PRIMARY RESEARCH PAPER

Allochthonous litter inputs, organic matter standing stocks, and organic seston dynamics in upland Panamanian streams: potential effects of larval amphibians on organic matter dynamics

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Abstract Allochthonous inputs of detritus represent an important energy source for streams in forested regions, but dynamics of these materials are not well studied in neotropical headwater streams. As part of the tropical amphibian declines in streams (TADS) project, we quantified benthic organic matter standing stocks and organic seston dynamics in four Panamanian headwater streams, two with (pre-amphibian decline) and two without (post-decline) healthy amphibian assemblages. We also measured direct litterfall and lateral litter inputs in two of these streams. Continuous litterfall and monthly benthic samples were collected for 1 year, and seston was collected 1–3 times/month for 1 year at or near baseflow. Direct litterfall was similar between the two streams examined, ranging from 934–1,137 g DM m^{-2} y^{-1}. Lateral inputs were lower, ranging from 140–187 g DM m^{-1} y^{-1}. Dead leaves (57–60%), wood (24–29%), and green leaves (8–9%) contributed most to inputs, and total inputs were generally higher during the rainy season. Annual habitat-weighted benthic organic matter standing stocks ranged from 101–171 g AFDM m^{-2} across the four study reaches, with ~4 × higher values in pools compared to erosional habitats. Total benthic organic matter (BOM) values did not change appreciably with season, but coarse particulate organic matter (CPOM, >1 mm) generally decreased and very fine particulate organic matter (VFPOM, 1.6–250 μm) generally increased during the dry season. Average annual seston concentrations ranged from 0.2–0.6 mg AFDM l^{-1} (fine seston, <754 μm >250 μm) and 2.0–4.7 mg AFDM l^{-1} (very fine, <250 μm >1.6 μm), with very fine particles composing 85–92% of total seston. Quality of fine seston particles in the two reaches where tadpoles were present was significantly higher (lower C/N) than the two where tadpoles had been severely reduced ($P = 0.0028$), suggesting that ongoing amphibian declines in this region are negatively influencing the quality of particles exported from headwaters. Compared to forested streams in other regions, these systems receive relatively high amounts of allochthonous litter inputs but have low in-stream storage.

Keywords Tropical streams · Leaf litter · Organic matter · Standing stocks · Organic seston · Larval amphibians

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Introduction

Detrital inputs from streamside vegetation are a major source of energy for streams, particularly headwaters draining forested catchments, where low light levels can greatly limit photosynthesis (Vannote et al., 1980; Wallace et al., 1997; Mosisch et al., 2001; Benfield, 2006). Because of the importance of these allochthonous energy sources, litter inputs and the internal storage and cycling of these materials in streams are well studied in many systems, particularly temperate-zone headwaters (e.g., Webster & Meyer, 1997; Webster et al., 1999). However, aside from a few isolated studies, most of which focused on decomposition and detritivore feeding (e.g., Padget, 1976; Benstead, 1996; Rosemond et al., 1998; March & Pringle, 2003; Rueda-Delgado et al., 2006; Wantzen & Wagner, 2006), there is scant quantitative information on inputs, storage, and cycling of allochthonous materials in tropical streams, even though they often drain heavily forested catchments, and thus allochthonous inputs are likely a major energy source (Araujo-Lima et al., 1986; Fittkau & Klinge, 1973; Henderson & Walker, 1986; Graca et al., 2001).

Studies of global patterns in litter production indicate that factors influencing litter inputs vary with latitude and temperature (Bray & Gorham, 1964, Meentemeyer et al., 1982). Peak litterfall in the tropics is often associated with rainfall and storm events, unlike temperate zones where seasonal patterns are related to temperature and photoperiod changes that trigger abscission (Covich, 1988). In addition, high productivity and longer growing seasons in tropical forests can result in nearly twice the amount of annual litterfall compared to temperate-zone forests (Brokaw, 1982; Leigh & Windsor, 1982). Hence, tropical streams draining forested catchments likely receive relatively high litter inputs on a year-round basis.

Along with inputs, organic materials must be retained in a stream reach until they can be processed if they are to contribute to local food webs (Jones, 1997; Lamberti & Gregory, 2006). Many tropical stream systems, particularly headwaters that drain rain and cloud forest systems, experience frequent scouring floods during their rainy seasons. More frequent and higher magnitude flooding in tropical headwaters likely decreases organic matter retention, and thus standing stocks, even when inputs are relatively high (Covich, 1988), which might limit the availability of detrital resources in these systems, despite high inputs.

