

Nutrients stimulate leaf breakdown rates and detritivore biomass: bottom-up effects via heterotrophic pathways

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Abstract Most nutrient enrichment studies in aquatic systems have focused on autotrophic food webs in systems where primary producers dominate the resource base. We tested the heterotrophic response to long-term nutrient enrichment in a forested, headwater stream. Our study design consisted of 2 years of pre-treatment data in a reference and treatment stream and 2 years of continuous nitrogen (N) + phosphorus addition to the treatment stream. Studies were conducted with two leaf species that differed in initial C:N,

Rhododendron maximum (rhododendron) and *Acer rubrum* (red maple). We determined the effects of nutrient addition on detrital resources (leaf breakdown rates, litter C:N and microbial activity) and tested whether nutrient enrichment affected macroinvertebrate consumers via increased biomass. Leaf breakdown rates were ca. 1.5 and 3× faster during the first and second years of enrichment, respectively, in the treatment stream for both leaf types. Microbial respiration rates of both leaf types were 3× higher with enrichment, and macroinvertebrate biomass associated with leaves increased ca. 2–3× with enrichment. The mass of N in macroinvertebrate biomass relative to leaves tended to increase with enrichment up to 6× for red maple and up to 44× for rhododendron leaves. Lower quality (higher C:N) rhododendron leaves exhibited greater changes in leaf nutrient content and macroinvertebrate response to nutrient enrichment than red maple leaves, suggesting a unique response by different leaf species to nutrient enrichment. Nutrient concentrations used in this study were moderate and equivalent to those in streams draining watersheds with altered land use. Thus, our results suggest that similarly moderate levels of enrichment may affect detrital resource quality and subsequently lead to altered energy and nutrient flow in detrital food webs.

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Introduction

Anthropogenic nutrient enrichment can profoundly change aquatic food webs and ecosystem function

(Carpenter et al. 1998; Smith et al. 1999). Research examining effects of nutrient enrichment in aquatic systems has focused on autotrophic food webs. Algal productivity and biomass in lakes and streams commonly increase due to nutrient enrichment (Elser et al. 1990; Carpenter et al. 1998; Francoeur 2001), and long-term nutrient enrichment in autotroph-based systems can lead to effects on higher order consumers (Peterson et al. 1993; Slavik et al. 2004).

Nutrient enrichment effects on basal resources of detrital food webs are potentially very different from previously observed effects on autotrophs. Detritus is an important energy source in many ecosystems, particularly via subsidies from adjacent ecosystems (Polis et al. 1997; Vanni et al. 2004; Moore et al. 2004). For example, food webs in forested headwater streams are often dependent on allochthonous leaves and wood as their primary energy source (Vannote et al. 1980; Wallace et al. 1999). Nutrient enrichment can reduce, rather than increase carbon availability in detritus-based systems via microbially driven increased processing rates (Elwood et al. 1981; Meyer and Johnson 1983; Robinson and Gessner 2000). Likewise, studies in terrestrial systems have shown loss of soil detrital carbon as a microbially mediated response to long-term nutrient enrichment (Mack et al. 2004).

The effects of nutrient enrichment on higher trophic levels may also differ in heterotrophic versus autotrophic food webs. Consumer biomass in primary producer-based systems typically increases in response to nutrient enrichment when the edibility of primary producers remains high (Rosemond et al. 1993; Brett and Goldman 1997; Gratton and Denno 2003; Gruner 2004). Less is known regarding detritivore responses, but the potential for nutrients to affect consumer energetics via detrital pathways is great. Detritus is higher in carbon-to-nutrient ratios than primary producers (Cross et al. 2005a), and nutrient stimulation of microbial activity on detrital substrata is predicted to lower C:N and C:P. Heterotrophic microbial activity on detritus has been shown to increase in response to increased nutrient availability (Elwood et al. 1981; Suberkropp and Chauvet 1995; Ramirez et al. 2003). However, the fate of such increased microbial activity is not well understood. Microbially mediated increases in detrital quality may lead to increased carbon and nutrient flow to consumers. Alternately, increased microbial activity may promote carbon loss from systems via increased respiration and export of particulate carbon. Such losses may negatively affect consumers that depend on detrital food resources. Nutrient enrichment has resulted in increased abundance, growth rates and production of detritivores in some studies (Pearson and

Connolly 2000; Rosemond et al. 2001; Cross et al. 2005b), but not in others (Elwood et al. 1981; Meyer and Johnson 1983; Newbold et al. 1983). Such differential responses likely depend on the extent of system-specific microbial nutrient limitation and the transfer efficiency of nutrients and carbon to consumers.

The response of microbial assemblages to nutrient enrichment likely depends on characteristics of detrital substrata. Allochthonous detritus differs in many aspects of structure and chemistry (e.g., lignin, C:N ratios, Melillo et al. 1982; Gessner and Chauvet 1994) and can differ across leaf species or types of detritus (Findlay et al. 2002). Detrital N content can have greater effects on leaf breakdown and food quality to invertebrates than external N concentrations (Chadwick and Huryn 2003). However, detrital nutrient content can also determine the response of attached microbial assemblages to external nutrient concentrations. These responses can be greater on detrital substrata that have relatively lower nutrient content (Peterson et al. 1993; Stelzer et al. 2003; Gulis et al. 2004) possibly resulting from the shortage of substratum-available nutrients. Thus, we predict that responses to nutrient enrichment will be determined in part by characteristics of detritus such as nutrient content.

We determined heterotrophic responses to nutrient enrichment in a forested headwater stream, in one of the first long-term studies to do so (but see Chadwick and Huryn 2003). Our objectives were to determine the effects of a 2-year experimental whole-stream enrichment on leaf breakdown rates, litter C:N, microbial activity and macroinvertebrate biomass. To determine potentially disparate effects of nutrient enrichment on leaf types of different quality, we examined the response of two dominant leaf species, red maple (*Acer rubrum* L.; low C:N) and rhododendron (*Rhododendron maximum* L.; high C:N). We predicted that nutrient enrichment would stimulate microbial activity associated with leaves, leading to increased detrital quality, macroinvertebrate biomass and subsequent leaf breakdown rates. We also predicted that rhododendron would show a stronger response to water column enrichment relative to red maple leaves due to its lower nutrient content.

Materials and methods

Study site

Our study was conducted from December 1998 to July 2002 in two fishless streams located at the Coweeta Hydrologic Laboratory (CHL), a USDA Forest Service

research facility and Long-Term Ecological Research site located in the Blue Ridge Mountain physiographic province in the southern Appalachian Mountains (North Carolina, USA). Macroinvertebrates in headwater streams at CHL are known to derive >95% of their energy from detrital pathways (Wallace et al. 1999; Hall et al. 2000). Both the reference stream (Catchment 53) and the treatment stream (Catchment 54) drain catchments of similar size (ca. 5.5 ha), aspect and elevation (ca. 850 m), and have similar stream-water chemistry, discharge and physical characteristics (Greenwood and Rosemond 2005). Ambient nutrient concentrations were <30 $\mu\text{g/l}$ dissolved inorganic nitrogen (DIN) and <10 $\mu\text{g/l}$ soluble reactive phosphorus (SRP).

