

Nutrient enrichment alters storage and fluxes of detritus in a headwater stream ecosystem

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Abstract. Responses of detrital pathways to nutrients may differ fundamentally from pathways involving living plants: basal carbon resources can potentially decrease rather than increase with nutrient enrichment. Despite the potential for nutrients to accelerate heterotrophic processes and fluxes of detritus, few studies have examined detritus–nutrient dynamics at whole-ecosystem scales. We quantified organic matter (OM) budgets over three consecutive years in two detritus-based Appalachian (USA) streams. After the first year, we began enriching one stream with low-level nitrogen and phosphorus inputs. Subsequent effects of nutrients on outputs of different OM compartments were determined using randomized intervention analysis. Nutrient addition did not affect dissolved or coarse particulate OM export but had dramatic effects on fine particulate OM (FPOM) export at all discharges relative to the reference stream. After two years of enrichment, FPOM export was 340% higher in the treatment stream but had decreased by 36% in the reference stream relative to pretreatment export. Ecosystem respiration, the dominant carbon output in these systems, also increased in the treatment stream relative to the reference, but these changes were smaller in magnitude than those in FPOM export. Nutrient enrichment accelerated rates of OM processing, transformation, and export, potentially altering food-web dynamics and ecosystem stability in the long term. The results of our large-scale manipulation of a detrital ecosystem parallel those from analogous studies of soils, in which net loss of organic carbon has often been shown to result from experimental nutrient addition at the plot scale. Streams are useful model systems in which to test the effects of nutrients on ecosystem-scale detrital dynamics because they allow both the tracking of OM conversion along longitudinal continua and the integrated measurement of fluxes of transformed material through downstream sites.

Key words: *Appalachian (USA) streams; Coweeta Hydrologic Laboratory, North Carolina, USA; detritus; ecological stoichiometry; nitrogen; nutrient limitation; organic matter budget; phosphorus; soils; streams.*

INTRODUCTION

Nutrient availability plays a central role in the dynamics of ecological systems (Søballe and Kimmel 1987, Vitousek and Howarth 1991). The strong linkages that exist between nutrient and carbon cycles influence plant productivity, decomposer activity, consumer

nutrition, and energy flow through food webs, from the level of cells to whole ecosystems (Sterner and Elser 2002, Cebrian 2004, Cebrian and Lartigue 2004). These linked biogeochemical cycles have long been of basic theoretical interest (Redfield 1958, Reiners 1986). From a more applied perspective, anthropogenic increases in nutrient mobilization have had dramatic and global effects on community- and ecosystem-level processes, reinforcing the need for improved understanding of the effects of nutrient enrichment in a diversity of ecosystem types (Vitousek et al. 1997, Falkowski et al. 2000, Elser et al. 2007).

Most knowledge regarding ecological impacts of nutrient enrichment is based on empirical and theoretical studies of material pathways dominated by living plants, in which biomass typically shows at least short-term increases as supplies of a limiting nutrient are elevated (Elser et al. 2007). However, the ultimate fate of an overwhelming proportion of plant production is to enter the detrital pool (Moore et al. 2004). For example, <20% of plant biomass produced in terrestrial ecosys-

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tems is consumed by herbivores, with the remainder being either consumed or stored as detritus (Cebrian 1999). From an ecosystem perspective, the response of donor-controlled detrital pathways to nutrients can be expected to differ fundamentally from those based on living plants because basal resources are typically expected to decrease rather than increase with nutrient enrichment (Rosemond et al. 2001). By reducing nutrient limitation of heterotrophic organisms, nutrient addition can result in loss of carbon along detritus-based pathways, a pattern observed at plot-level scales in soils, forest litter, and aquatic detritus in many different biomes (e.g., Robinson and Gessner 2000, Sundareshwar et al. 2003, Mack et al. 2004, Cleveland and Townsend 2006).

Examining effects of nutrients on detrital resources at larger (i.e., ecosystem-level) scales requires measurement of inputs, storage, and outputs of all major organic matter (OM) compartments, usually over relatively long time scales. Tracking the input and fate of OM represents a considerable challenge across the variety of detrital pathways observed in terrestrial and aquatic ecosystems (e.g., headwater streams vs. soils). However, the processes and biota involved in comminution of coarse OM to fine particulate and dissolved OM and eventual conversion to CO_2 are qualitatively similar among different ecosystems, differing only in temporal and spatial scale. Streams for example can be viewed as "stretched soil cores," in which the tight cycling of carbon and nutrients typical of soils is elongated into a spiral by longitudinal transport (Wagener et al. 1998). From this perspective, stream ecosystems provide a useful model system in which to test the effects of nutrient addition on ecosystem-level detrital dynamics. Pervasive unidirectional flow accelerates the decomposition of coarse OM inputs, while physically elongating this process (i.e., conversion to dissolved and particulate OM and CO_2) along an easily accessed linear continuum. Moreover, focused transport along discrete channels facilitates the integrated measurement of fluxes of exported material through downstream weir sites.

Here, we use stream ecosystems to examine the effects of nutrient enrichment on detrital dynamics at relatively large temporal and spatial scales. We conducted a two-year, low-level nutrient (nitrogen [N] and phosphorus [P]) addition to a detritus-based headwater stream ecosystem at Coweeta Hydrologic Laboratory, North Carolina, USA. We used comprehensive OM budgets and detailed analyses of exports for the manipulated and a reference ecosystem to examine the relative sensitivity of different OM pools and outputs (exports and community respiration) to nutrient enrichment.

