase until the second year of FLA (Fig. 2D). During FLA, monthly standing crops of leaf material in the treatment stream dropped to 0 g AFDM/m² by the summer months of each year (monthly data not shown). Mean annual leaf litter standing crops reached levels similar to those of pretreatment during the second year of FLA. During the mixed leaf addition (MLA) year, leaf litter standing crop in the treatment stream was similar to that of the reference stream. In spite of continuous efforts to remove all wood from the treatment stream following small and large wood removal, wood standing crops never reached zero and ranged from 20–96 g AFDM/m² (Fig. 2C and Appendix A) as storms uncovered wood previously buried beneath the surface of the stream bed. Benthic organic matter standing crops on the steep-gradient rock face substrate was a small fraction of that of mixed substrate in both streams (Appendix A). There were no differences ($P > 0.05$, RIA) in organic matter standing crops associated with treatments on rock face substrates except for wood during the SWR period.

Organic matter export

Total CPOM export did not differ significantly between streams until small wood removal (Fig. 3A). When data from both years of SWR were combined, there was no statistical difference in total CPOM export between streams; however, when each year was analyzed separately, total CPOM export was significantly lower in the treatment stream during year two of SWR ($P < 0.0001$, RIA). Leaf export from the treatment stream declined immediately after the start of litter exclusion and remained low until leaves were reintroduced ($P < 0.001$ to $P < 0.05$, RIA) (Fig. 3B). Leaf export from the treatment stream increased during leaf addition years but remained significantly lower than that from the reference stream ($P < 0.01$ to $P < 0.0001$, RIA). With the decline in leaf standing crops during litter exclusion and the concomitant loss of retentive material, wood export from the treat-

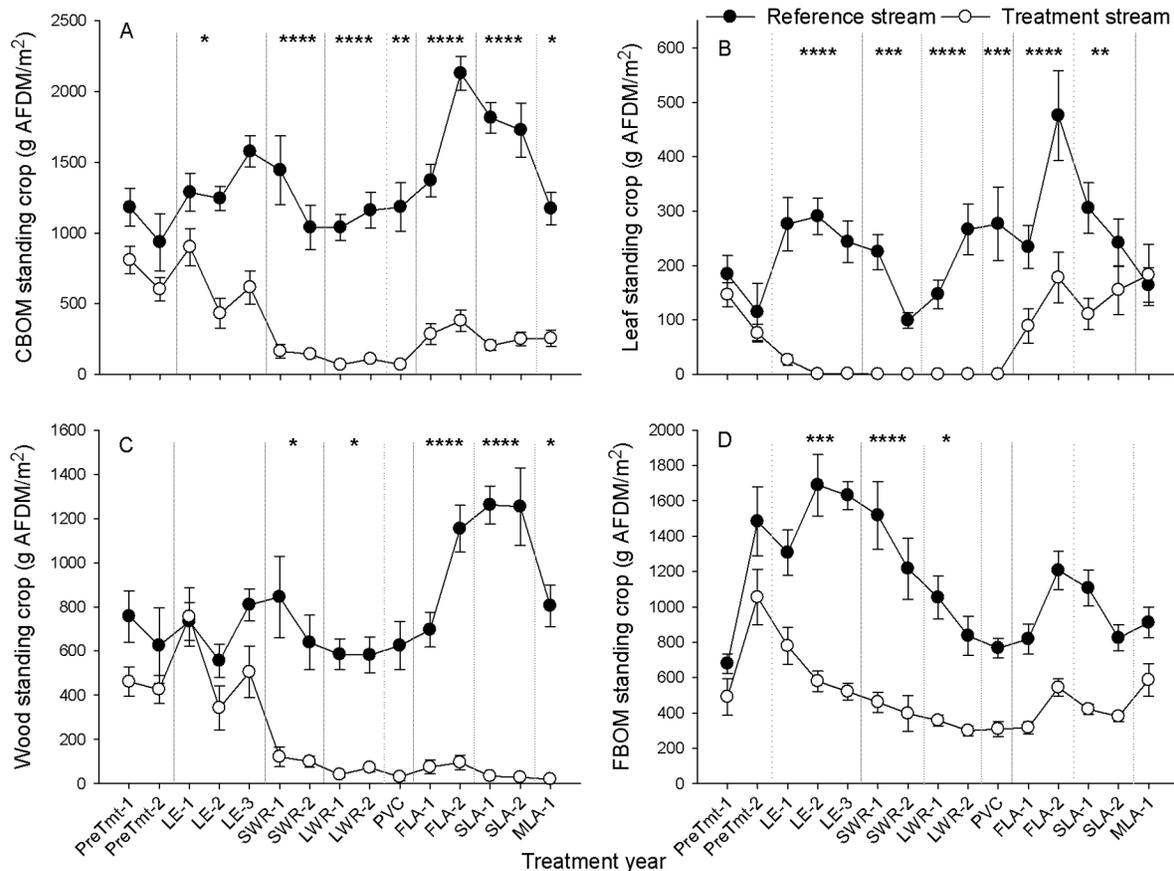


Fig. 2. Average (\pm SE) annual standing crop of (A) total coarse benthic organic matter (CBOM), (B) leaf, (C) wood, and (D) fine benthic organic matter (FBOM) in mixed substrate habitats of the reference and treatment streams during each pretreatment (PreTmt), litter exclusion (LE), small wood removal (SWR), large wood removal (LWR), PVC pipe addition (PVC), fast leaf addition (FLA), slow leaf addition (SLA), and mixed leaf addition (MLA) year. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

ment stream increased significantly ($P < 0.01$, RIA) and declined following year one of small wood removal (year two $P < 0.01$, RIA) (Fig. 3C).

FPOM export was about 9.5 times that of CPOM in both streams (Figs. 3 and 4 and Appendix B). The proportion of total POM export as FPOM was lowest in the autumn and highest in the spring. Prior to litter exclusion, annual FPOM export from the treatment stream exceeded that of the reference stream (Fig. 4). Annual FPOM export from the treatment stream was significantly greater than from the reference stream during the first three years of litter exclusion ($P < 0.05$, RIA) and then decreased for the duration of the experiment (Fig. 4). Although total FPOM export changed signifi-

cantly with these manipulations, FPOM concentration was consistently higher in the reference stream (Fig. 5), which had lower annual discharge than the treatment stream (Table 1). Differences in FPOM concentration between streams were significant during only the LWR ($P < 0.001$, RIA) and PVC ($P < 0.05$, RIA) manipulation periods.