As coarse organic materials that are retained in a stream reach break down, smaller particles that are more amenable to transport are formed. Export of these particles in the form of organic seston represents an important energy source for filter-feeding invertebrates and fishes and downstream food webs (Vannote et al., 1980; Wotton, 1990; Wallace & Webster, 1996). Organic seston dynamics have been examined for a variety of streams in temperate regions (e.g., Golladay, 1997; Wallace et al., 1991; Whiles & Dodds, 2002), and linkages with other consumers have been made (Grafius & Anderson, 1979; Wallace & Merritt, 1980; Richardson, 1984), but there is much less known about seston dynamics in tropical headwaters.

As part of the tropical amphibian declines in streams (TADS) project, an investigation of the ecological consequences of catastrophic amphibian declines in Central America, our goal was to develop detrital energy budgets for headwater streams in the Panamanian uplands. In doing so, we quantified annual litter inputs to two stream reaches and benthic organic matter standing stocks and organic seston dynamics in four reaches, including sites with and without stream-breeding amphibian assemblages. We then compared our estimates to similar, better-studied streams in North America and Europe. We hypothesized that these neotropical headwater streams would receive relatively high litter inputs, particularly during the rainy season, but would have overall low retention of these materials because of frequent high flows. We also hypothesized that tadpole extirpations, which represent the removal of abundant grazers and detritivores from these systems, would reduce seston concentrations and quality because of reduced generation of fecal materials that are of relatively high quality (Whiles et al., 2006).

Methods

Study sites

The study streams are all 100-m reaches of high gradient, upland headwaters draining mostly secondary growth, pre-montane to very moist montane

rainforest catchments in central and northwestern Panamá (Andrada, 2000; Guerra & Valdespino, 2002). The rainy season in this region generally lasts from May–December, with relatively drier conditions from January–April. Physical attributes of each study reach are summarized in Table 1. El Copé study reaches (El Copé 1 and El Copé 2) are 2nd order, 100-m reaches of the Río Guabal located in the Parque Nacional General de División Omar Torrijos Herrera, Coclé, Panamá. This park is located on the eastern end of the Cordillera Central (8°40′ N, 80°35′ W) at ~700 m above sea level. Fortuna study streams included a 1st order (Fortuna 2) and a 2nd order (Fortuna 1) reach located in the Reserva Forestal Fortuna, Chiriquí, Panamá (1,000–1,400 m elevation). This region is ~200 km west of El Copé (8°42′ N, 82°14′ W).

At the time of this study, El Copé harbored a diverse amphibian fauna, with at least 40 species in riparian habitats, 22 of which had stream-dwelling larvae (Lips et al., 2006). Tadpole densities of up to $50/m^2$ were commonly observed in the El Copé study streams (Ranvestel et al., 2004; Whiles et al., 2006). Most of these tadpoles are grazers or detritivores, representing the only vertebrate grazers in these headwater systems (Ranvestel, 2002). Fortuna once harbored a similarly abundant and diverse

stream-breeding amphibian assemblage, but a massive decline associated with chytridiomycosis in 1997–1998 severely reduced amphibian populations from the Fortuna streams (Lips, 1999). Over two years of monitoring at the Fortuna streams revealed that tadpole densities have declined to $<1/m^2$ (Lips, unpublished data). Stream invertebrate and fish assemblages are similar between the Fortuna and El Copé stream reaches (Addames, 1977; de Sousa, 1999; Colón-Gaud, unpublished data).

Litter inputs

Litter inputs were quantified for one stream reach at El Copé and one at Fortuna for one year beginning July 2004. Twelve plastic laundry baskets (1,809 cm^2 sampling area), fitted with a 363-μm Nitex mesh, were secured within the stream channel to collect direct inputs. Twelve plastic containers (linear area = 33 cm, height of opening = 19 cm, fitted with a 363-μm Nitex mesh) were secured along the stream bank (six on each side) to collect lateral inputs. Lateral traps were placed in areas with gentle inclines down to the stream and the bottom of the opening of each was flush with the ground (Wallace et al., 1995). Holes in direct and lateral collectors