METHODS

Site description

The two streams used for this study are first-order, and drain adjacent catchments (C53 and C54) at the Coweeta Hydrologic Laboratory (CHL) Long Term

Ecological Research site, Macon County, North Carolina, USA, a 2185-ha forested basin located in the Blue Ridge physiographic province of the southern Appalachian Mountains (Swank and Crossley 1988). Our study used whole reaches (headwater seep to weir) as experimental units. Reach lengths were 145 m for C53 and 260 m for C54. The two streams have very similar physical and chemical characteristics (i.e., watershed area, slope, elevation, discharge, temperature, pH; see Lughart and Wallace 1992), but have differed since July 2000 in concentrations of dissolved N and P as a result of our experimental nutrient enrichment of C54 (see *Experimental nutrient addition*, below). Ambient concentrations of inorganic N and P in these streams are very low ($[\text{NO}_3^- + \text{NO}_2^-]$ -N average, 17 $\mu\text{g/L}$, range, 4–40 $\mu\text{g/L}$; NH_4^+ -N average, 10 $\mu\text{g/L}$, range, below detection to 30 $\mu\text{g/L}$; soluble reactive phosphorus [SRP] average, 4 $\mu\text{g/L}$, range, below detection to 22 $\mu\text{g/L}$). Vegetation is dominated by mixed hardwoods (primarily oak, maple, and poplar), with a dense understory of *Rhododendron maximum* L. that shades the streams throughout the year. Headwater streams at CHL are extremely heterotrophic; allochthonous inputs of detritus provide >90% of the organic matter (OM) available for secondary production (Cross et al. 2007).

Experimental nutrient addition

Our study consisted of a one-year pretreatment period (July 1999–June 2000) followed by a two-year experimental nutrient addition (July 2000–June 2002) to C54. Beginning 11 July 2000, N (NH_4NO_3) and P (K_2HPO_4 and KH_2PO_4) were dripped continuously into C54 to elevate concentrations of dissolved inorganic N and P approximately 6- to 15-fold along the lower 190-m, permanently flowing reach (see Gulis et al. [2004] for a full description of the flow-proportional, longitudinal dripper system). Discharge of both streams was monitored continually at an H-flume (Cuffney and Wallace 1988) at the base of each reach. Concentrations of $[\text{NO}_3^- + \text{NO}_2^-]$ -N, NH_4 -N, and soluble reactive phosphorus (SRP) were measured every two weeks at the weir of the reference stream and at several locations along the treatment stream (APHA 1998). Water temperature was monitored every 30 min in both streams with Optic StowAway temperature probes (Onset Computer Corporation, Bourne, Massachusetts, USA).

OM inputs

Litterfall was estimated using 5–8 direct-fall traps (0.25 m^2) placed along each stream. Lateral litter inputs were estimated using 5–8 lateral traps ($0.5 \text{ m long} \times 0.2 \text{ m high} \times 0.3 \text{ m deep}$). Litter from both trap types was collected monthly, except during periods of peak litterfall (October–December) when collections were made approximately every two weeks. Organic material entering traps was separated into leaf litter and non-leaf particulate OM (e.g., wood, flowers, bryophytes), oven-dried (60°C for 5 d), weighed, ashed (500°C for 1–4

h), and reweighed to determine ash-free dry mass (AFDM). Direct and lateral inputs were converted to grams of AFDM per square meter of bankful stream area. Comparison with long-term data indicated that nonrepresentative trap placement had resulted in overestimation of lateral inputs into the treatment stream over the three years of the study. Lateral input data for the treatment stream were subsequently corrected using paired data from the eight original traps and seven new traps (16 additional collections between March 2006 and February 2007).

Dissolved organic carbon (DOC) concentrations in groundwater were estimated with grab samples collected from each headwater seep at ~2-week intervals and analyzed using a Shimadzu TOC-5000A total organic-carbon analyzer (Shimadzu Scientific Instruments, Columbia, Maryland, USA). Dissolved OM (DOM) concentration was assumed to be DOC concentration \times 2 (Webster and Meyer 1997). Total DOM input was calculated as the product of the mean seep concentration at the start and end of each two-week interval and total discharge during the interval. Net primary production (NPP) by periphyton was estimated using monthly chlorophyll *a* standing crops on ceramic tiles (Greenwood and Rosemond 2005) and an empirically derived ratio of chlorophyll *a* standing crop to NPP rate obtained from Coweeta streams (Hains 1981). NPP on bedrock habitats (i.e., by mosses) was assumed to be 10.9 times that of periphyton (Hains 1981). Areal gross primary production (GPP) was calculated as $\text{NPP} \times 2$ (Webster and Meyer 1997), weighted by the proportions of mixed (i.e., cobble, gravel, and sand) substrate (for periphyton GPP) and bedrock outcrop (for moss GPP) in each stream. Throughfall (channel interception of precipitation-derived DOM) was assumed to be 16 g AFDM \cdot m $^{-2}$ \cdot yr $^{-1}$ (Meyer and Tate 1983). Inputs that were based on assumptions (i.e., GPP, DOM throughfall) were a relatively small proportion of total inputs (<4% in the reference stream, <12% in the treatment stream) and thus these assumptions are unlikely to have a critical effect on the annual budgets.