Inorganic export

Differences in gravel and total inorganic export between streams were greatest during litter exclusion and small wood removal ($P < 0.05$ and $P < 0.0001$, RIA) (Fig. 6A–B and Appendix B). Gravel export was 7 \times higher in the treatment stream than in the reference stream during year

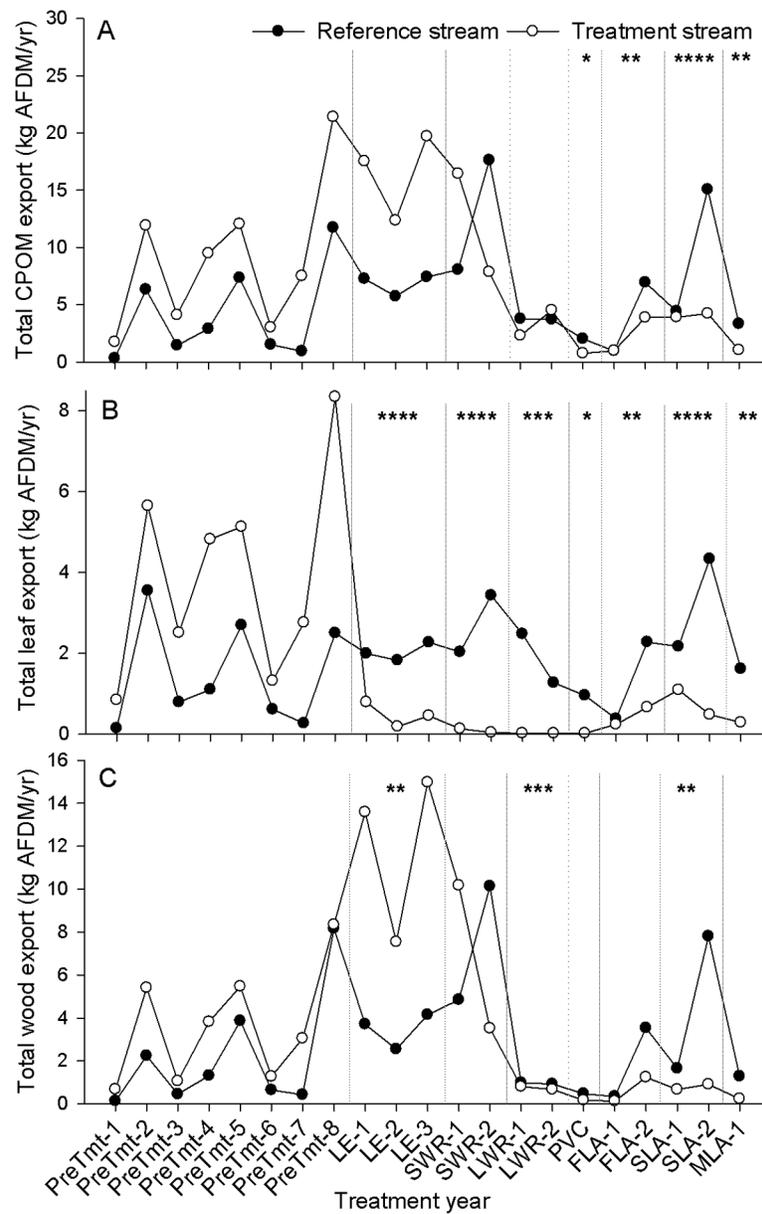


Fig. 3. Annual export of (A) coarse particulate organic matter (CPOM), (B) leaf, and (C) wood from reference and treatment streams during each pretreatment (PreTmt), litter exclusion (LE), small wood removal (SWR), large wood removal (LWR), PVC pipe addition (PVC), fast leaf addition (FLA), slow leaf addition (SLA), and mixed leaf addition (MLA) year. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

one of SWR (Fig. 6A). Following the SWR period, gravel and total inorganic export declined in the treatment stream. Total inorganic export was dominated by fine inorganic particles (FIP) (Fig. 6B and Fig. 7). Largest differences in FIP export between streams occurred during the SWR ($P <$

0.0001, RIA). Following SWR there was a large decrease in FIP export in the treatment stream during the LWR, PVC, and leaf addition periods. Fine inorganic particulate concentrations were similar in both streams until the LWR period, when concentrations differed significantly be-

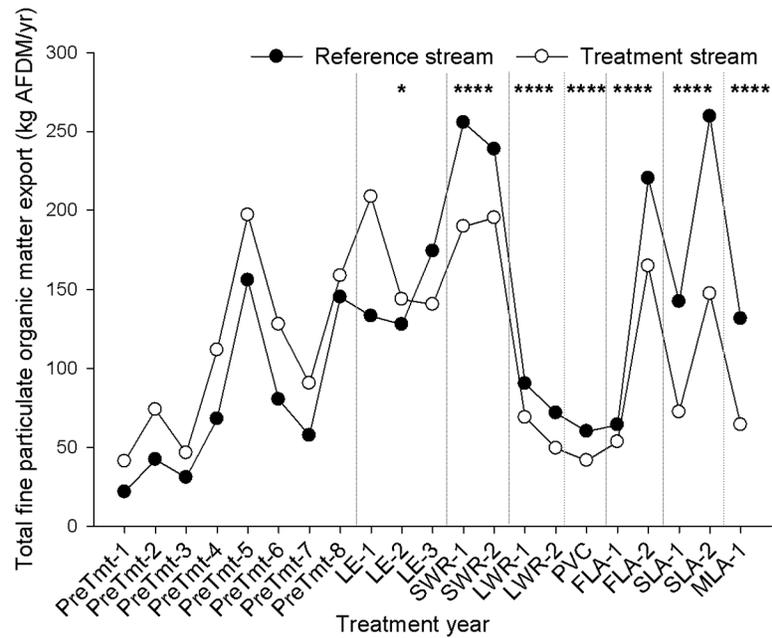


Fig. 4. Annual export of fine particulate organic matter from reference and treatment streams during each pretreatment (PreTmt), litter exclusion (LE), small wood removal (SWR), large wood removal (LWR), PVC pipe addition (PVC), fast leaf addition (FLA), slow leaf addition (SLA), and mixed leaf addition (MLA) year. * $P < 0.05$; **** $P < 0.0001$.

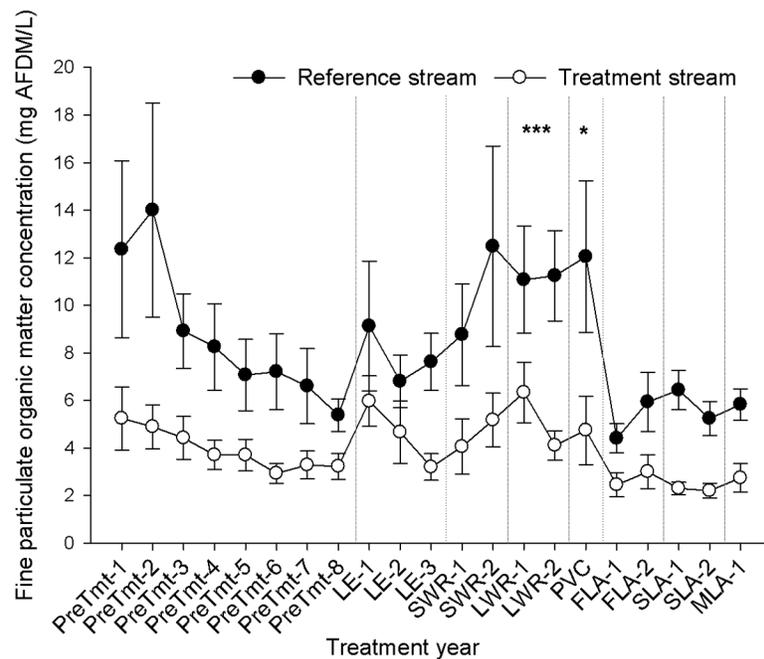


Fig. 5. Average (\pm SE) annual fine particulate organic matter concentrations for reference and treatment streams during each pretreatment (PreTmt), litter exclusion (LE), small wood removal (SWR), large wood removal (LWR), PVC pipe addition (PVC), fast leaf addition (FLA), slow leaf addition (SLA), and mixed leaf addition (MLA) year. * $P < 0.05$; *** $P < 0.001$.