Nutrient enrichment

The treatment stream was continuously enriched with NH_4NO_3 and $\text{KH}_2\text{PO}_4 + \text{K}_2\text{HPO}_4$ (in a molar N:P ratio of 11:1 with a stream water target N:P of ca. 15:1) along the entire 150-m study reach for 2 years beginning 11 July 2000 (methods detailed in Greenwood and Rosemond 2005). Stream water nutrient concentrations were measured at least bimonthly from both streams throughout the study (details in Greenwood and Rosemond 2005).

Leaf breakdown and litter quality

Single species leaf packs containing either red maple or rhododendron leaves were deployed in the treatment and reference streams to determine breakdown rates. Leaf packs were made with plastic mesh pecan bags (22 \times 40 cm, 5-mm mesh) to allow access by stream invertebrates. Freshly abscised leaves were collected each year near the study streams, air-dried in the laboratory for several weeks and weighed into packs of 15 ± 0.25 g rhododendron or 5 ± 0.25 g red maple and placed into bags. Sets of 35 leaf packs per species per stream were deployed throughout the stream reach for a total of four seasons on 2 December 1998 and 14 December 1999 [for pre-treatment years 1 and 2 (PY1, PY2)], and on 7 December 2000 and 5 December 2001 [for enrichment years 1 and 2 (NY1, NY2)]. A new set of leaf packs was deployed each year. Between 3 and 6 rhododendron and 3 and 5 red maple leaf packs were collected at increasingly spaced intervals up to 400 days for rhododendron and 200 days for red maple (details on retrieval dates in Appendix S1). Leaf packs collected from the field were frozen for later processing.

Within 6 months of collection, material from thawed leaf packs was rinsed to remove foreign material from

the leaves. Leaf particles >4 mm were dried, weighed, and a sub-sample combusted at 500°C to determine remaining ash-free dry mass (AFDM). Leaf breakdown rates were determined using the negative exponential model (Petersen and Cummins 1974). Ball-milled material from dried leaves was analyzed for total C and total N by micro-Dumas combustion (NA1500 CHN Analyzer, Carlo Erba Strumentazione, Milan). Leaf packs collected with less than 5% of their original weight were not included in the calculation of breakdown rates or in C:N analyses. This is a common practice since data from these leaf packs can fluctuate greatly and lead to large variation in model fit for the whole time course (Chung et al. 1993).

Microbial activity

Microbial respiration rates were measured as oxygen uptake during the first four retrieval dates for rhododendron and first three retrieval dates for red maple during NY2 ($n=3$ for each date) from both streams. Measurements were limited to dates when leaf material was still intact enough to cut leaf disks. Within 1 h of leaf pack collection, ten disks were cut with an 18-mm diameter cork borer from leaf material in each pack. Disks were placed in stream water in a 29-ml glass chamber incubated in the stream in the dark. Oxygen concentrations were measured three times during the 20-min incubation with a YSI 5100 dissolved oxygen meter using a YSI 5010 self-stirring oxygen probe, which capped each chamber (Gulis and Suberkropp 2003). An incubation with only stream water served as a blank. Oxygen consumption was calculated by subtracting the slope of the regression of oxygen concentration over time of the stream water blank from the regression slope of the sample. Units were mg O_2 per leaf AFDM per hour. The AFDM from the leaf discs used for respiration was added back to leaf pack AFDM values for calculating breakdown rates. Unfortunately, pretreatment data were not collected for respiration, limiting our ability to attribute treatment effect to any changes we measured in respiration. However, similar respiration measurements were performed on naturally occurring leaves from both streams starting 1 year before enrichment and continued through the time period of our study (K. Suberkropp, unpublished data), allowing us to corroborate any trends in our results.

Macroinvertebrate response

Invertebrates were sorted from leaf material at the time leaf packs were processed for AFDM remaining.

Invertebrates were preserved in 7–8% formalin stained with phloxine-B to facilitate sorting. Macroinvertebrates were identified and biomass quantified for both leaf types from both streams on three dates spaced throughout the deployment for each of the 4 years (PY1: days 14, 70 and 169; PY2: days 14, 55 and 160; NY1: days 14, 55 and 170; NY2: days 14, 55 and 135). Insects were identified to the lowest taxonomic level practical, usually genus. Chironomidae were separated into Tanypodinae and non-Tanypodinae. Macroinvertebrates were measured to the nearest 0.5 mm to estimate biomass as AFDM using length–weight regressions (Benke et al. 1999). Functional feeding groups were designated based on Merritt and Cummins (1996) and trophic analyses of these taxa (Hall et al. 2000; Cross 2004).

Leaf and macroinvertebrate N content

The effect of nutrient enrichment on the relative amount of N contained in macroinvertebrate biomass versus leaf litter standing crop was quantified. The amount of N contained in the average biomass of macroinvertebrates for the second year of pretreatment and both years of enrichment (from the same three dates as macroinvertebrate community analysis) was calculated by assuming that, on average, macroinvertebrate biomass was 10% N, as determined from a study from the same streams ($n=100$; mean =10.02; SD=1.16; Cross et al. 2003). The amount of N in leaves was determined from the C:N value and dry weight of leaves from individual leaf packs.

Statistical analyses

Since only one reference and one experimental stream were used, this experiment was not strictly replicated, violating assumptions of inferential statistics (Hurlbert 1984). However, the catchment-level spatial scale of the experiment, in addition to the multiple years of data acquired, were essential for understanding ecosystem-level processes, and the paired-system experiment is considered an acceptable approach to detect the effects of experimental manipulations (Carpenter 1989). Also, in this study, the relative differences between the treatment and reference systems were known prior to our experimental manipulation, in some cases for data spanning 2 years, allowing us to use a before–after control–impact (BACI) type of analysis (Stewart-Oaten et al. 1986), which is appropriate for non-replicated studies. However, some variables were not amenable to BACI analysis due to a lack of pre-treatment data (see below). Appropriateness of para-

metric versus nonparametric tests was determined by testing the data for normality by fitting to a normal distribution model.

Breakdown rates were compared using BACI analysis where the difference (d) in breakdown rates between streams for each date was calculated, and then d was subjected to a two-way analysis of variance (ANOVA) with leaf species and time (pre-treatment vs. post-treatment) as the two factors. A significant time effect would indicate a treatment effect. Breakdown rates were also compared to nearly 20 years of previously determined breakdown rates of rhododendron and red maple leaves from our study streams as well as others at CHL. Comparisons of data from this study to 95% confidence intervals of the longer-term data allow us to compare our treatment effect to effects of large-scale climatic and spatial variation.

Macroinvertebrate biomass was expressed per leaf pack and per gram AFDM of leaf material remaining in the leaf pack. Macroinvertebrate biomass per leaf pack was considered a conservative normalization to examine nutrient response since leaf pack AFDM was predicted to decrease with nutrient enrichment, thus potentially resulting in greater relative consumer biomass. Macroinvertebrate biomass per g AFDM of leaf material remaining was considered an examination of the ability of leaf material to support higher macroinvertebrate biomass due to increased quality. Responses of both forms of macroinvertebrate biomass were examined in a BACI-type analysis where d in average biomass between streams for each date was calculated and then subjected to a Mann–Whitney U test (data did not fit a normal distribution model) to compare biomass before versus after enrichment.