Benthic OM storage

Samples of stored OM were collected separately from mixed substrate and bedrock-outcrop habitats on a monthly basis. Mixed-substrate samples were collected at four random locations in each stream with a stovepipe core sampler (400 cm 2); all material was removed to a depth of ~15 cm. Bedrock samples were taken at three randomly determined locations in each stream by brushing and scraping moss and associated particles from a known area (15 \times 15 cm) into a Hess sampler net (250- μ m mesh size) pressed flush against the bedrock. Benthic samples were processed according to Lugthart and Wallace (1992). Briefly, coarse particulate OM (CPOM; >1 mm) was sorted into leaf and non-leaf material, dried (60°C), weighed, ashed (500°C), and reweighed to quantify AFDM. Fine particulate OM

(FPOM; <1 mm) was subsampled, filtered onto pre-ashed, pre-weighed glass-fiber filters (Gelman A/E), and AFDM was quantified as above. Areal estimates of OM storage were habitat-weighted as above.

OM outputs

Attempts to use whole-stream metabolism methods for measuring ecosystem respiration were unsuccessful due to high reaeration rates in these exceptionally shallow, high-gradient streams (P. J. Mulholland, *unpublished data*). Whole-stream respiration was consequently estimated by summing compartment-specific rates. We assumed that autotrophic respiration was $\text{GPP} \times 0.5$ (Webster and Meyer 1997). Heterotrophic respiration was estimated using the combined products of mean monthly benthic storage and mass-specific respiration rates measured at a representative range of temperatures for each of the three dominant storage pools: leaf litter, wood (=non-leaf CPOM), and FPOM. In all cases, replicated samples were incubated for ~30 min in chambers (~30-mL volume with a mechanical stirrer) at ambient stream temperature. Oxygen uptake rates were measured with YSI 5100 dissolved-oxygen meters (YSI Corporation, Yellow Springs, Ohio, USA). Leaf-litter respiration rates were measured monthly between June 1999 and July 2002; monthly rates were summed to calculate annual respiration for each budget year. Wood respiration rates were determined four times between November 2004 and August 2005 (Gulis et al. 2008) and FPOM respiration rates were measured on 18 dates between June 2005 and June 2006 (A. D. Rosemond and C. J. Tant, *unpublished data*). Respiration rates for wood and FPOM were obtained during continuation of the nutrient addition but after the 1999–2002 period considered in this paper. However, differences in dissolved-nutrient concentrations and leaf-litter respiration rates between the reference and treatment stream did not differ greatly between the 2000–2002 and 2004–2006 periods (A. D. Rosemond and K. Suberkropp, *unpublished data*). Consequently, we believe that wood and FPOM respiration rates measured in the treatment stream in 2004–2006 are a satisfactory approximation of the 1999–2002 rates. We regressed wood and FPOM respiration rates against incubation temperature and used the resulting relationships and mean monthly stream temperatures to estimate in situ respiration rates for these two compartments. Respiration rates in chambers would overestimate in situ respiration because most OM is buried and likely to be respired at rates well below those measured under well-oxygenated conditions. We therefore assumed that 80% of the OM (i.e., that below the top 3 cm) respired at half the rate of OM measured in chambers (based on decreases in microbial biomass with sediment depth in similar streams; Findlay et al. 2002).

Total CPOM outputs were measured in each stream using a coarse collecting trap (4-mm steel mesh) installed above the weir in each stream (Wallace et al. 1995).

Material in the trap was collected at ~2-week intervals and quantified as for litter storage above. FPOM outputs (<4 mm) were sampled continuously in each stream with a Coshcocton proportional subsampler that allowed independent measures of discharge and FPOM export, as well as the incorporation of FPOM export during storms (Cuffney and Wallace 1988; see Plate 1). FPOM outputs were quantified at ~2-week intervals. DOM outputs were estimated by collecting grab samples at each flume at ~2-week intervals and analyzing as above. DOM concentrations at the start and end of each 2-week interval were averaged and multiplied by total interval discharge to estimate total DOM export. Storm concentrations were rarely sampled so we may have underestimated total DOM export (Meyer and Tate 1983).

Statistical analyses

OM input, storage and output data were used to construct annual OM budgets (July–June) for each of the three years in each stream. We used randomized intervention analysis (RIA; Carpenter et al. 1989) to test null hypotheses of no change in export variables in the treatment stream relative to the reference stream following initiation of nutrient addition. Time-series data were visually examined to determine the direction (positive or negative) of the response. Data were $\log(x + 1)$ -transformed to meet assumptions of normality and homogeneity of variance. Some dates were missing from the time series (e.g., because of missing samples). These dates were excluded from RIA, while appropriate long-term means were used for missing dates in the compilation of the budgets. To examine interactions between nutrient enrichment and magnitude of FPOM export during storms, we plotted FPOM export (g AFDM) against cumulative water export (L) for each ~2-week sampling interval. Significant differences among budget years in the slopes and intercepts of these relationships were tested using analysis of covariance (ANCOVA) with water export as the covariate. ANCOVAs were run separately for each stream (and without the interaction term) after preliminary analyses revealed that slopes differed between streams but did not differ among years within streams. Significant differences in intercept among years were followed by Tukey honestly significant difference (hsd) tests. Data were log-transformed prior to ANCOVA to meet assumptions of normality and homogeneity of variance.

RESULTS

The experimental nutrient addition elevated background concentrations of nutrients by 6–15 times in the treatment stream (C54): $[\text{NO}_3^- + \text{NO}_2^-]\text{-N}$ (mean, 309 $\mu\text{g/L}$; range, 11–1711 $\mu\text{g/L}$), $\text{NH}_4^+\text{-N}$ (mean, 106 $\mu\text{g/L}$; range, 6–566 $\mu\text{g/L}$), and SRP (mean, 51 $\mu\text{g/L}$; range, below detection to 268 $\mu\text{g/L}$). Annual mean discharge during the three years of the study ranged between 0.20 and 0.46 L/s in the reference stream and between 0.38

and 0.62 L/s in the treatment stream. Such low discharges constitute drought conditions based on mean discharge data for the two streams during four years (1985–1988) that included the wettest and driest years in a 55-yr precipitation record (reference: 0.71 L/s, treatment: 1.1 L/s; Wallace et al. 1991). Water temperature ranged from 1° to 19°C during the study and did not differ between the two streams.