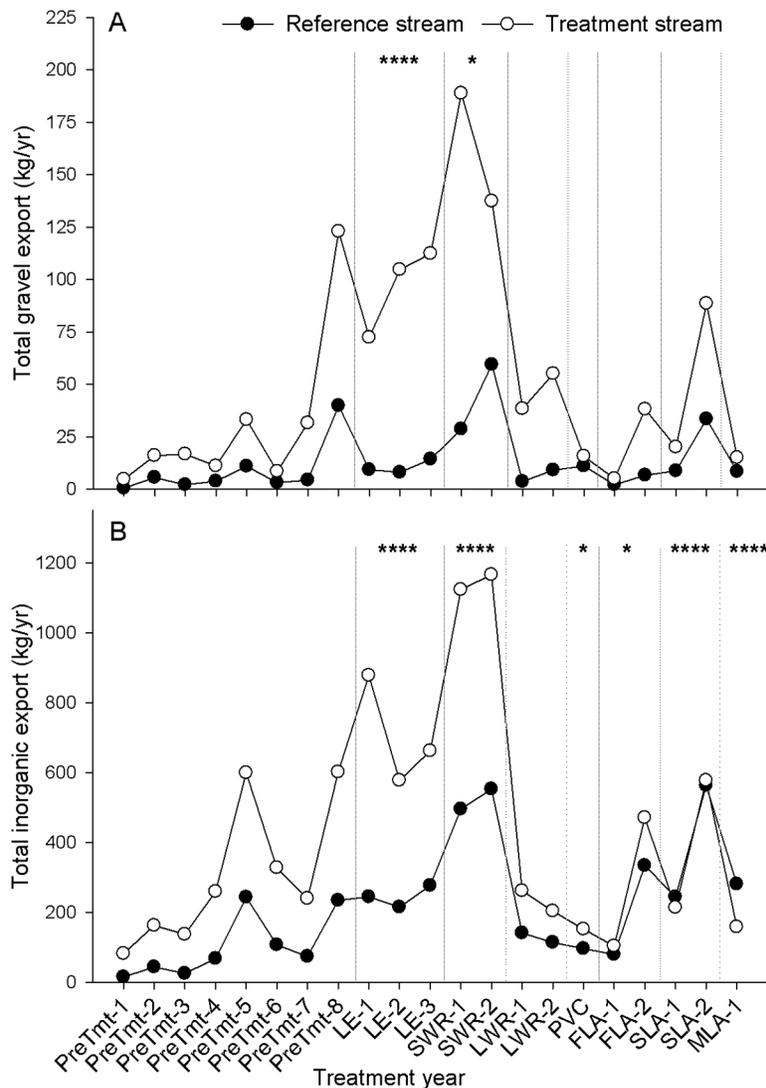


Fig. 6. Annual export of (A) gravel and (B) total inorganic matter from reference and treatment streams during each pretreatment (PreTmt), litter exclusion (LE), small wood removal (SWR), large wood removal (LWR), PVC pipe addition (PVC), fast leaf addition (FLA), slow leaf addition (SLA), and mixed leaf addition (MLA) year. * $P < 0.05$; **** $P < 0.0001$.

tween streams ($P < 0.05$, RIA), as well as during the SLA and MLA periods (Fig. 8, $P < 0.01$ to < 0.001 , RIA). In all three cases these significant differences in FIP concentrations were a result of lower concentrations in the treatment stream compared to the reference stream (Fig. 8).

Export vs. discharge relationships

Relationships between organic matter export and maximum discharge during each sampling

interval for the treatment stream varied with the manipulation (Fig. 9). Leaf export slopes in the treatment stream were significantly lower during the LE, SWR, LWR, PVC addition, and FLA periods than during pretreatment (Fig. 9A). During the leaf addition period there was a progressive increase in slope of the leaf export versus maximum discharge relationship, and during the SLA and MLA periods, slopes did not differ significantly from pretreatment in the

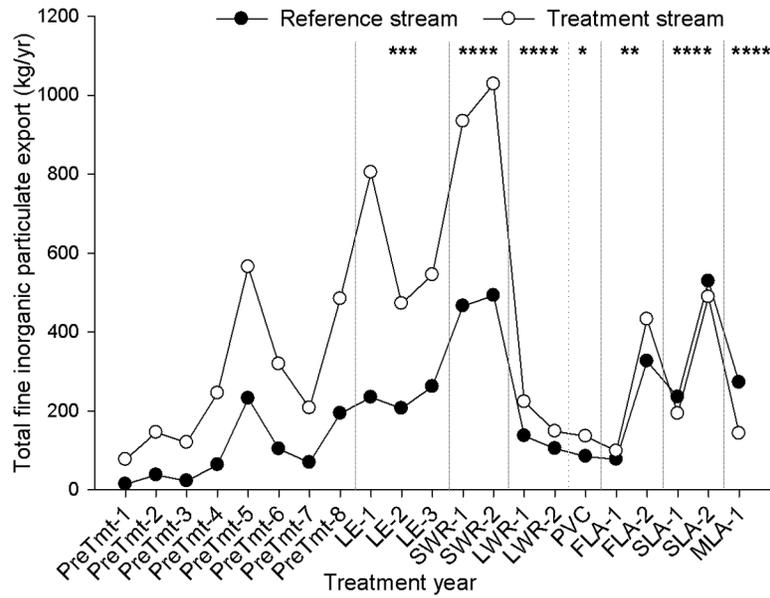


Fig. 7. Annual export of fine inorganic matter from reference and treatment streams during each pretreatment (PreTmt), litter exclusion (LE), small wood removal (SWR), large wood removal (LWR), PVC pipe addition (PVC), fast leaf addition (FLA), slow leaf addition (SLA), and mixed leaf addition (MLA) year. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

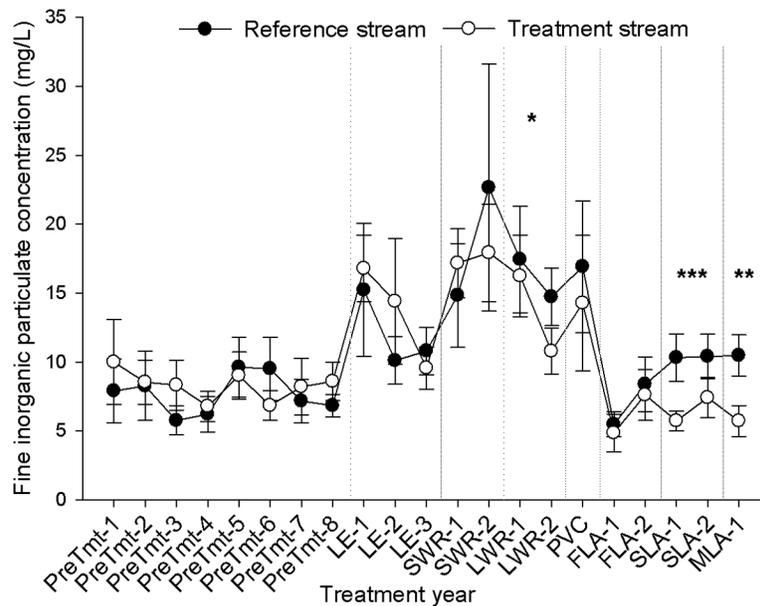


Fig. 8. Average (\pm SE) annual fine inorganic particulate concentrations for reference and treatment streams during each pretreatment (PreTmt), litter exclusion (LE), small wood removal (SWR), large wood removal (LWR), PVC pipe addition (PVC), fast leaf addition (FLA), slow leaf addition (SLA), and mixed leaf addition (MLA) year. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