For variables where BACI analysis was inappropriate because of ≤ 1 year of pre-treatment data, we compared 95% confidence intervals between streams to determine whether treatment effects were significant. The slopes and 95% confidence intervals of log leaf C:N versus time were compared between reference and enrichment conditions for each year individually. Means and 95% confidence intervals of respiration rates and macroinvertebrate N:leaf N were compared between streams to assess potential treatment effects.

To examine the potentially different response of the two leaf types of different quality, the magnitude of nutrient enrichment effects on rhododendron versus red maple leaves was examined by comparing responses of variables in the treatment stream relative to a reference condition for each leaf type during both years of enrichment. For breakdown rates and macroinvertebrate biomass, the values for the treatment stream in NY1 and NY2 were compared with average

pretreatment values from both streams. Average respiration rates in the treatment stream were compared to average rates in the control stream during NY2. Because of interannual variability, leaf C:N comparisons were made between slopes of the regression lines for both streams during each year of enrichment individually. Macroinvertebrate N:leaf N was also compared between streams individually for each year. Statistical tests were performed with Systat (Version 11, Systat Software Inc., Richmond, CA).

Results

Nutrient enrichment

The enrichment increased DIN ca. 13× to approximately 400 µg/l and SRP ca. 5× to approximately 45 µg/l in the treatment stream. The average stream water molar N:P ratio was 20:1, and stock solution was added at a molar N:P ratio of approximately 11:1, suggesting that there was relatively greater P uptake. P limitation was also detected in earlier nutrient uptake studies at CHL (Munn and Meyer 1990). The nutrient concentrations in the treatment stream were within the range of those found in streams regionally with different land use types (Scott et al. 2002). Nutrient concentrations in the reference stream remained consistent throughout the study (Greenwood and Rosemond 2005).

Leaf breakdown

Differences in breakdown rates were significantly greater between streams after enrichment vs. before enrichment (Fig. 1; $F_1=9.78$; $P=0.035$). There was no

significant effect on species ($F_1=0.25$; $P=0.65$) or the species–time interaction ($F_1=0.73$; $P=0.44$). By NY2, the number of days to 95% loss (an estimate of the ‘life span’ of leaves in the study stream) decreased over threefold in the treatment stream relative to the reference stream for both leaf types (Appendix S1). Also see Appendix S1 for annual plots of leaf breakdown. In a comparison of breakdown rates to 17 (rhododendron) and 18 (red maple) years of previously published data from CHL, both leaf types were within 1.5 standard deviations (SD) of the long-term average for leaf breakdown under reference conditions. With enrichment, rhododendron breakdown rates were ca. 3 and 9 SD higher than long-term averages and red maple breakdown rates were ca. 1.5 and 4.5 SD higher than long-term averages during NY1 and NY2, respectively (details in Appendix S2).

Litter quality

C:N of leaf material declined significantly through time for all years measured and for both leaf types, suggesting that microbial biomass on leaf material increased as decay of organic matter progressed ($P<0.0001$ for regressions of each line, Fig. 2). For rhododendron, 95% confidence intervals of the slopes of C:N versus time overlapped between streams during PY2 (Fig. 2a), but did not overlap between streams in NY1 (Fig. 2c) and NY2 (Fig. 2e), indicating relatively greater microbial biomass on leaf material in the treatment stream with nutrient addition. Results were similar for red maple with overlap of slope confidence intervals between streams during PY2 (Fig. 2b), but no overlap between streams for NY1 (Fig. 2d) and NY2 (Fig. 2f).

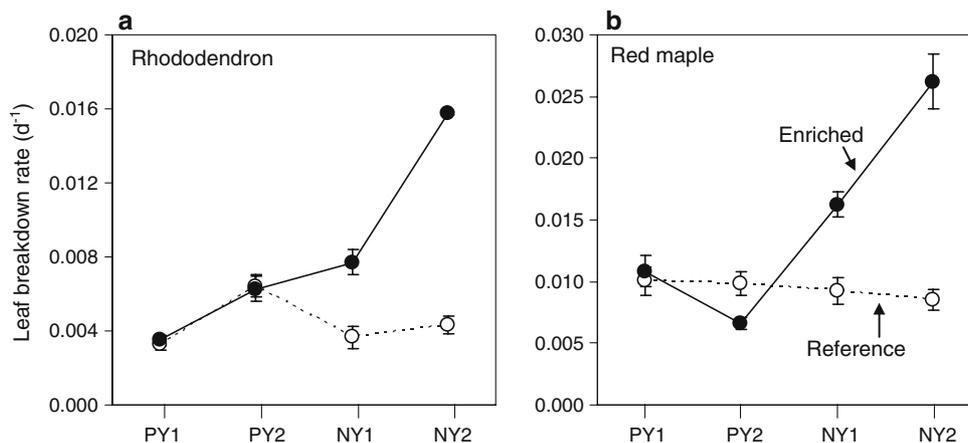


Fig. 1 Leaf breakdown rates (\pm SE) for **a** rhododendron (*Rhododendron maximum*) and **b** red maple (*Acer rubrum*) leaves during 2 years of pre-treatment (PY1, PY2) and 2 years of nutrient enrichment (NY1, NY2) in reference (open circle) and treatment

(filled circle) streams at the Coweeta Hydrologic Laboratory. Breakdown rates are calculated as the negative slope of \ln percent leaf AFDM remaining versus days in stream