Although similar in geomorphology, catchment size and mean discharge, the organic matter (OM) budgets of the two streams differed in some respects during the pretreatment period. First, the reference stream had greater FPOM export (Fig. 1), despite slightly lower mean discharge (possibly as a result of a higher proportion of total discharge as storm flow in this stream; J. B. Wallace, *unpublished data*). Higher export of FPOM from the reference stream may explain the second difference between the two streams: the reference stream had much lower FPOM storage than the treatment stream. Consequently, estimates of total heterotrophic respiration rates were higher in the treatment stream during the pretreatment period because of a higher contribution from the FPOM compartment.

In the reference stream, inputs and outputs of OM were similar among years. OM inputs were relatively constant in the reference stream over the three years, except for non-leaf particulate OM, which was affected by variable wood inputs (Fig. 1). Inputs from in-stream primary production and of DOM from the seep were consistently low. Similarly, in-stream OM storage and respiration rates differed little among the three years, except for a slight increase in non-leaf storage (Fig. 1). Leaf-litter storage declined by only 6% over the three years. Outputs of FPOM from the reference stream declined by 36% over the three years, from 565 g AFDM/m² to 360 g AFDM/m² (Fig. 1), presumably as a function of low discharge during this drought period. DOM export from the reference stream was variable over the three-year period (i.e., 12–26% of total organic matter output).

In the treatment stream, particulate OM inputs were lower over the three years than in the reference stream (Fig. 1). Inputs from in-stream primary production increased after nutrient addition started at the end of the first year, but still represented a minor part of the OM budget (i.e., <10% of total organic matter inputs; Fig. 1). Dissolved inputs were low and similar to those into the reference stream. Storage of non-leaf CPOM in the treatment stream remained relatively constant over the three years of the study, while storage of FPOM declined slightly. The largest change in storage was in leaf litter, which declined by 69% during the two years of nutrient addition compared to the first (pretreatment) year.

Nutrient addition had two major effects on OM export from the treatment stream. First, heterotrophic respiration increased substantially relative to the pre-