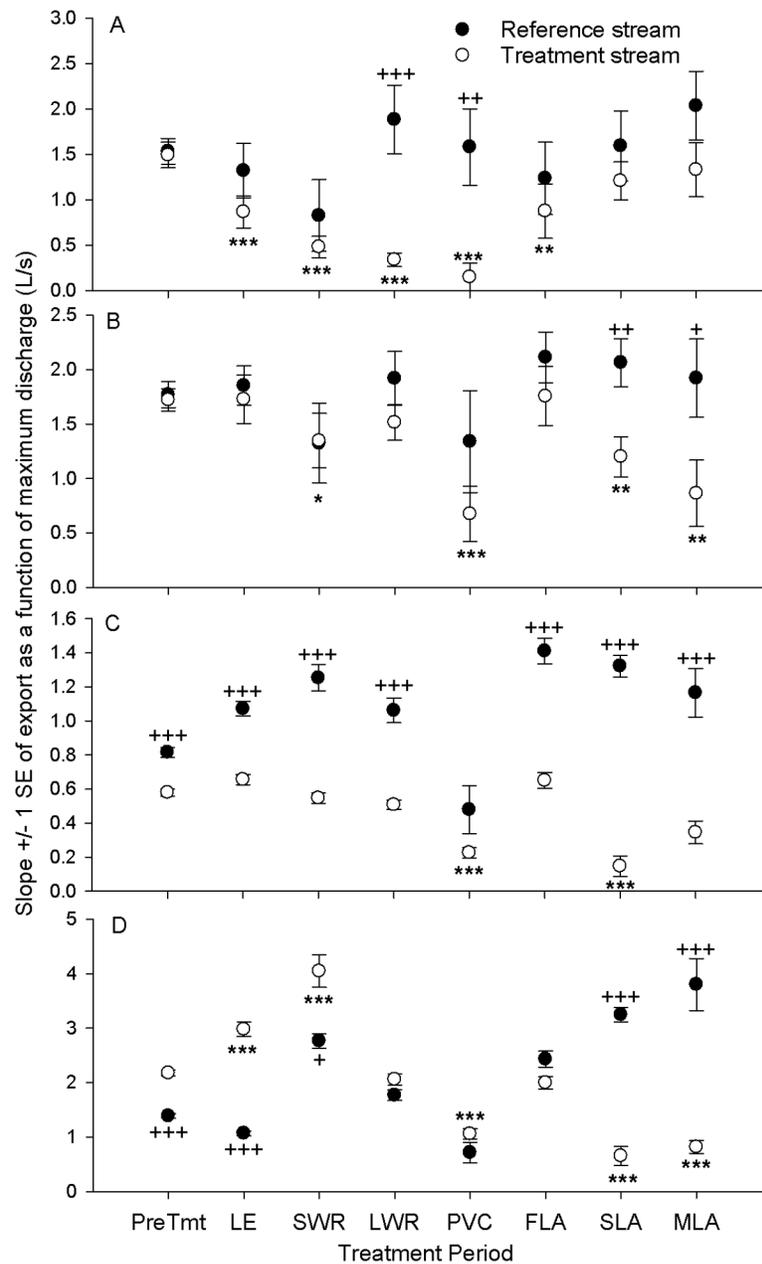


Fig. 9. Mean slopes \pm 1 SE of export of leaf, wood, fine organic and fine inorganic matter (g ash-free dry mass for organic matter; g for inorganic matter) per collection interval as a function of maximum discharge (L/s) based on linear regressions through the origin with maximum discharge as x and organic or inorganic matter exported as y. $P < 0.05$ for all regressions. P represents probability of differences in slopes for the export/maximum discharge relationship between streams (+ for $P < 0.05$; ++ for $P < 0.01$; +++ for $P < 0.001$) and between pre- and post-treatment periods within the treatment stream (*) (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$). Treatment periods are: pretreatment (PreTmt), litter exclusion (LE), small wood removal (SWR), large wood removal (LWR), PVC pipe addition (PVC), fast leaf addition (FLA), slow leaf addition (SLA), and mixed leaf addition (MLA).

treatment stream or between streams (Fig. 9A). Wood export versus maximum discharge relationships in the treatment stream differed from pretreatment during the SWR, PVC, SLA, and MLA periods when the slope of the regression was significantly lower in the treatment stream (Fig. 9B). The slope of the FPOM export vs. maximum discharge relationship in the treatment stream differed significantly from pretreatment only during the PVC and SLA years (Fig. 9C). During the LE and especially the SWR periods, the slopes of the FIP export vs. maximum discharge regressions in the treatment stream were greater than any other period (Fig. 9D).

Discharge

The long-term discharge data set (1985–2006) for the treatment and reference streams included the wettest and driest years at Coweeta based on yearly departures from mean annual precipitation at Coweeta (63-year precipitation record) (Fig. 10A). Mean annual discharges in the reference and treatment streams during the study ranged from 0.22 and 0.37 L/s during 2000–2001 to 1.20 and 2.38 L/s during 1989–1990, respectively (Table 1). The highest daily discharges during this study occurred during a large storm in January 1998 and during Hurricane Ivan in September 2004.

Cumulative export

Cumulative export of FPOM from the treatment stream exceeded that of the reference stream throughout the pretreatment and the treatment periods until the last three years of the study when cumulative FPOM export from the reference stream surpassed that of the treatment stream (Fig. 10B). Cumulative FIP export in the treatment stream exceeded that of the reference stream by >3.5 metric tons over the 21-yr period (Fig. 10C). Differences in cumulative FIP export between streams were greatest during the LE and SWR periods. Large infrequent storms can occur during drought or wet years; however, the departure from mean annual precipitation (Fig. 10A) shows that during years of low precipitation, the slopes of the cumulative export (Fig. 10B, C) are lower than during wet years when precipitation and discharge are elevated.

Relationship between standing crop and export

A greater proportion of stream benthic organic matter standing crop was exported from the treatment stream than from the reference stream for much of the study (Table 3). During the first 3 years of litter exclusion and wood removal periods the ratio of CPOM export to benthic standing crop in the treatment stream exceeded that of the reference stream by $\sim 12\times$ (Table 3). The greatest difference in the ratio occurred during the SWR period when the ratio in the treatment stream exceeded that of the reference stream by $>29\times$. During the MLA year the ratio was identical in both streams, whereas during the fast and slow leaf addition periods the ratio in the treatment stream was $3\times$ greater than in the reference stream. During the litter exclusion and wood removal periods leaf export/benthic standing crop ratios in the treatment stream exceeded those of the reference stream by an average of $>85\times$, with the greatest difference in year one of SWR when the ratio was $>361\times$ higher in the treatment stream (Table 3). During the litter addition periods leaf export to standing crop ratios in the treatment stream were similar to or less than those in the reference stream.