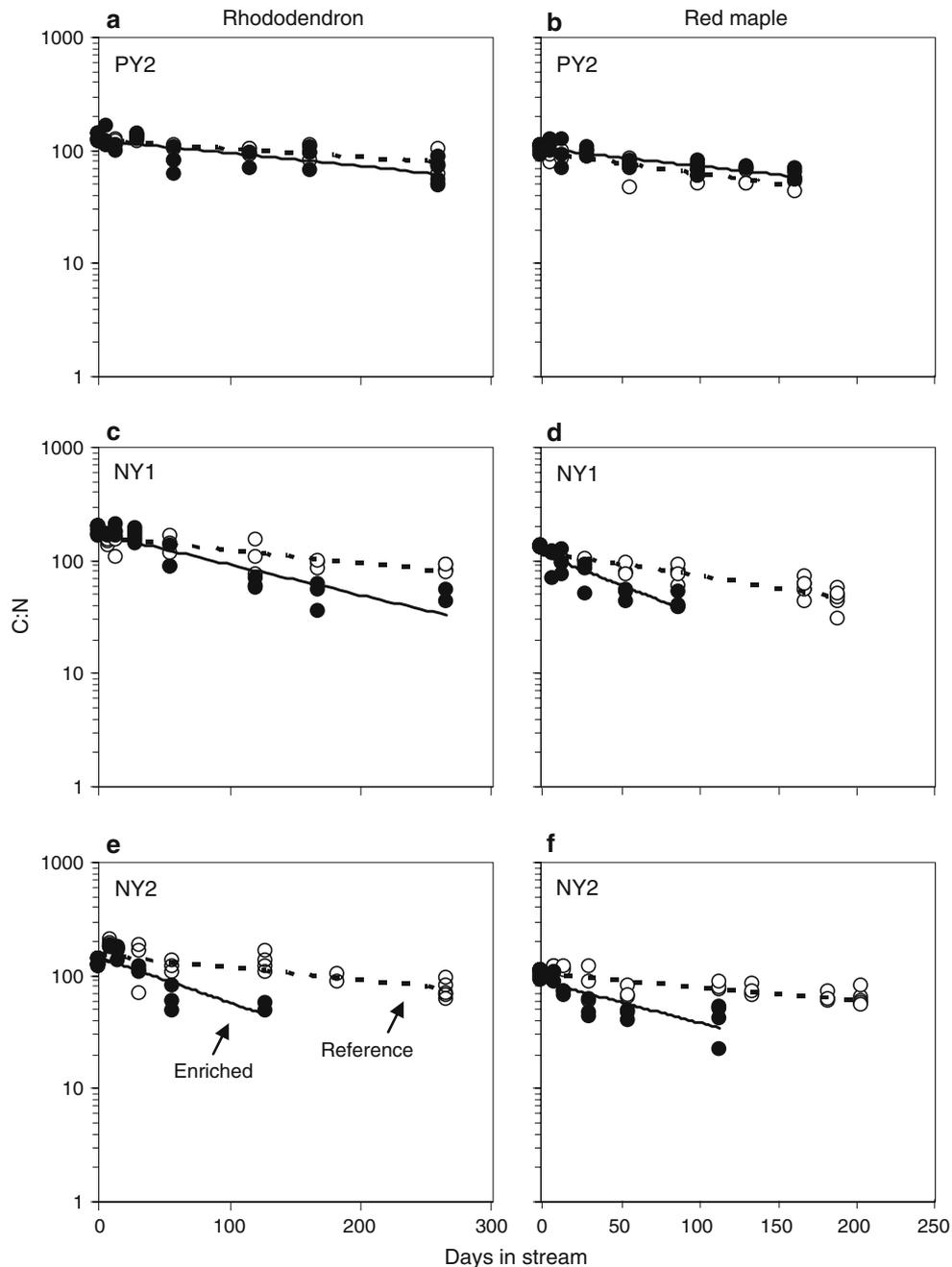


Fig. 2 Carbon-to-nitrogen ratio (C:N) of (**a, c, e**) rhododendron and (**b, d, f**) red maple leaves versus the number of days in the reference (*open circle*) and treatment (*filled circle*) streams. **a** PY2, reference slope = -0.001 (95% CI ± 0.001), treatment slope = -0.001 (± 0.001); **b** PY2, reference slope = -0.002 (± 0.001), treatment slope = -0.002 (± 0.001); **c** NY1, reference

slope = -0.001 (± 0.001), treatment slope = -0.003 (± 0.001); **d** NY1, reference slope = -0.002 (± 0.001), treatment slope = -0.006 (± 0.002); **e** NY2, reference slope = -0.001 (± 0.001), treatment slope = -0.004 (± 0.002); **f** NY2, reference slope = -0.001 (± 0.001), treatment slope = -0.004 (± 0.002)

Microbial activity

Respiration rates on rhododendron leaves were higher in the treatment stream relative to the reference stream, ($0.20 \text{ mg O}_2 \text{ mg leaf AFDM}^{-1} \text{ h}^{-1}$ vs. $0.06 \text{ mg O}_2 \text{ mg leaf AFDM}^{-1} \text{ h}^{-1}$) without overlap of

95% confidence intervals on the last three sampling dates (Fig. 3a). Respiration rates for red maple were also generally higher in the treatment stream ($0.44 \text{ mg O}_2 \text{ g leaf AFDM}^{-1} \text{ h}^{-1}$ vs. $0.15 \text{ mg O}_2 \text{ g leaf AFDM}^{-1} \text{ h}^{-1}$, Fig. 3b), but 95% confidence intervals were only separated clearly for the second date. With-

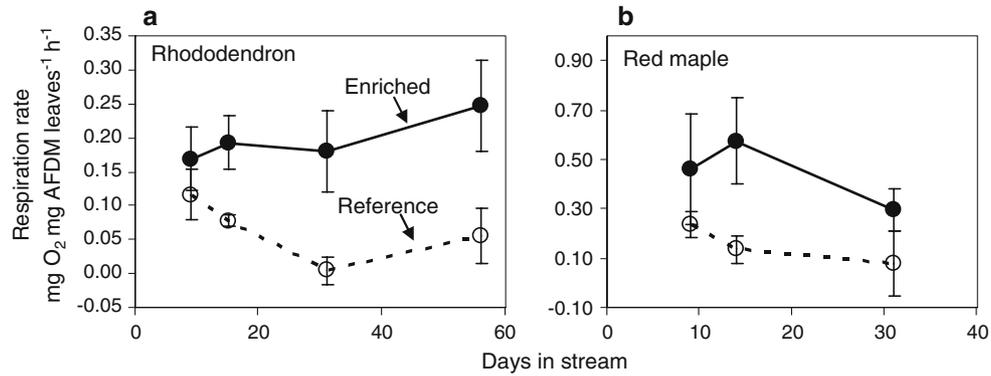


Fig. 3 Respiration rates [mg O₂ per mg ash free dry mass (AFDM) per hour, ±95% CI] from **a** rhododendron and **b** red maple leaf pack discs during the second year of enrichment (NY2) from the reference (*open circle*) and treatment (*filled circle*) streams

out pretreatment data, changes in respiration rates resulting from enrichment cannot be definitively shown. However, respiration rates from leaf species collected randomly in the treatment and reference streams were similar between streams prior to the experimental enrichment, but were ca. 2× higher in the treatment stream after enrichment (K. Suberkropp, unpublished data). These data integrate over variability due to leaf species and colonization time and show a similar trend to the differences in respiration we measured on single-species leaf packs between streams.

Macroinvertebrate response

Nutrient enrichment resulted in significant differences in mean biomass of macroinvertebrates between streams in rhododendron leaf packs when normalized either by leaf pack or AFDM remaining (Fig. 4a, c; Table 1). A similar pattern was also observed for average biomass of shredders (the biomass dominant) and total primary consumers (i.e., non-predators), although these differences were not statistically significant for biomass measured per leaf pack (Fig. 4a, c; Table 1). The difference in average biomass between streams of

Fig. 4 Average invertebrate biomass (±SE) of shredders (*solid bars*), gatherers (*dark grey bars*), filterers (*light grey bars*), and predators (*open bars*) in **(a, c)** rhododendron and **(b, d)** red maple leaf packs for reference and treatment streams during 2 years of pre-treatment (PY1, PY2) and 2 years of enrichment (NY1, NY2) as expressed as **(a, b)** mg per leaf pack and **(c, d)** mg per g leaf AFDM remaining. *Arrows* indicate start of nutrient enrichment