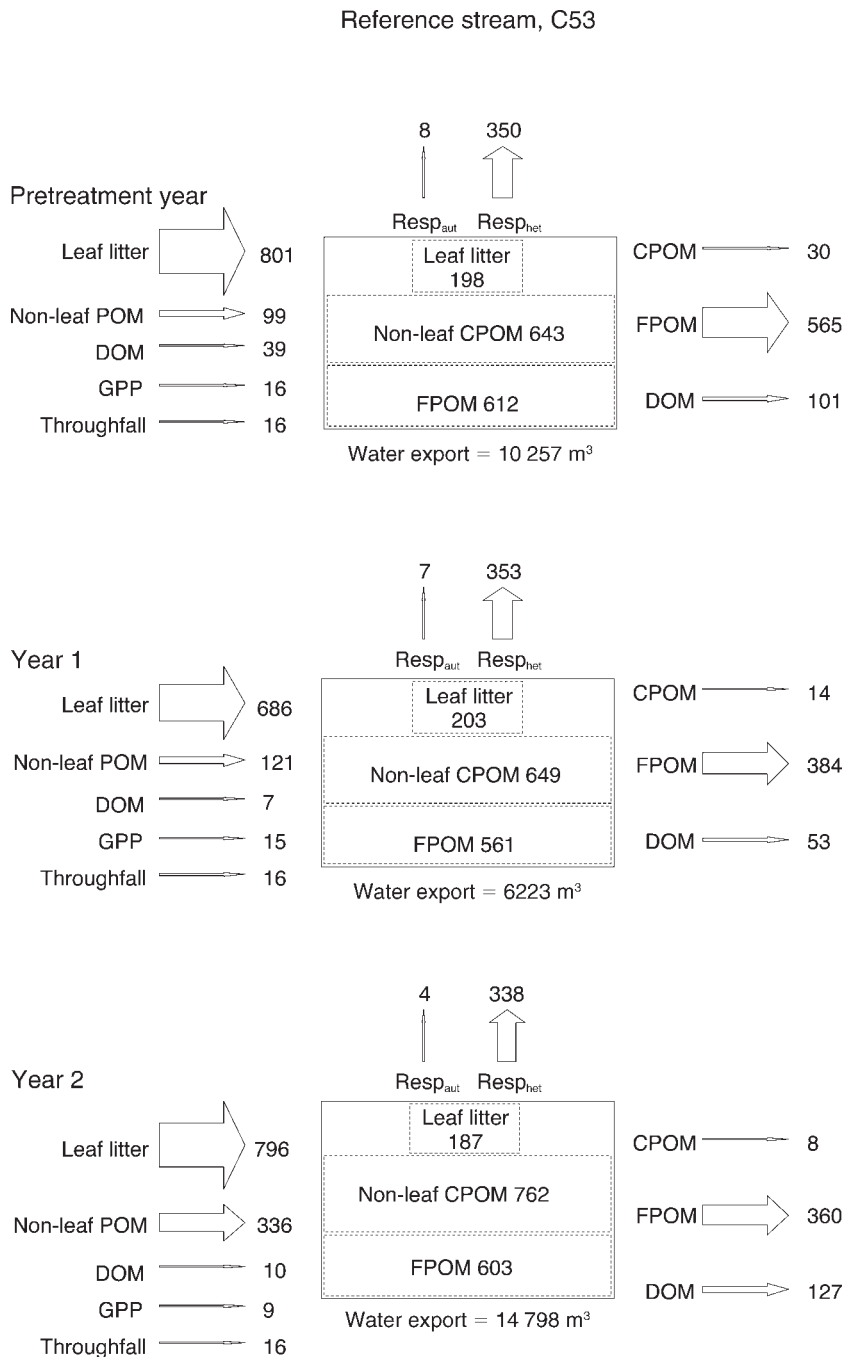


FIG. 1. Organic-matter budgets for the reference (C53) and treatment (C54) streams at the Coweeta Hydrologic Laboratory, North Carolina, USA, during the pretreatment year (July 1999–June 2000) and years 1 and 2 of nutrient enrichment (July 2000–June 2002, shaded boxes in C54). Inputs and outputs (arrows) are in grams of ash-free dry mass per square meter per year ($\text{g AFDM}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), and mean storage pools (boxes) are in $\text{g AFDM}/\text{m}^2$. Key to abbreviations: CPOM, coarse particulate organic matter; FPOM, fine particulate organic matter; DOM, dissolved organic matter; GPP, gross primary production; Resp_{aut} , autotrophic respiration; Resp_{net} , heterotrophic respiration.

treatment year ($746 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$), to $1063 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ and $955 \text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in Years 1 and 2 of the nutrient addition, respectively (Fig. 1). Changes in areal heterotrophic respiration over time were influenced both by declines in storage of OM (Fig. 1) and increases in compart-

specific respiration rates (Fig. 2). Second, total export of FPOM increased dramatically following nutrient addition (randomized intervention analysis [RIA], $P < 0.0001$), due to increased suspended FPOM concentration (RIA, $P < 0.0001$; Fig. 3a). Annual FPOM export

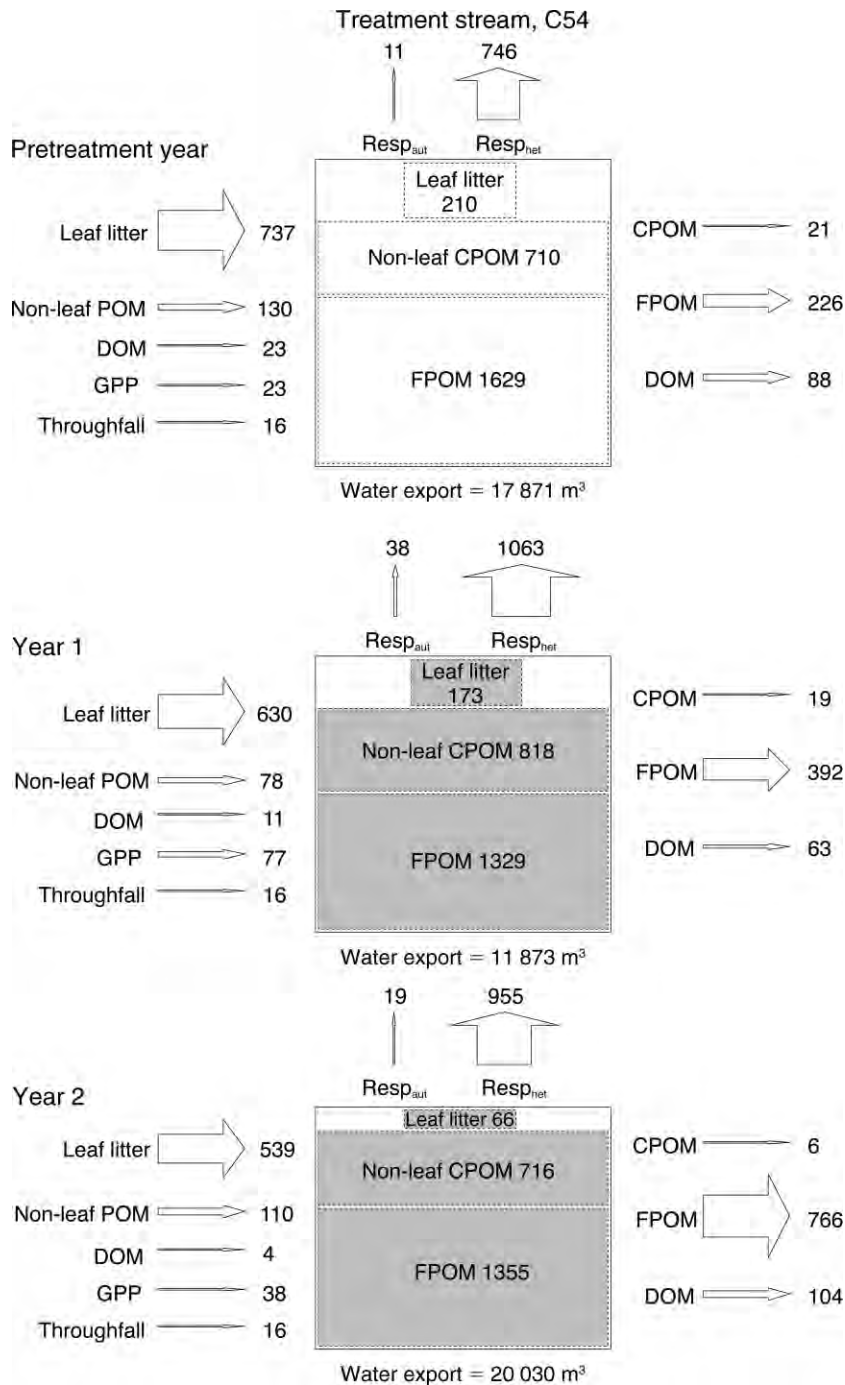


FIG. 1. Continued.