Export/standing crop ratios for each stream were higher for FPOM than the other forms of particulate organic matter (Table 3). The average ratio in the reference stream during the litter exclusion and wood removal periods was $74\times$ greater for FPOM than leaf material and $40\times$ greater for FPOM than CPOM. During the same time period, the average export/standing crop ratio for the treatment stream was similar for FPOM and leaf material and $4\times$ greater for FPOM compared to CPOM. During the two years of slow leaf addition and the year of mixed leaf addition, the ratio for FPOM was lower in the treatment stream than that in the reference stream (Table 3).

DISCUSSION

CPOM and FPOM standing crop

Results from this long-term manipulation support our first prediction that benthic standing crop of organic matter would decrease in the treatment stream during the litter exclusion, wood removal, and PVC addition periods and then increase with the reintroduction of leaves of

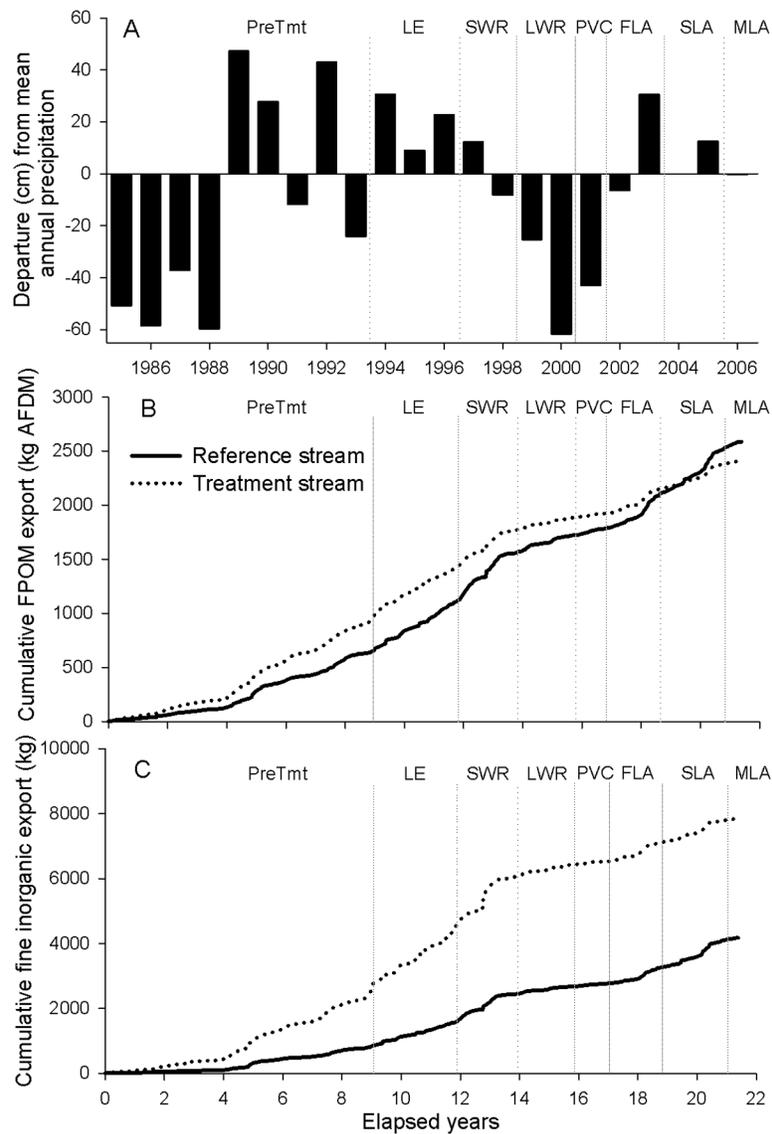


Fig. 10. (A) Yearly departures from mean annual precipitation during the study period. Cumulative export of (B) fine particulate organic matter (FPOM) export and (C) fine inorganic matter from reference and treatment streams vs. elapsed years during study period from 1985 to 2006. Treatment periods are: pretreatment (PreTmt), litter exclusion (LE), small wood removal (SWR), large wood removal (LWR), PVC pipe addition (PVC), fast leaf addition (FLA), slow leaf addition (SLA), and mixed leaf addition (MLA).

various detrital qualities. Unexpectedly, we observed a very rapid decline in leaf standing crop to the point where 0 g AFDM/m² of leaf litter remained in the treatment stream after only one year of litter exclusion. Differences between leaf standing crop in the treatment and reference streams remained significantly different until the reintroduction of mixed leaf species in the last

year of the study. We observed a very rapid response of ecosystem processes to the loss of leaf standing crop, which demonstrated the critical role of leaf litter in regulating ecosystem function in headwater streams draining forested watersheds (e.g., Wallace et al. 1997b, 1999, Meyer et al. 1998, Webster et al. 2001, Eggert and Wallace 2003a, 2003b, Johnson and Wallace

Table 3. Average annual habitat-weighted standing crop (kg), total annual export (kg), and ratio of total annual export to average annual standing crop of benthic organic matter in reference stream (RS) and treatment stream (TS) during treatment periods.

Treatment period	Average standing crop (kg)		Total annual export (kg)		Annual export/average standing crop	
	RS	TS	RS	TS	RS	TS
Coarse particulate organic matter						
Pre-Tmt	143.21	129.59	11.73	21.39	0.082	0.165
LE-1	196.97	193.72	7.27	17.52	0.037	0.090
LE-2	188.95	93.38	5.73	12.35	0.028	0.132
LE-3	239.44	132.96	7.43	19.69	0.031	0.148
SWR-1	108.41	3.98	8.06	16.43	0.074	4.128
SWR-2	197.17	31.06	17.62	7.85	0.089	0.252
LWR-1	159.08	15.14	3.76	2.30	0.024	0.152
LWR-2	176.32	21.75	3.71	4.52	0.021	0.208
PVC	181.57	15.68	2.03	0.75	0.011	0.048
FLA-1	209.90	61.74	0.97	0.97	0.005	0.016
FLA-2	323.84	82.03	6.94	3.88	0.021	0.047
SLA-1	276.10	44.21	4.42	3.91	0.017	0.088
SLA-2	262.02	54.28	15.07	4.22	0.058	0.078
MLA-1	178.68	55.57	3.33	1.03	0.019	0.019
Leaves						
Pre-Tmt	94.99	16.29	2.50	8.34	0.026	0.512
LE-1	111.74	5.70	1.99	0.79	0.018	0.138
LE-2	84.29	0.15	1.83	0.18	0.022	1.200
LE-3	122.69	0.28	2.27	0.45	0.018	1.607
SWR-1	56.06	0.01	2.03	0.13	0.036	13.002
SWR-2	120.67	0.03	3.43	0.04	0.028	1.333
LWR-1	88.53	0.03	2.48	0.02	0.028	0.667
LWR-2	88.02	0.13	1.27	0.02	0.014	0.153
PVC	95.00	0.07	0.96	0.02	0.010	0.286
FLA-1	105.75	19.32	0.38	0.24	0.004	0.012
FLA-2	174.67	38.58	2.28	0.66	0.013	0.017
SLA-1	190.83	23.99	2.17	1.09	0.011	0.026
SLA-2	189.50	33.55	4.33	0.48	0.023	0.014
MLA-1	121.91	39.47	1.61	0.29	0.013	0.007
Fine particulate organic matter						
Pre-Tmt	201.88	227.20	144.96	158.52	0.718	0.698
LE-1	197.93	170.59	133.00	208.58	0.672	1.223
LE-2	255.90	125.02	127.66	143.63	0.499	1.149
LE-3	247.11	112.61	174.14	140.39	0.705	1.247
SWR-1	32.15	14.01	255.58	189.74	7.951	13.547
SWR-2	185.34	100.07	238.64	195.23	1.288	1.951
LWR-1	160.51	78.30	90.18	68.82	0.562	0.879
LWR-2	144.43	67.59	71.58	49.27	0.496	0.729
PVC	116.85	71.19	59.95	41.49	0.513	0.583
FLA-1	126.15	66.87	64.07	53.32	0.508	0.797
FLA-2	179.50	121.50	220.22	164.72	1.227	1.356
SLA-1	168.54	91.13	142.18	72.21	0.844	0.792
SLA-2	125.87	82.31	259.50	147.11	2.062	1.787
MLA-1	139.63	108.81	131.34	64.16	0.941	0.590