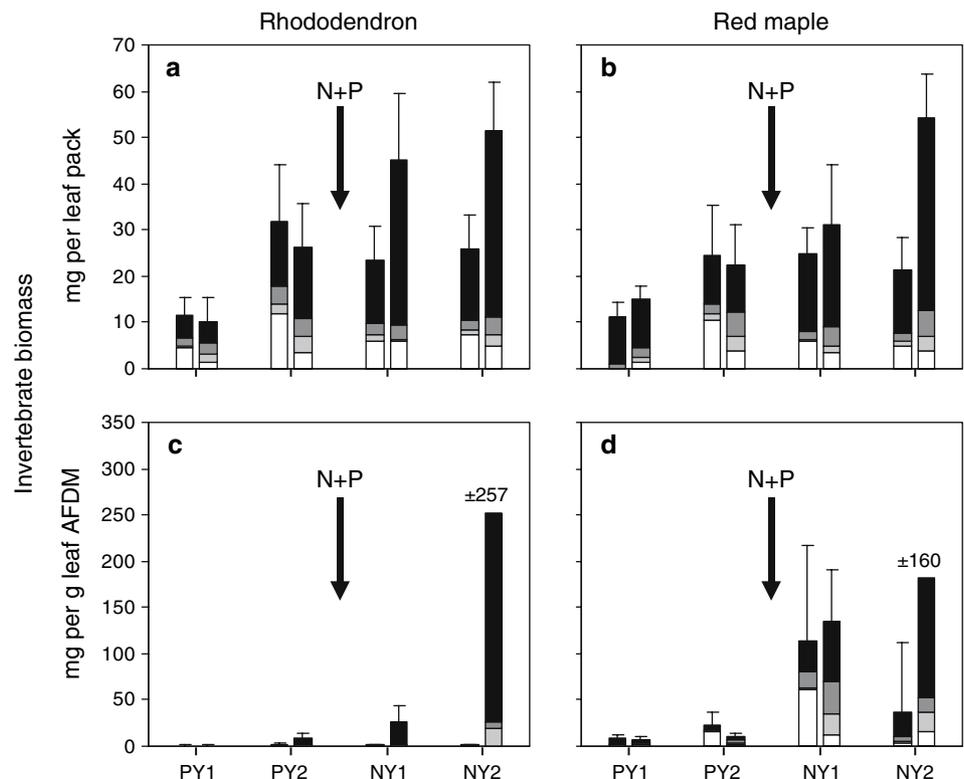


Table 1 Average difference (*d*) of invertebrate biomass between the reference and treatment streams with standard error (SE) and results of Mann–Whitney *U* test (*n*=12) on *d* to test for differences in *d* before versus after the start of nutrient enrichment

	Rhododendron			Red maple		
	Avg. <i>d</i> (SE)	<i>U</i>	<i>P</i>	Avg. <i>d</i> (SE)	<i>U</i>	<i>P</i>
Invertebrate biomass per leaf pack						
Total	9.9 (5.5)	31	0.037	55.3 (38.0)	23	0.42
Shredders	11.7 (5.0)	30	0.055	53.7 (37.6)	25	0.26
Gatherers	0.9 (0.8)	24	0.92	2.7 (1.0)	21	0.63
Filterers	0.7 (0.4)	9	0.15	1.4 (0.8)	21	0.63
Primary consumers	13.3 (5.0)	30	0.055	22.9 (14.9)	25	0.26
Predators	3.3 (1.5)	29	0.078	2.4 (2.6)	18	1.00
Invertebrate biomass per g leaf afdm remaining						
Total	75.3 (66.8)	31	0.037	30.6 (20.8)	28	0.11
Shredders	63.4 (55.6)	31	0.037	28.1 (14.4)	34	0.010
Gatherers	1.9 (1.6)	27	0.15	6.2 (3.3)	31	0.037
Filterers	4.9 (4.6)	17	0.87	9.2 (5.8)	26	0.20
Primary consumers	70.3 (61.8)	31	0.037	43.3 (20.2)	32	0.025
Predators	5.0 (5.0)	27	0.15	13.0 (13.5)	19	0.87

Tests were performed individually for both leaf types [rhododendron (*Rhododendron maximum*) and red maple (*Acer rubrum*)]. Biomass was measured as both per leaf pack and per g leaf AFDM remaining in leaf packs. “Primary consumers” = shredders + gatherers + filterers. *P* values in boldface are *P*<0.05, and all significant effects were positive

filterers and predators showed no significant changes after enrichment (Fig. 4a, c; Table 1).

There were similar, but less consistent effects of nutrients on the biomass of macroinvertebrates in red maple leaf packs. Macroinvertebrate biomass was significantly higher for shredders, gatherers and primary consumers after the enrichment in the treatment stream when normalized by AFDM (Fig. 4b, d; Table 1). However, biomass was not significantly differ-

ent between streams when measured per leaf pack (Fig. 4b, d; Table 1). Data on macroinvertebrate biomass response for individual dates for both leaf species are shown in Appendix S3.

Macroinvertebrate assemblages were similar between leaf types regarding distribution of functional feeding groups (Fig. 4). However, red maple supported more macroinvertebrate biomass per leaf mass compared to rhododendron (on average about 15× and 3× under reference and enriched conditions, respectively) (Fig. 4). See Appendix S4 for responses of individual taxa to nutrient enrichment.

Leaf and macroinvertebrate N content

The ratio of macroinvertebrate total N to leaf total N per leaf pack was similar between streams during PY2 (PY1 was not tested) for rhododendron (Fig. 5a) and red maple (Fig. 5b). During NY1 and NY2, ratios were on average higher in the treatment stream relative to the reference for both leaf types; however, there was not good separation of 95% confidence intervals (Fig. 5). Values were highest in the treatment stream during the second year of enrichment, but were also associated with high variability (Fig. 5).

Relative response of leaf species to nutrient enrichment

Characteristics of rhododendron and red maple leaves, and macroinvertebrates associated with them, were similarly affected by nutrient enrichment (Table 2). The response to nutrient enrichment was greater in NY2 than NY1 for nearly all variables, and by NY2, a relatively greater response to nutrients was observed for rhododendron than red maple for all variables

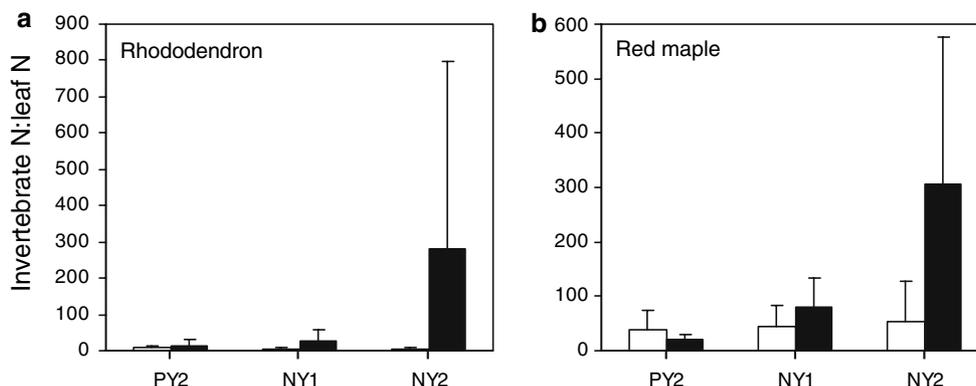


Fig. 5 Average ratio (+95% CI) of total nitrogen contained in invertebrate biomass to total nitrogen contained in leaves for leaf packs for reference (*open bars*) and treatment (*solid bars*) in the

second year of pre-treatment (PY2) and both years of nutrient enrichment (NY1, NY2)

Table 2 Magnitude of effect, or the relative response, of variables to enrichment vs. a reference condition, for rhododendron (*Rhododendron maximum*) and red maple (*Acer rubrum*)

	Rhododendron		Red maple	
	NY1	NY2	NY1	NY2
^a Breakdown rate (k day ⁻¹)	1.6	3.2	1.7	2.8
^b Respiration		3.1		3.0
^c C:N	4.5	5.2	1.5	3.2
^a Invertebrate biomass per leaf pack	2.3	2.6	1.7	3.0
^a Invertebrate biomass per g leaf AFDM	7.1	71.6	10.6	14.3
^c Invertebrate total N:leaf total N	6.3	44.3	1.8	5.8

Boldface indicates the leaf type with a stronger response to enrichment

^a Both years of enrichment in the treatment stream were compared with the average breakdown rates from both streams during the 2 years of pre-treatment

^b Average values across all dates were compared between streams

^c Comparisons were made between streams separately for each year

except macroinvertebrate biomass normalized per leaf pack (Table 2).