per unit area increased by 1.7 times and 3.4 times in the first and second year of nutrient addition, respectively (Fig. 1). This several-fold increase occurred during a period in which FPOM export from the reference stream declined due to drought conditions. These changes caused a reversal of the pretreatment difference in FPOM export between the two streams (i.e., the treatment stream began exporting more FPOM than

the reference stream; Fig. 3b) and contributed to substantial annual deficits of OM in the treatment stream's OM budget relative to the reference stream. The balance of OM inputs and outputs in the treatment stream revealed a net loss of OM (-1143 g AFDM/m^2) during the second year of nutrient addition, while the same calculations revealed a net accrual of OM in the reference stream during the same year ($+330 \text{ g}$

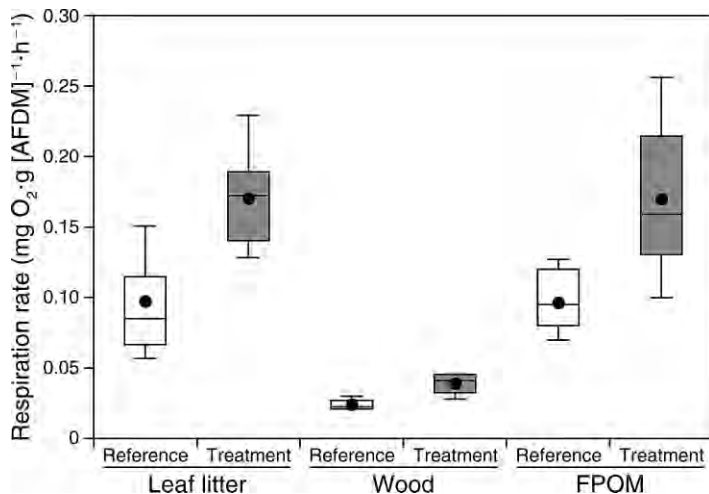


FIG. 2. Box plots of mass-specific respiration rates of the three major organic-matter storage pools in the reference and treatment streams. The top and bottom horizontal lines and the line through the middle of the box correspond to the 75th, 25th, and 50th (median) percentiles, respectively; the whiskers extend from the 10th percentile to the 90th percentile; and the solid circle represents the arithmetic mean. Data for leaf litter were collected between June 1999 and July 2002 (reference) and between August 2000 and July 2002 (treatment). Data for wood were collected between November 2004 and August 2005 (reference and treatment). Data for fine particulate organic matter (FPOM) were collected between June 2005 and June 2006 (reference and treatment). See *Methods: OM outputs* for a description of how these rates were used to estimate annual whole-ecosystem heterotrophic respiration.

AFDM/m²). Export of CPOM (>4 mm) and DOM, both relatively small fractions of total export, showed no significant change with nutrient addition (RIA, $P = 0.25$ and 0.22 , respectively).

Slopes of the relationship between water export and FPOM export differed significantly between streams ($P = 0.002$), but did not differ among years for each stream ($P > 0.75$ for both streams; Fig. 4). After removal of the interaction term in the ANCOVA, intercepts of the relationship in the reference stream were significantly different among years ($P = 0.009$); the intercept for Year 2 was significantly lower than the intercepts for the pretreatment year and Year 1 of the nutrient manipulation ($P < 0.05$, Tukey hsd test; Fig. 4a). Intercepts of the relationship between water export and FPOM export in the treatment stream were significantly different among years ($P < 0.0001$); the intercepts for Years 1 and 2 of the nutrient manipulation were successively higher than the intercept for the pretreatment year. Both of these year-to-year increases were significant ($P < 0.05$, Tukey hsd test; Fig. 4b).

DISCUSSION

The results of our two-year N + P addition showed that low-level nutrient enrichment of a detritus-based ecosystem led to faster processing of CPOM (coarse particulate organic matter) to FPOM (fine particulate organic matter) and CO₂. Much of the FPOM produced was subsequently exported from the system, resulting in greatly increased rates of carbon loss. This increased rate of carbon loss occurred despite drought conditions under which carbon accrued in the reference ecosystem. FPOM export and demands for respiration during the second year of nutrient enrichment of the treatment stream exceeded annual OM inputs by >1000 g AFDM (ash-free dry mass)/m². Such large annual deficits in OM suggest an important role for long-term storage in explaining our results. Specifically, the increases in FPOM export we observed could only have resulted

from increased processing of buried CPOM or increased mobilization of buried FPOM (or both), in addition to the production of FPOM from recent inputs of OM. However, changes in measured storage of OM in the treatment stream did not reflect the reductions expected from such large annual deficits. Although all components of our budgets were subject to some measurement