Notes: Treatment periods were pretreatment (Pre-Tmt); litter exclusion years one through three (LE-1, LE-2, LE-3); small wood removal years one and two (SWR-1, SWR-2); large wood removal years one and two (LWR-1, LWR-2); PVC addition year (PVC); fast leaf addition years one and two (FLA-1, FLA-2); slow leaf addition years one and two (SLA-1, SLA-2); mixed leaf addition year (MLA-1). Organic matter standing crop and annual export were corrected for differences in bottom wetted area between streams.

2005).

Although the initial standing crop of leaf litter was reduced rapidly, a large standing crop (>5 kg AFDM/m²) of wood remained in the treatment stream prior to SWR and LWR (Wallace et al. 2000, 2001). We conducted the wood removal in a two-step process over four years to compare

differences in ecosystem response to the removal of small and large wood separately. Over 4.76 kg of wood per m² of stream was removed from the treatment stream during the SWR (>1.54 kg/m²) and LWR (3.22 kg/m²) periods (Wallace et al. 2000). Small wood (SW) removed by hand was ~10% greater than that estimated by line

intersect methods (Wallace et al. 2000). In contrast, large wood (LW) removed was only 30% of the line intersect methods, but still within the 95% CI of the line estimates because of the patchy distribution of LW (Wallace et al. 2001). The SW in benthic samples following SWR and LWR in the treatment stream was a result of wood that was buried below the surface of the stream bed and became exposed over time following repeated storms and scouring of the stream bed.

The standing crop of FBOM never declined to levels below ~ 0.3 kg AFDM/m² (LWR year two and the PVC addition year) in the mixed substrates of the treatment stream, which was greater than expected (prediction two). The high ratio of export/standing crop ratio in the treatment stream indicates that despite ongoing litter exclusion followed by wood removal, FBOM standing crop in the stream bed was being renewed. As noted elsewhere (e.g., Ward et al. 1994) there are other potential sources of FPOM, which include soil organic matter (Sollins et al. 1985), fine litterfall and frass, overland flow from the banks during storms, and continued fragmentation of some wood buried within the stream bed. Other potential sources include any instream primary production from mosses and/or periphyton, which would be minor in these shaded headwaters, or the release of buried FBOM during storms. Regardless of the source, these results reinforce the concept that it is extremely difficult, if not impossible, to disrupt inputs into a given ecosystem when that system is located “downhill” in the landscape from the donor system (e.g., Polis et al. 1997, Pace et al. 2004, Rubbo et al. 2006).

In sharp contrast to mixed substrate habitats, standing crops of organic matter on the moss-covered rock outcrop substrates exhibited fewer differences between the reference stream and treatment stream. Wood was the only category of benthic organic matter on the rock face substrate that showed any significant difference between streams and this was only during the SWR period when the reference stream exceeded that of the treatment stream. The moss-covered substrates are steep-gradient areas with little organic matter retention other than a limited amount of FPOM retained within the moss (Huryn and Wallace 1985). Undoubtedly the

interception of suspended FPOM by the moss on the shallow bedrock substrates ensures an ample food supply for the invertebrates because animals on bedrocks showed few significant responses to manipulation (Wallace et al. 1997b, 1999).

Export of organic and inorganic particulate matter and relationships with discharge

As predicted, leaf export decreased each year with ongoing litter exclusion and did not increase until the litter addition years (Fig. 1A and B). Unexpectedly, export of leaves of all three detrital qualities remained significantly lower in the treatment stream than in the reference stream due to consumption by the large abundances of shredders in the treatment stream (J. B. Wallace, S. Eggert, J. Meyer, and J. Webster, *unpublished data*). We expected that wood export per unit discharge would decline throughout the litter exclusion period and be nominal during the wood removal periods; however, we did not foresee the large amount of buried wood in the treatment stream that surfaced following storms. As evident from the comparisons of annual export versus maximum discharge, the manipulations changed the export response of the treatment stream to increased discharge particularly for leaf export and FIP export. The response of FPOM export per unit maximum discharge during the LE, SWR, and LWR manipulations was especially difficult to predict (Fig. 1A) due to the reduction in FBOM generation and standing crop associated with the loss of quickly broken down leaves. We attribute the year one increase in FPOM export per unit maximum discharge in the treatment stream to reduced retention associated with leaf exclusion and wood removal as well as a slow decline in FBOM standing crops. FPOM export declined significantly in the treatment stream with the addition of PVC as retention structure, as well as during the slow leaf addition period where the presence of longer breakdown leaf species served to retain more FBOM. As expected the mixed breakdown leaf species added during the MLA period resulted in export levels more similar to pre-treatment levels (Fig. 1B). These results not only indicate that leaf litter of varying qualities, small wood, and large wood are all important in the retention of FPOM, but the quality of detrital inputs as sources of

FBOM all increase the complexity of organic matter dynamics in these headwater streams.

Gravel and FIP export were also strongly related to the presence or absence of organic matter in the stream bottom, particularly the presence of small wood which we did not anticipate (prediction four). Fine inorganic export per unit maximum discharge increased significantly in the treatment stream during the SWR period. Following the pulse of sediment export during the LE and SWR periods, there was little readily transportable inorganic material remaining on and within the stream bed of the treatment stream and FIP export declined. In another large-scale (175-m reach) debris dam removal, Bilby (1981) reported a 72% loss in fine sediments stored behind debris dams that were collected in the ponding basin below the dam removal reach. The remaining inorganic substrate in our treatment stream consisted primarily of coarse sediments (pebbles and cobbles), which were no longer embedded in fine sediments, a result also noted by Díez et al. (2000) in their wood removal manipulation. As expected, FIP export declined during the leaf addition periods with the fast breakdown leaves having the least retentive capacity compared to the addition of slow and mixed leaf species (Fig. 1B).

Cumulative export

Cumulative FPOM export was greater from the treatment stream during the first 18 years of the study, primarily as a result of greater discharge from the treatment stream which drains a slightly larger catchment than does the reference stream. Long-term exclusion of organic matter inputs, combined with wood removal, produced a cumulative shift in total FPOM export by the 19th year of the study with cumulative export in the reference stream exceeding that of the treatment stream, despite higher discharge in the treatment stream during every year of the study. This is undoubtedly attributable to declining availability of FPOM per unit stream bed for transport in the treatment stream. The decline in FPOM availability in the treatment stream was especially noticeable during the LE, SWR, and LWR periods. These time periods correlate strongly with the reduction of shredder invertebrate production, which is a large source of FPOM

through detrital breakdown of CPOM (e.g., Wallace et al. 1982).