Discussion

Nutrient effects on basal resources in detritus vs. primary producer-based food webs

Our study showed that nutrient enrichment affected heterotrophic food web pathways in a forested headwater stream via increased detrital quality and accelerated breakdown rates. This response contrasts with responses of autotroph based systems to nutrient enrichment, in which both the quality and quantity of autotrophic resources can increase (Francoeur 2001; Elser et al. 2001). Because detritus is donor-controlled in some heterotrophic systems, rates of carbon loss may not affect supply, but potentially the timing of availability of organic matter to consumers. Many headwater streams rely on the pulse of leaf litter that enters streams in the autumn, and macroinvertebrate production is often timed to utilize this resource, which becomes less available through the year (Wallace et al. 1997; Stone and Wallace 1998). Invertebrates with short life cycles may ultimately benefit from the increased quality of detritus resulting from nutrient enrichment, but some long-lived taxa may be negatively affected by reductions in quantity. Thus,

faster breakdown rates may affect timing of food availability for some taxa and shift consumer species assemblages toward shorter-lived taxa that are not dependent on continuous availability of detritus (Cross et al. 2005b).

Our long-term nutrient enrichment not only had effects on organic matter resources, but resulted in increased biomass of some detritivorous consumers. These results are similar to previously observed increased herbivore biomass in response to nutrient enrichment (Rosemond et al. 1993; Brett and Goldman 1997; Gratton and Denno 2003; Gruner 2004). Such effects on consumers have also been observed in previous work examining heterotrophic pathways in short-term studies (Pace and Funke 1991; Pearson and Connolly 2000; Robinson and Gessner 2000; Rosemond et al. 2001; Gruner 2004). These empirical findings suggest that bottom-up factors are important in structuring food webs of both types of systems. However, these bottom-up effects apparently occur largely via changes in food quality (nutrient content) and/or microbial activity in detritus-based systems and occur via a combination of changes in quality and quantity (increased primary production) in autotroph based systems. Modeling consumer response to bottom-up effects typically has focused on the quantitative change in basal resources (Wootton and Power 1993). Our results suggest that a refined view of bottom-up effects in detritus-based systems will require determination of heterotrophic microbial turnover and production rates and changes in detrital quality to ultimately predict effects on higher order consumers.

Nutrient effects on consumers via detrital pathways

The mechanisms by which consumer biomass may increase via nutrient enrichment in detritus-based systems appear to be mediated by heterotrophic microbes. Evidence of increased microbial activity or colonization in our study included increased leaf-associated respiration and %N content. Although our experimental design limits our interpretation of our microbial response being due to differences between streams, other studies have similarly found detritus-associated microbial biomass increases in response to nutrient enrichment (Elwood et al. 1981; Suberkropp and Chauvet 1995; Ramirez et al. 2003; Gulis and Suberkropp 2004). Increased microbial activity has been associated with short-term increases in abundance, biomass or growth of detritivores (Pearson and Connolly 2000; Robinson and Gessner 2000; Rosemond et al. 2001). These findings illustrate that increased heterotrophic microbial activity not only leads to

increased carbon losses from systems via respiration, but can result in increased consumer carbon (Pearson and Connolly 2000; Robinson and Gessner 2000; Rosemond et al. 2001). Growth rates and survivorship for several taxa, which were quantified concurrently with the present study, increased with enrichment in mixed benthic substrata in the study stream, while the standing crop of coarse particulate organic matter declined (Cross et al. 2005b, 2006). These results further implicate nutrient-mediated increased microbial activity and detrital quality as pathways by which consumer biomass can increase in response to nutrient enrichment in detritus-based ecosystems.

Biomass and energy pyramids in detritus-based aquatic food webs are similar to those in terrestrial ecosystems, since large stores of carbon support a relatively smaller quantity of consumer biomass (Chapin et al. 2002). In our study, we found that nutrient enrichment stimulated microbial activity and thus, presumably, the turnover of detritus-associated microbial carbon pools. Nutrient enrichment resulted in greater AFDM of macroinvertebrate consumers relative to leaf AFDM than was found under reference conditions. Thus, nutrient enrichment may slightly shift the shape of detritus-based pyramids to include greater mass in consumers and less in basal resources than in unenriched systems, trending towards structures more similar to 'high turnover' biomass pyramids of primary producer-based aquatic systems.

Pyramids of nutrient storage are predicted to be similar to those of biomass (Chapin et al. 2002), and we also saw trends of increased relative mass of N in consumers versus leaf packs that paralleled the observed shifts in carbon. Our data are limited in scale to the 'resources islands' that leaf packs represent, and consumers in leaf packs likely draw from other basal resources in the stream. This effect was due to a combination of increased mass of macroinvertebrates, decreased mass of leaves and increased leaf N content. A comprehensive analysis of the allocation of nutrients and carbon should be addressed on a whole-system basis and/or assessed explicitly with tracer experiments. Our stream-wide assessment of C, N and P allocation from this experimental manipulation showed higher than predicted macroinvertebrate C production relative to leaf standing crop during enrichment (Cross et al. 2006). Likewise, using macroinvertebrate production, macroinvertebrate N and P content and leaf N and P content on a stream-wide scale show greater storage of N and P in macroinvertebrates than in detrital resources under enriched conditions compared to long-term trends in the reference and other CHL streams (W.F. Cross, unpublished data). These data

suggest that nutrient enrichment effects can extend beyond basal resources and result in greater storage of N and C in consumers.

Detrital quality as a predictor of response to enrichment

The responses of the two leaf species we tested were unique and, in part, predictable based on initial C:N. Our results identified substratum C:N as a potentially important species trait in determining the effects of nutrient enrichment on basal resources (functional response trait, *sensu* Hooper et al. 2005). Our results are consistent with previous studies showing lower vs. higher quality substrata responding more strongly to nutrient enrichment (Stelzer et al. 2003). Generally, red maple leaves showed characteristics of a higher quality leaf type with breakdown rates 1.5–3× faster, respiration rates 2–4× higher and macroinvertebrate biomass per leaf pack 2–50× higher compared to rhododendron under reference conditions. By NY2, rhododendron, the lower quality leaf type, generally showed larger magnitudes of response to enrichment compared to red maple. Similarly, during this stream enrichment, lower quality wood substrata showed a relatively stronger response to nutrient enrichment compared to higher quality leaves in C:N and breakdown rate (Gulis et al. 2004). At naturally low nutrient concentrations in aquatic systems, microbes on different detrital substrata likely compete for nutrients (Tank and Webster 1998). Results of our study show that when nutrient limitation is released, microbes on poor quality substrata may respond the most. Thus, variation within substrata (leaf accumulations with leaves of varying quality) might affect microbial competitive outcomes.