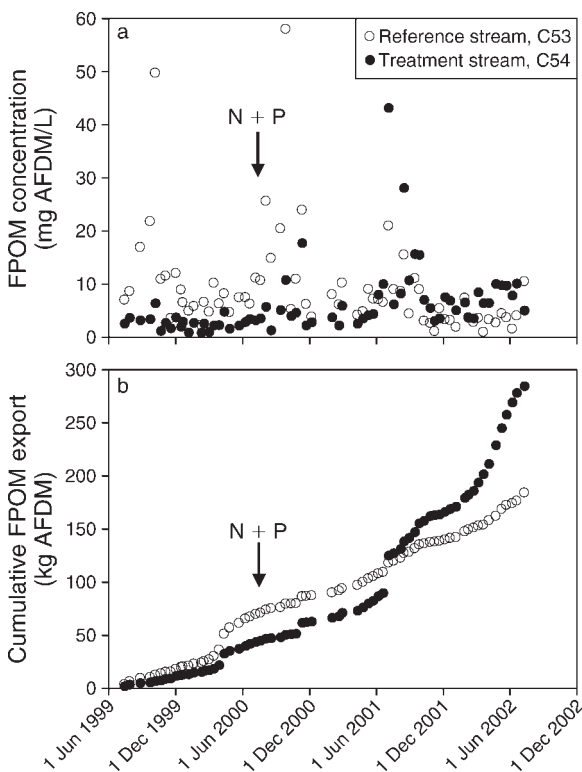


FIG. 3. (a) Concentration of suspended fine particulate organic matter (FPOM) and (b) cumulative FPOM export in the reference and treatment streams, July 1999–June 2002. An arrow indicates the start of nutrient addition to the treatment stream (C54).

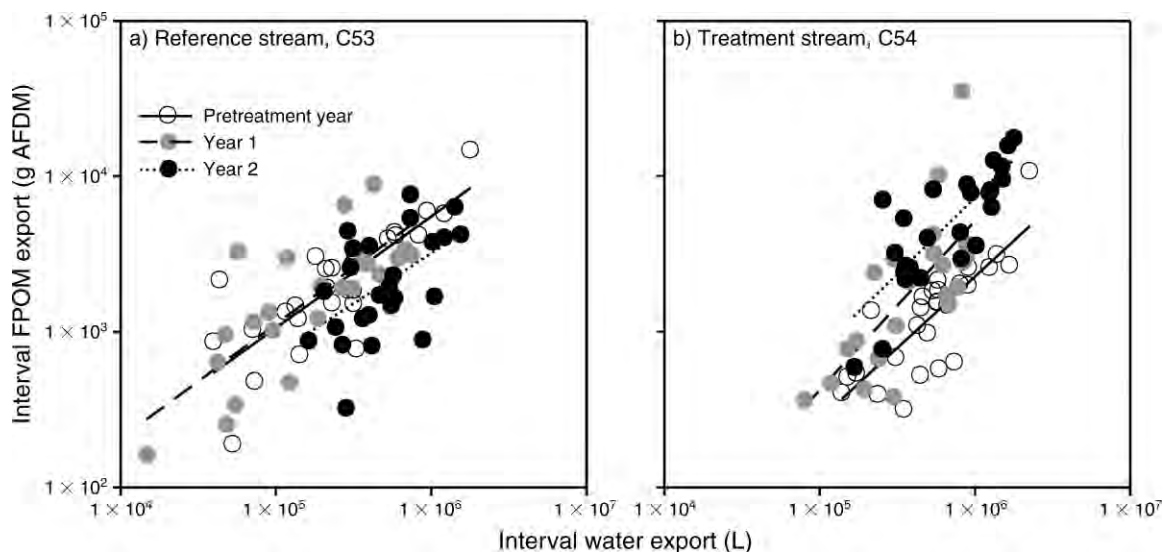


FIG. 4. Relationships between fine particulate organic matter (FPOM) export and water export during sampling intervals (~ 14 d) for each budget-year in (a) the reference stream, C53, and (b) the treatment stream, C54.

error, the core samples used to estimate storage most likely underestimated the amount of buried OM (i.e., below 15 cm depth) in our study streams. Deeply buried stores of detritus are therefore the most likely source of the large increases in FPOM export that we observed in the treatment stream.

The potential for mobilization of buried carbon by nutrient enrichment highlights the parallels between our results and the responses to nutrient enrichment observed in many terrestrial (soil and litter) systems. Losses of OM from litter layers and soils as a result of experimental nutrient enrichment have been observed at plot-levels in tropical (e.g., Cleveland and Townsend 2006), temperate (e.g., Pregitzer et al. 2004,) and arctic ecosystems (e.g., Mack et al. 2004). Specific mechanisms of OM loss vary among terrestrial studies. For example, the OM pool most sensitive to nutrient enrichment ranges from litter layers (e.g., Cleveland et al. 2006) to deeply buried carbon that is hundreds of years old (e.g., Nowinski et al. 2007). Although net loss of OM from soils is a common consequence of experimental nutrient enrichment, some studies have shown neutral or negative effects of nutrients on litter or soil OM processing (e.g., Neff et al. 2002, Hobbie 2008). The variability in nutrient effects observed in terrestrial studies is still poorly understood, but it likely reflects the great diversity in substrate quality found in soil OM, with associated potential for nutrient-induced inhibition of enzyme activity or formation of decay-resistant compounds (Bradford et al. 2008, Hobbie 2008). For example, N addition to alpine meadow plots accelerated processing of light soil OM fractions, while stabilizing soil OM compounds in heavy, mineral-associated fractions with much longer turnover times (Neff et al. 2002). Total OM pools in headwater streams likely lack

the latter type of more recalcitrant OM (the “passive” pool sensu Trumbore 1997), being dominated by a low diversity of relatively labile (“fast-cycling”; Trumbore 1997) OM compartments composed of plant material in various states of degradation, flocculated particles, and microbial biomass. Hence, heterotrophic processes in headwater streams may be more likely to respond positively to nutrient addition than those in many soils.