Cumulative FIP export, unlike that of cumulative FPOM export, was greater from the treatment stream than the reference stream throughout pretreatment and all subsequent years. In fact, throughout the first 12 years of study, FIP export from the treatment stream always exceeded that of the reference stream, as shown by the increasing trajectory of total export in the treatment stream. However, there was a very large increase in cumulative inorganic export following SWR; thereafter, there was a decline in the slope of cumulative export from the treatment stream which tended to resemble that of the reference stream. We attribute this to the large pulse of FIP export occurring after small wood removal which depleted the readily transportable inorganic material from the stream bed.

Relationship between standing crop and export

The ratio of average annual organic matter export/average annual standing crop was lowest for total CPOM, which indicates that the streams are highly retentive of CPOM inputs (prediction five). Previous studies in these and nearby catchments have documented the high retention of CPOM and slow downstream movement of even small diameter twigs and leaves in these streams (Webster et al. 1994, Wallace et al. 1995). The much higher ratios of FPOM export/standing crop suggests much higher turnover rates for FPOM than for CPOM. Furthermore, standing crop and export values, without even considering respiration losses, dictate that there must be continued replenishment of the FPOM resource. Deposition, storage, and resuspension of FPOM is well documented from larger second-order reaches of streams (Newbold et al. 2005) and turnover lengths of FPOM increase in larger downstream reaches (Webster et al. 1999, Minshall et al. 2000). Our results suggest FPOM turnover may be greater than commonly expected in these highly retentive headwater streams.

Importance of allochthonous subsidies on abiotic ecosystem processes in headwater streams

Allochthonous subsidies of varying quantity and quality from a donor system can strongly influence food web dynamics and metabolism of the recipient system (e.g., Polis et al. 1997,

Richardson et al. 2010, Marcarelli et al. 2011) as demonstrated in streams (e.g., Nakano et al. 1999, Wallace et al. 1999), container habitats (e.g., Murrell et al. 2011), caves (e.g., Huntsman et al. 2011, Schneider et al. 2011), and oceanic islands (e.g., Polis and Hurd 1996). Inputs of terrestrial detritus can also regulate key ecosystem processes such as nutrient retention (Webster et al. 2001) and DOC export (Meyer et al. 1998) in small streams. By conducting this detritus manipulation in distinct stages and multiple years per treatment, (i.e., reductions in leaf litter, small wood, large wood followed by the addition of PVC retention structures and leaves of varying detrital complexity), we were able to show that the quantity and quality of allochthonous subsidies can also strongly impact additional abiotic aspects of ecosystems (i.e., the physical structure of the stream channel as well as the transport dynamics of inorganic particles). This approach demonstrated that leaf and wood subsidies can affect more than just stream energetics, and helped resolve differences in allochthonous organic matter function, particularly that of small versus large wood in streams and the functional complexity of leaf detritus.

Much attention to the role of wood in streams has been given to large wood, (e.g., Gregory et al. 2003, Wipfli et al. 2007). Previous wood removal manipulations in headwater streams in which all wood (large and small) was removed, resulted in immediate declines in standing crops of CBOM (Bilby and Likens 1980, Angermeier and Karr 1984) and increased export of inorganic particles (Bilby 1981, Díez et al. 2000), FPOM, and CPOM (Bilby and Likens 1980). In Virginia, a five-fold increase in the number of debris dams in a low-gradient headwater stream resulted in 6–11× increases in organic matter storage (Smock et al. 1989). Other studies have demonstrated that small wood alone can be important for the retention of leaves in headwater streams (Trotter 1990, Pretty and Dobson 2004). Results from the exclusion/removal phase of our study demonstrated that leaves and small wood are both extremely important in retention (Fig. 1A). Due to the immediate loss of CBOM (primarily leaf) standing crop during the first three years and ongoing litter exclusion, we were unable to document declines in CBOM standing crop associated with small wood removal alone.

However FBOM standing crop declined significantly during the initial three years of litter exclusion and declined even more following the removal of small wood (prediction two). Total inorganic export, gravel export, FPOM export, as well as FIP concentrations unexpectedly peaked in the treatment stream during SWR. Although representing only 32% of the total wood standing crop in the treatment stream, these results make a strong case for small wood being much more important in retention in headwater streams than previously thought.

Many of the trends in export and storage were reversed during the five-year addition phase of this experiment (Fig. 1B). However most trends never reached levels observed during the pre-treatment period. The addition of artificial retention structures reduced gravel and CPOM export, and to a lesser extent FIP exports. Results from the leaf addition manipulations showed that the quality and functional diversity of the detritus resource in a donor-based ecosystem regulates ecosystem structure and function because the complexity of detritus controls its persistence and availability to retain particles within a reach. Leaf standing crops in the treatment stream were more similar to those in the reference stream during the mixed leaf addition year than during the fast and slow leaf addition years. The largest reductions in total and fine inorganic export and total CPOM export occurred with the addition of mixed breakdown leaf species. The incomplete recovery of FBOM standing crops in the treatment stream after five years of leaf additions suggests that restoration of the storage capacity of these systems may require many years. From an ecosystem restoration perspective our results suggest that: (1) structural components, preferably organic in form, should be added to stream beds to provide the physical complexity needed to slow the export of inorganic and large organic materials to downstream reaches, (2) a mixture of riparian tree species should be planted during restoration efforts to provide the functional complexity needed (i.e., fast, medium, and slow breakdown rates) to allow persistence and availability of allochthonous resources throughout the restoration period, and (3) complete recovery of some ecosystem processes may take years.

CONCLUSIONS

The 13-yr organic matter manipulation of this forested, headwater stream demonstrated that these streams are highly dependent on the surrounding forest for their organic matter as litter exclusion reduced leaf standing crop by 100% within one year. Wood export declined much more slowly than leaf material. Although representing a smaller proportion of total wood standing crop than LW, removal of SW resulted in much greater increases in export of FPOM and coarse and fine inorganics, indicating SW has a more important role in retention than previously realized. FPOM standing crops declined continually during the LE, SWR, and LWR periods and increased only when PVC retention structures or leaves were added. After five years of adding leaves of various detrital qualities, FPOM standing crops still had not reached pre-treatment levels, suggesting that it would take many years of leaf inputs plus the reintroduction of wood before the organic matter pools would recover in this stream. These results imply that anthropogenic disturbances that alter the quantity or quality of allochthonous subsidies to headwater streams can change the physical structure of the system enough to significantly reduce organic carbon retention which ultimately can alter stream food webs. Additionally, sufficient inputs of diverse forms of organic matter (i.e., functional mixtures of leaf species and wood) can ameliorate export of inorganic sediments to downstream reaches, benefitting not only the proximate portions of the ecosystem but also downstream reaches of the watershed.

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SUPPLEMENTAL MATERIAL

APPENDIX A

Table A1. Average annual standing crop (g AFDM/m²) of fine and coarse benthic organic matter (FBOM and CBOM, respectively) in the mixed substrate and moss-covered bedrock substrate of reference and treatment watersheds during treatment periods.