Table 1 Physical characteristics of the El Copé and Fortuna study reaches

Characteristic	El Copé 1	El Copé 2	Fortuna 1	Fortuna 2
Stream order	2	2	2	1
Mean width (m)	3.28	3.55	3.37	2.01
Mean depth (m)	0.12	0.15	0.15	0.11
Streambed area (m^2)	328	355	337	201
Canopy cover (%)	74	67	68	74
Habitat composition (%)				
Riffle/run	74	48	60	83
Pool	26	52	40	17
Substrate composition (%)				
Cobble and larger	25	23	23	25
Pebble	25	24	22	28
Gravel	20	18	16	21
Sand	10	12	30	8
Silt	20	23	9	18
Mean annual water temp (°C)	20.7	21.0	17.4	18.1
Mean annual discharge (l/s)	78	113	88	31
Mean annual precipitation (cm)	350	350	450	450

allowed for water drainage. Direct and lateral collectors were all placed above the surface of the stream and frequently checked to assure that materials collected were not submerged or displaced during peak flow events.

All materials that accumulated in traps were collected at least once monthly and placed in plastic bags. More frequent collection of materials was not possible due to the remote locations and distance between sites. However, visual inspection indicated that decomposition of materials in the collectors was minor and thus should not have influenced the patterns we observed. Nonetheless, some decomposition and possible consumption of materials, particularly fruits and seeds, may have taken place and our input estimates are thus conservative. Materials were separated into green leaves, dead leaves, wood, reproductive (fruit, seed, flowers), and miscellaneous categories (moss, lichens, epiphytes, unidentified materials). Sorted samples were then dried (55°C) for 72 h and weighed to obtain g dry mass (DM) m^{-2} for direct litterfall and g DM m^{-1} length of stream for lateral inputs.

Benthic organic matter standing stocks

Monthly benthic organic matter samples were collected from all four stream reaches for one year beginning in June 2003. On each sampling date, three samples were collected from depositional habitats (pools) using a stovepipe benthic corer (sampling area = 314 cm^2) and four were collected from erosional habitats (riffle/runs) using a Surber sampler (sampling area = 930 cm^2, 250-μm mesh). Organic material from samples was separated into CPOM (>1 mm) and FPOM (<1 mm > 250 μm) using nested sieves. CPOM was further separated into leaves, wood, reproductive (fruit, seed, flowers), and miscellaneous categories (moss, epiphytes, unidentified small detritus) before drying. Sorted CPOM categories and FPOM samples were dried (55°C) for 48 h, transferred to a dessicator for 24 h, and then weighed to obtain DM. Samples were then ashed (500°C) for 1 h and reweighed to obtain ash-free dry mass (AFDM). Large samples were subsampled before combustion and % AFDM estimates applied to total sample masses.

Very fine particulate organic matter (VFPOM) was collected with each stovepipe benthic core and Surber sample. Because the mesh on the Surber sampler was 250 μm, an additional core sample was collected next to each Surber sample to estimate VFPOM for these samples. For each VFPOM sample, all material including water from within the corer was removed, placed in a graduated bucket, and the volume recorded. Material was then stirred vigorously and poured through a 250-μm sieve. A sample of material that passed through the sieve was collected in a numbered plastic sample bottle for later filtering. In the laboratory, VFPOM samples were shaken and a subsample was filtered through a glass fiber filter (particle retention size = 1.6 μm). Estimates of total AFDM were obtained using the same methods described above for CPOM and FPOM and correcting for subsamples.

Organic matter standing stocks (g AFDM m^{-2}) were estimated for depositional and erosional habitats; habitat-weighted values were obtained by summing habitat-specific values multiplied by the proportion of the respective habitat type available in 100-m study reaches.

Organic seston

Seston was sampled during baseflow or near-baseflow conditions in all four stream reaches ∼2–3 times per month for one year beginning June 2003. Water samples collected from the main channel of each stream were processed with a wet filtration system consisting of a series of stacked sieves with mesh sizes of 754, 250, 98 μm, similar to the one described by Whiles & Dodds (2002). Water samples were agitated and poured through the filtration system into a graduated bucket and the total volume of water sieved was recorded. Materials in the 754-, 250-, and 98-μm sieves were rinsed into a labeled sample bottle for later filtering. A subsample of the water that passed through all sieves (<98 μm) was also collected from the graduated bucket. All size fractions were filtered and processed to obtain AFDM using methods described above for VFPOM. Portions of filters were removed with a cork borer before ashing and analyzed for carbon and nitrogen content on a Thermo FlashEA 1112 NC Analyzer. For analyses,

particles were grouped into fine (250–754 μm) and very fine (1.6–250 μm) size classes.