Our results show that rates of conversion of total CPOM (recent plus buried) to FPOM and subsequent FPOM transport were strongly controlled by ambient nutrient concentrations at our study site. Two years of low-level N + P addition changed the magnitude of FPOM export from the treatment stream relative to the reference stream. Increases in FPOM export from the treatment stream occurred across the entire range in stream discharge, despite three years of drought conditions and the consequently reduced potential for transport. Parallel studies in the reference and treatment streams showed a strong positive effect of nutrient enrichment on detrital processing rates and associated microbial respiration (Gulis and Suberkropp 2003, Gulis et al. 2004, Greenwood et al. 2007) and bacterial, fungal, and invertebrate production (Cross et al. 2006, Gulis et al. 2008; K. Suberkropp, *unpublished data*), driven by reduced stoichiometric constraints on consumer metabolism and growth (Cross et al. 2003, 2007). It therefore appears likely that the higher rates of respiration and OM export that we observed in the treatment stream were driven largely by increased activity of a previously nutrient-limited heterotrophic community.

The important role of consumers in explaining our results is supported by previous research at our study site. Small forest streams at Coweeta (North Carolina, USA) are extremely retentive of CPOM, their primary



PLATE 1. Field apparatus for independent measurement of stream discharge and export of fine particulate organic matter (FPOM) from the reference stream (C53) at Coweeta Hydrologic Laboratory, North Carolina, USA. Discharge is measured by a calibrated bubble flow-meter in the H-flume. A flow-proportional sample of streamwater exiting the flume is captured by the hollow blade (4-mm aperture) of a Coshocton wheel sampler (see inset). The continuous sample flows to a series of three settlement barrels (main photo). Export of FPOM to the barrels was quantified every ~14 d in this study and subsequently corrected for settlement efficiency and proportion captured. The coarse particulate organic matter trap (4-mm mesh) is immediately upstream of the flume. An identical system was used at the terminus of the treatment stream (C54). Photo credits: S. L. Eggert (main photo) and Deanna Connors (inset).

OM source. CPOM exports from the reference and treatment streams are typically <2.5% of CPOM inputs and <4% of total OM export (Cuffney et al. 1990, Wallace et al. 1995). Particulate OM export is consequently dominated by suspended FPOM (Wallace et al. 1991). Although peak FPOM export coincides with storms, manipulations of invertebrate biomass (using insecticide) have showed that the role of invertebrate feeding activity (especially by shredding detritivores) is at least as important as discharge in controlling the magnitude of FPOM export from these headwater stream ecosystems (Cuffney and Wallace 1989, Wallace et al. 1991). Invertebrates are therefore a key component of CPOM processing at the ecosystem scale, typically consuming up to a quarter of the leaf litter entering these small streams (Cuffney et al. 1990, Cross et al. 2007). Consumption of CPOM by invertebrates is intimately associated with colonization and conditioning by fungi and bacteria and it is this microbial community that

must carry out the balance of biological processing of CPOM to FPOM (Cummins 1974).

Although the elevated rate of FPOM export was driven by increases in both invertebrate and microbial production, the relative importance of these two groups likely differed. Consumption of leaf litter by invertebrates increased to 35% of inputs in the treatment stream during the second year of nutrient addition (compared to 12% in the reference stream; Cross et al. 2007). Assuming 5% assimilation efficiency of CPOM (excluding microbial biomass; Cross et al. 2007), this consumption resulted in fecal FPOM production of 179 g AFDM/m² in the treatment stream relative to the reference stream (88 g AFDM/m²). This difference in fecal FPOM production accounts for only 22% of the difference in FPOM export between the two streams for that year. The majority of the increase in FPOM export observed in the treatment stream can therefore be attributed to elevated processing by the microbial

community (particularly fungi; K. Suberkropp, *unpublished data*), as well as other factors such as sloughing of microbial biomass (including extracellular products), physical flocculation, and reduced physical retention of FPOM due to lower CPOM storage (Short and Ward 1981).

The results of our large-scale nutrient addition support ecological theory that predicts that detritus-based ecosystems should respond to elevated nutrients in a fundamentally different way than systems that are net autotrophic and based on living plant material (Polis and Strong 1996, Rosemond et al. 2001). Donor-controlled systems such as soils, forested headwater streams and caves contain assemblages dominated by heterotrophic organisms that consume, rather than produce, OM. If these organisms are limited by nutrient availability, enrichment can accelerate the rate at which they process and mineralize OM, leading to increased community respiration and comminution of OM, with consequently reduced standing crop of OM and increased export of transportable OM (i.e., to downstream reaches of streams or deeper soil horizons). In contrast, systems containing a significant living-plant component typically respond to elevated nutrients by increasing primary production and plant biomass. Thus, more often than not, nutrient enrichment results in accumulation of OM in living-plant-based systems (Elser et al. 2007), rather than increased loss or export.

Headwater forest streams are classic examples of donor-controlled systems, supporting communities that rely on physical retentiveness for storage of pulsed, external resource inputs utilized for consumer growth (Cuffney et al. 1990). However, the storage capacity of ecosystems for OM is obviously limited. In fact, OM storage in wetted channels of headwater streams at Coweeta likely exceeds annual OM export by only 1.2 to 3.7 times (Cuffney and Wallace 1989; this study). Storage of deeply buried OM is undoubtedly difficult to quantify, even in the stream ecosystems we used in this study. However, during the course of our study, ratios of storage to export in the reference stream increased from 1.4 to 1.9, while almost halving (from 2.3 to 1.2) in the treatment stream. These divergent trends highlight the potential for long-term shifts in OM storage as a result of nutrient addition to detrital ecosystems. Accelerated loss rates of OM in response to nutrient addition, if maintained, could potentially lead to altered intra- and interannual availability of detritus and to related changes in the temporal stability that this resource confers to terrestrial and aquatic food webs and ecosystem processes (DeAngelis and Mulholland 2004, Moore et al. 2004).

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