Nutrient response can be greatest when water column nutrients are most limiting (for substrata with high C:N) and perhaps are amplified by the increased palatability of substrata to consumers. Consumption rates of leaves are generally faster when the quality to consumers is higher (Kaushik and Hynes 1971). The stronger macroinvertebrate response in rhododendron versus red maple leaf packs may derive from the relatively poorer quality of rhododendron leaves under reference conditions and reflect a potentially greater importance of macroinvertebrates compared to microbial activity in the processing of rhododendron leaves under enriched conditions. Consistent with this hypothesis, an earlier study showed a greater reduction of breakdown rates of rhododendron vs. red maple leaves when invertebrates were experimentally removed (Wallace et al. 1982; Chung et al. 1993).

Predicting long-term ramifications of nutrient enrichment of detritus-based systems

A particular strength of our study was that we maintained a consistent elevated level of enrichment for 2 years as in a true press experiment (*sensu* Bender et al. 1984), and long-term enrichments to study detritus-based systems are rare (but see Chadwick and Huryn 2003). On the whole, greater effects of nutrients were observed in the second year of enrichment, particularly in leaf breakdown and macroinvertebrate biomass, compared to the first year of enrichment. The difference between the first and second years of enrichment could be largely a result of an additional increase in invertebrate activity (i.e., feeding) during the second year. Microbial biomass and production did not differ considerably between the first and second enrichment years (K. Suberkropp, unpublished data). However, macroinvertebrate biomass from this study and macroinvertebrate secondary production (Cross et al. 2006) were roughly 20% higher during the second versus first enrichment year. Greater nutrient effects on leaf breakdown in the second vs. first treatment year may have been due to a lagged invertebrate response in the treatment stream that required more than 1 year to occur. There is evidence of increased growth rates of macroinvertebrates in the treatment stream (Cross et al. 2005b), which could manifest during the second year of enrichment and beyond. A continuation of the nutrient enrichment experiment has shown that leaf breakdown rates for both rhododendron and red maple increased further during the third year and again in the fourth year of enrichment (A.D. Rosemond, unpublished data), which may be largely a result of increased invertebrate feeding.

In spite of the increase in food quality to consumers, it seems likely that the increased rates of detrital processing may result in food limitation to some consumers since the timing of food availability in the study reach has been truncated. With nutrient enrichment, time to 95% loss of red maple leaves was reduced from almost 1 year to less than 6 months. Likewise, time to 95% loss of rhododendron leaves was reduced from nearly 2 years to less than 1 year, a very fast rate of loss for this recalcitrant species. Thus, the effect of nutrients on the timing of leaf availability may be especially important to longer-lived detrital consumers, and particularly in the summer months, when most leaf types are relatively unavailable and detritivores would normally depend more on recalcitrant leaf types such as rhododendron (Schofield et al. 2001).

Conclusion

Even with relatively moderate levels of nutrient enrichment, we have shown fundamental changes in detrital processing in headwater forested stream. Just as nutrient enrichment in autotroph-based systems can result in greater herbivore biomass, we have also shown increased detritivore biomass via bottom-up processes. The effects of nutrient enrichment, however, have not reached equilibrium after 2 years of continuous enrichment. Thus, ecosystem function in southern Appalachian forested headwater streams is potentially very sensitive to nutrient loading, and impacts of nutrient enrichment may continue to increase over time. Leaf litter is the dominant food source in most temperate forested streams (Vannote et al. 1980), and dead organic matter is the dominant basal food resource in many ecosystems (Hedin 1991). If nutrient enrichment similarly affects carbon loss in other systems (e.g., Mack et al. 2004, but see Ågren et al. 2001; Franklin et al. 2003), the effects of global nutrient enrichment on organic matter dynamics and detritivores may be profound.

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References

- Ågren GI, Bosatta E, Magill AH (2001) Combining theory and experiment to understand effects of inorganic nitrogen on litter decomposition. *Oecologia* 128:94–98
- Bender EA, Case TJ, Gilpin ME (1984) Perturbation experiments in community ecology: theory and practice. *Ecology* 65:1–13
- Benke AC, Huryn AD, Smock LA, Wallace JB (1999) Length–mass relationships for freshwater macroinvertebrates in North American with particular reference to the southeastern United States. *J North Am Benthol Soc* 18:308–343
- Brett MT, Goldman CR (1997) Consumer versus resource control in freshwater pelagic food webs. *Science* 275:384–386
- Carpenter SR (1989) Replication and treatment strength in whole-lake experiments. *Ecology* 70:453–463