Site	Treatment period	Total CBOM	Leaves	Wood	Moss	FBOM
Mixed substrate						
Reference	PreTmt-1	1181	184	757	0	679
	PreTmt-2	935	115	625	0	1483
	LE-1	1287	276	734	0	1307
	LE-2	1244	291	556	0	1688
	LE-3	1575	244	809	0	1631
	SWR-1	1443	225	845	0	1518
	SWR-2	1039	99	639	0	1216
	LWR-1	1038	147	585	0	1053
	LWR-2	1159	266	582	0	836
	PVC	1183	277	625	0	767
	FLA-1	1371	234	696	0	818
	FLA-2	2129	476	1154	0	1206
	SLA-1	1814	306	1261	0	1106
	SLA-2	1728	242	1254	0	824
	MLA-1	1172	164	805	0	911
	Treatment	PreTmt-1	808	147	461	0
PreTmt-2		602	76	426	0	1054
LE-1		900	26	755	0	779
LE-2		432	1	343	0	579
LE-3		615	1	505	0	521
SWR-1		163	0	122	0	460
SWR-2		143	0	100	0	397
LWR-1		68	0	41	0	358
LWR-2		108	0	72	0	299
PVC		69	0	31	0	309
FLA-1		284	89	75	0	316
FLA-2		379	178	96	0	544
SLA-1		203	111	34	0	421
SLA-2		250	155	29	0	380
MLA-1		255	183	20	0	587

Table A1. Continued.

Site	Treatment period	Total CBOM	Leaves	Wood	Moss	FBOM	
Bedrock substrate							
Reference	PreTmt-1	51	31	21	19	40	
	PreTmt-2	34	6	11	9	19	
	LE-1	46	20	16	7	20	
	LE-2	19	1	2	13	14	
	LE-3	41	17	7	12	26	
	SWR-1	16	4	3	6	19	
	SWR-2	17	2	1	9	28	
	LWR-1	39	25	2	4	26	
	LWR-2	21	12	1	3	16	
	PVC	15	5	3	3	24	
	FLA-1	50	24	10	4	19	
	FLA-2	38	25	6	5	20	
	SLA-1	36	21	6	7	25	
	SLA-2	16	4	1	8	24	
	MLA-1	28	7	5	13	35	
	Treatment	PreTmt-1	43	13	9	12	26
		PreTmt-2	31	4	2	15	19
		LE-1	9	0	1	7	15
		LE-2	18	0	4	9	12
		LE-3	26	1	7	13	22
SWR-1		15	0	3	10	22	
SWR-2		13	0	1	8	16	
LWR-1		17	0	1	12	22	
LWR-2		34	1	2	15	17	
PVC		23	0	2	10	25	
FLA-1		20	6	5	2	16	
FLA-2		34	11	4	13	22	
SLA-1		17	6	1	9	21	
SLA-2		18	6	1	9	20	
MLA-1		24	5	1	16	26	

Notes: Treatment periods were pretreatment years 1 and 2 (PreTmt-1, PreTmt-2); litter exclusion years 1 through 3 (LE-1, LE-2, LE-3); small wood removal years 1 and 2 (SWR-1, SWR-2); large wood removal years 1 and 2 (LWR-1, LWR-2); PVC addition year (PVC); fast leaf addition years 1 and 2 (FLA-1, FLA-2); slow leaf addition years 1 and 2 (SLA-1, SLA-2); mixed leaf addition year (MLA-1). Annual averages based on September to August data of each treatment year.

APPENDIX B

Table B1. Total annual export (kg AFDM) of inorganic particulates, and fine benthic organic matter and coarse particulate organic matter (FBOM and CPOM, respectively) from reference and treatment streams during treatment periods.

Site	Treatment period	Total inorganic	Gravel	Fine inorganic	Total CPOM	Leaves	Wood	FBOM	
Reference	PreTmt-1	14.75	0.51	14.20	0.31	0.14	0.13	21.54	
	PreTmt-2	43.56	5.54	37.58	6.33	3.55	2.24	42.13	
	PreTmt-3	24.73	2.08	22.52	1.45	0.79	0.45	30.69	
	PreTmt-4	67.35	3.84	63.18	2.90	1.10	1.32	67.86	
	PreTmt-5	242.74	10.88	231.44	7.34	2.70	3.86	155.70	
	PreTmt-6	106.73	3.13	103.52	1.52	0.61	0.64	80.23	
	PreTmt-7	73.57	4.35	69.17	0.94	0.27	0.43	57.35	
	PreTmt-8	233.80	39.85	193.40	11.73	2.50	8.16	144.96	
	LE-1	244.03	9.28	234.35	7.27	1.99	3.71	133.00	
	LE-2	214.69	8.02	206.34	5.73	1.83	2.54	127.66	
	LE-3	276.18	14.32	261.53	7.43	2.27	4.15	174.14	
	SWR-1	495.21	28.63	465.84	8.06	2.03	4.85	255.58	
	SWR-2	552.51	59.41	492.34	17.62	3.43	10.13	238.64	
	LWR-1	140.60	3.60	136.65	3.76	2.48	0.99	90.18	
	LWR-2	113.71	9.07	104.43	3.71	1.27	0.92	71.58	
	PVC	95.67	11.04	84.52	2.03	0.96	0.47	59.95	
	FLA-1	79.23	2.08	77.08	0.97	0.38	0.34	64.07	
	FLA-2	333.30	6.63	325.95	6.94	2.28	3.53	220.22	
	SLA-1	244.13	8.73	235.09	4.42	2.17	1.65	142.18	
	SLA-2	562.41	33.46	528.35	15.07	4.33	7.80	259.50	
	MLA-1	280.62	8.37	272.06	3.33	1.61	1.28	131.34	
	Treatment	PreTmt-1	81.50	4.63	76.62	1.75	0.84	0.68	41.02
		PreTmt-2	162.37	15.95	145.09	11.91	5.64	5.40	73.75
		PreTmt-3	136.91	16.67	119.99	4.10	2.51	1.06	46.37
		PreTmt-4	258.85	11.10	245.05	9.49	4.82	3.82	111.51
		PreTmt-5	598.76	33.14	564.93	12.05	5.13	5.47	197.02
		PreTmt-6	327.19	8.46	318.55	3.01	1.32	1.27	127.77
		PreTmt-7	239.40	31.50	207.40	7.50	2.76	3.05	90.37
PreTmt-8		601.07	122.88	484.01	21.39	8.34	8.34	158.52	
LE-1		877.74	72.35	804.20	17.52	0.79	13.58	208.58	
LE-2		577.06	104.67	471.93	12.35	0.18	7.54	143.63	
LE-3		661.71	112.33	544.58	19.69	0.45	14.97	140.39	
SWR-1		1122.97	188.77	933.65	16.43	0.13	10.18	189.74	
SWR-2		1165.75	137.35	1028.15	7.85	0.04	3.52	195.23	
LWR-1		261.32	38.35	222.91	2.30	0.02	0.80	68.82	
LWR-2		203.58	55.04	148.40	4.52	0.02	0.67	49.27	
PVC		151.45	15.73	135.70	0.75	0.02	0.17	41.49	
FLA-1		103.22	4.97	98.20	0.97	0.24	0.13	53.32	
FLA-2		470.38	38.08	432.11	3.88	0.66	1.24	164.72	
SLA-1		213.59	20.06	193.35	3.91	1.09	0.67	72.21	
SLA-2		577.30	88.49	488.68	4.22	0.48	0.91	147.11	
MLA-1		157.78	15.00	142.74	1.03	0.29	0.23	64.16	

Notes: Treatment periods were as in Appendix A. Total export based on September 1 to August 31 data of each treatment year.