- Carpenter SR, Caraco NF, Correll DL, Howarth R.W, Sharpley AN, Smith VH (1998) Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecol Appl* 8:559–568
- Chadwick MA, Huryn AD (2003) Effects of a whole-catchment N addition on stream detritus processing. *J N Am Benthol Soc* 22:194–206
- Chapin III FS, Matson PA, Mooney HA (2002) Principles of terrestrial ecosystem ecology. Springer Berlin Heidelberg, New York
- Chung K, Wallace JB, Grubaugh JW (1993) The impact of insecticide treatment on abundance, biomass and production of litterbag fauna in a headwater stream: a study of pretreatment, treatment and recovery. *Limnologia* 28:93–106
- Cross WF (2004) Nutrient enrichment of a detritus-based stream ecosystem: effects on invertebrate community structure and function. Dissertation, University of Georgia Athens
- Cross WF, Benstead JP, Rosemond AD, Wallace JB (2003) Consumer-resource stoichiometry in detritus-based streams. *Ecol Lett* 6:721–732
- Cross WF, Benstead JP, Frost PC, Thomas SA (2005a) Ecological stoichiometry in freshwater benthic systems: recent progress and perspectives. *Freshw Biol* 50:1895–1912
- Cross WF, Johnson BR, Wallace JB, Rosemond AD (2005b) Contrasting response of stream detritivores to long-term nutrient enrichment. *Limnol Oceanogr* 50:1730–1739
- Cross WF, Wallace JB, Rosemond AD, Eggert SL (2006) Nutrient enrichment alters predicted consumer-resource dynamics in a detritus-based stream ecosystem. *Ecology* 87:1556–1565
- Elser JJ, Marzolf ER, Goldman CR (1990) Phosphorus and nitrogen limitation of phytoplankton growth in the freshwaters of North America: a review and critique of experimental enrichments. *Can J Fish Aquat Sci* 47:1468–1477
- Elser JJ, Hayakawa K, Urabe J (2001) Nutrient limitation reduces food quality for zooplankton: *Daphnia* response to seston phosphorus enrichment. *Ecology* 82:898–903
- Elwood JW, Newbold JD, Trimble AF (1981) The limiting role of phosphorus in a woodland stream ecosystem: effects of P enrichment on leaf decomposition and primary producers. *Ecology* 62:146–158
- Findlay S, Tank J, Dye S, Valett HM, Mulholland PJ, McDowell WH, Johnson SL, Hamilton SK, Edmonds J, Dodds WK, Bowden WB (2002) A cross-system comparison of bacterial and fungal biomass in detritus pools of headwater streams. *Microb Ecol* 43:55–66
- Francoeur SN (2001) Meta-analysis of lotic nutrient amendment experiments: detecting and quantifying subtle responses. *J North Am Benthol Soc* 20:358–368
- Franklin O, Högberg P, Ekblad A, Ågren GI (2003) Pine forest floor carbon accumulation in response to N and PK additions: bomb ¹⁴C modelling and respiration studies. *Ecosystems* 6:644–658
- Gessner MO, Chauvet E (1994) Importance of stream microfungi in controlling breakdown rates of leaf litter. *Ecology* 75:1807–1817
- Gratton C, Denno RF (2003) Inter-year carryover effects of a nutrient pulse on *Spartina* plants, herbivores, and natural enemies. *Ecology* 84:2692–2707
- Greenwood JL, Rosemond AD (2005) Periphyton response to long-term nutrient enrichment in a shaded headwater stream. *Can J Fish Aquat Sci* 62:2033–2045
- Gruner DS (2004) Attenuation of top-down and bottom-up forces in a complex terrestrial community. *Ecology* 85:3010–3022
- Gulis V, Suberkropp K (2003) Leaf litter decomposition and microbial activity in nutrient-enriched and unaltered reaches of a headwater stream. *Freshwater Biol* 48:123–134
- Gulis V, Suberkropp K (2004) Effects of whole-stream nutrient enrichment on the concentration and abundance of aquatic hyphomycete conidia in transport. *Mycologia* 96:57–65
- Gulis V, Rosemond AD, Suberkropp K, Weyers HS, Benstead JP (2004) Effects of nutrient enrichment on the decomposition of wood and associated microbial activity in streams. *Freshw Biol* 49:1437–1447
- Hall RO, Wallace JB, Eggert SL (2000) Organic matter flow in stream food webs with reduced detrital resource base. *Ecology* 81:3445–3463
- Hedin LO (1991) Cross-system comparisons of detritus food webs. In: Cole J, Lovett G, Findlay S (eds) Comparative analyses of ecosystems: patterns, mechanisms, and theories. Springer, Berlin Heidelberg New York, pp 346–347
- Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* 75:3–35
- Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. *Ecol Monogr* 54:187–211
- Kaushik NK, Hynes HBN (1971) The fate of dead leaves that fall into streams. *Arch Hydrobiol* 68:465–515
- Mack MC, Schuur EAG, Bret-Harte MS, Shaver GR, Chapin III FS (2004) Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature* 431:440–443
- Melillo JM, Aber JD, Muratore JF (1982) Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology* 63:621–626
- Merritt RW, Cummins KW (eds) (1996) An introduction to the aquatic insects of North America. Kendall/Hunt Publishing Company, Dubuque
- Meyer JL, Johnson C (1983) The influence of elevated nitrate concentration on rate of leaf decomposition in a stream. *Freshw Biol* 13:177–183
- Moore JC, Berlow EL, Coleman DC, de Ruiter PC, Dong Q, Hastings A, Johnson NC, McCann KS, Melville K, Morin PJ, Nadelhoffer K, Rosemond AD, Post DM, Sabo JL, Scow KM, Vanni MJ, Wall DH (2004) Detritus, trophic dynamics and biodiversity. *Ecol Lett* 7:584–600
- Munn NL, Meyer JL (1990) Habitat-specific solute retention in two small streams: an intersite comparison. *Ecology* 71:2069–2082
- Newbold JD, Elwood JW, Schulze MS, Stark RW, Barmeier JC (1983) Continuous ammonium enrichment of a woodland stream: uptake kinetics, leaf decomposition, and nitrification. *Freshw Biol* 13:193–204
- Pace ML, Funke E (1991) Regulation of planktonic microbial communities by nutrients and herbivores. *Ecology* 72: 904–914
- Pearson RG, Connolly NM (2000) Nutrient enhancement, food quality and community dynamics in a tropical rainforest stream. *Freshw Biol* 43:31–42
- Petersen RC, Cummins KW (1974) Leaf processing in a woodland stream. *Freshw Biol* 4:343–368
- Peterson BJ, Deegan L, Helfrich J, Hobbie JE, Hullar M, Moller B, Ford TE, Hershey A, Hiltner A, Kipphut G, Lock MA, Fiebig DM, McKinley V, Miller MC, Vestal JR, Ventullo R, Volk G (1993) Biological responses of a tundra river to fertilization. *Ecology* 74:653–672
- Polis GA, Anderson WB, Holt RD (1997) Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu Rev Ecol Syst* 28:289–316
- Ramirez A, Pringle CM, Molina L (2003) Effects of stream phosphorus levels on microbial respiration. *Freshw Biol* 48:88–97

- Robinson CT, Gessner MO (2000) Nutrient addition accelerates leaf breakdown in an alpine springbrook. *Oecologia* 122:258–263
- Rosemond AD, Mulholland PJ, Elwood JW (1993) Top-down and bottom-up control of stream periphyton: effects of nutrients and herbivores. *Ecology* 74:1264–1280
- Rosemond AD, Pringle CM, Ramirez A, Paul MJ (2001) A test of top-down and bottom-up control in a detritus-based food web. *Ecology* 82:2279–2293
- Schofield KA, Pringle CM, Meyer JL, Sutherland AB (2001) The importance of crayfish in the breakdown of rhododendron leaf litter. *Freshw Biol* 46:1191–1204
- Scott MC, Helfman GS, McTammany ME, Benfield EF, Bolstad PV (2002) Multiscale influences on physical and chemical stream conditions across Blue Ridge landscapes. *J Am Water Resour As* 38:1379–1392
- Slavik K, Peterson BJ, Deegan LA, Bowden WB, Hershey AE, Hobbie JE (2004) Long-term responses of the Kuparuk River Ecosystem to phosphorus fertilization. *Ecology* 85:939–954
- Smith VH, Tilman GD, Nekola JC (1999) Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. *Environ Pollut* 100:179–196
- Stelzer RS, Heffernan J, Likens GE (2003) The influence of dissolved nutrients and particulate organic matter quality on microbial respiration and biomass in a forest stream. *Freshw Biol* 48:1925–1937
- Stewart-Oaten A, Murdoch WW, Parker KR (1986) Environmental impact assessment: “Pseudoreplication” in time? *Ecology* 67:929–940
- Stone MK, Wallace JB (1998) Long-term recovery of a mountain stream from clear-cut logging: the effects of forest succession on benthic invertebrate community structure. *Freshw Biol* 39:151–169
- Suberkropp K, Chauvet E (1995) Regulation of leaf breakdown by fungi in streams: influences of water chemistry. *Ecology* 76:1433–1445
- Tank JL, Webster JR (1998) Interaction of substratum and nutrient availability on wood biofilm processes in streams. *Ecology* 79:2168–2179
- Vanni MJ, DeAngelis DL, Schindler DE, Huxel GR (2004) Overview: cross-habitat flux of nutrients and detritus. In: Polis GA, Power ME, Huxel GR (eds) *Food webs at the landscape level*. University of Chicago Press, Chicago, pp 3–11
- Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE (1980) The River Continuum Concept. *Can J Fish Aquat Sci* 37:130–137
- Wallace JB, Webster JR, Cuffney TF (1982) Stream detritus dynamics: regulation by invertebrate consumers. *Oecologia* 53:197–200
- Wallace JB, Eggert SL, Meyer JL, Webster JR (1997) Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science* 277:102–104
- Wallace JB, Eggert SL, Meyer JL, Webster JR (1999) Effects of resource limitation on a detrital-based ecosystem. *Ecol Monogr* 69:409–442
- Wootton JT, Power ME (1993) Productivity, consumers, and the structure of a river food chain. *Proc Natl Acad Sci* 90:1384–1387