Relationships between C and N in seston collected from El Copé and Fortuna streams were examined using linear regression techniques, and differences between these relationships for each site (differences in slopes and elevation of slopes) were assessed using analysis of covariance (ANCOVA, $\alpha = 0.05$) to assess differences in slopes (SAS Institute, Carey, North Carolina). If slopes did not differ, differences in elevation of slopes at the mid-point of the x-axis were statistically compared ($\alpha = 0.05$). Differences in elevation of slopes were not tested for if slopes differed because the relationship between the two slopes therefore changes significantly across x-axis values.

Results

Litter inputs

Total annual inputs were slightly higher at El Copé than Fortuna (Table 2). Although total inputs were generally higher across sites in the wet season (Table 2) because it constitutes most of the year (8 months; May–December), rates of direct litterfall inputs were 1.2–1.9× higher in the dry season (Table 2). Lateral inputs contributed 13–14% of total annual litter inputs at both sites, representing 16% of total litter inputs during the wet season and 10–11% of total inputs during the dry season. Dead leaves comprised more than half of all inputs at both sites, followed by wood (24–29%), green leaves (8–9%), and reproductive parts (1–5%). Miscellaneous inputs (moss, lichens, epiphytes, unidentified materials) were highly variable throughout the year and were generally higher during sampling intervals with strong storms.

Benthic organic matter standing stocks

Total BOM standing stocks were similar across sites, with habitat-weighted values ranging from 101–171 g AFDM m^{-2} (Table 3). Total BOM standing stocks in depositional habitats were 4–9× higher than erosional habitats in all four streams during the wet season, and 2–4× higher during the dry season,

Table 2 Total and mean monthly (±1 SE) litter inputs to the El Copé (El Copé 1) and Fortuna (Fortuna 1) study streams during the wet and dry seasons

| | Total inputs | | | | Monthly average inputs | | | |
| | El Copé | | Fortuna | | El Copé | | Fortuna | |
	Direct	Lateral	Direct	Lateral	Direct	Lateral	Direct	Lateral
Wet season								
Green leaves	54.2	6.7	32.8	6.0	6.8 ± 3.0	0.8 ± 0.2	4.1 ± 0.5	0.8 ± 0.2
Dead leaves	389.1	104.2	300.4	54.4	48.6 ± 10.9	13.0 ± 6.6	37.6 ± 3.0	6.8 ± 1.2
Wood	172.8	20.3	116.1	11.2	21.6 ± 12.2	2.5 ± 1.3	14.5 ± 4.3	1.4 ± 0.4
Reproductive	3.5	1.3	27.2	4.4	0.4 ± 0.2	0.2 ± 0.8	3.4 ± 1.3	0.6 ± 0.2
Miscellaneous	84.4	–	0.9	13.0	10.6 ± 11.2	–	0.1 ± 0.1	1.6 ± 1.7
Total	704.0	132.5	477.4	89.0	88.0 ± 34.6	16.5 ± 7.8	59.7 ± 5.1	11.2 ± 1.7
Dry season								
Green leaves	49.2	8.9	36.4	5.7	12.3 ± 5.1	2.2 ± 0.8	9.1 ± 3.1	1.4 ± 0.5
Dead leaves	272.5	32.8	220.7	33.3	68.1 ± 25.6	8.2 ± 3.0	55.2 ± 13.3	8.3 ± 2.3
Wood	109.3	12.9	183.8	4.5	27.3 ± 21.4	3.2 ± 1.4	46.0 ± 33.1	1.1 ± 0.5
Reproductive	1.9	0.2	15.3	7.3	0.5 ± 0.3	0.1 ± 0.1	3.8 ± 1.6	1.8 ± 1.5
Miscellaneous	–	–	–	–	–	–	–	–
Total	432.9	54.8	456.2	50.8	108.2 ± 52.1	13.7 ± 4.5	114.1 ± 47.3	12.6 ± 3.7

The sum of the wet season and dry season inputs is total annual inputs. Direct litterfall is in g dry mass (DM) m^{-2} of stream area. Lateral inputs are in g DM m^{-1} length of stream channel. Reproductive materials = seeds, fruits, nuts, and flowers. Miscellaneous = whole plants, epiphytes, and unidentified materials. Dash = no material

Table 3 Mean benthic organic matter (BOM) standing stocks in erosional and depositional habitats of each study stream during the dry and wet season

	El Copé 1		El Copé 2		Fortuna 1		Fortuna 2	
	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
Erosional								
Total CPOM	27.1 ± 10.7	45.2 ± 19.7	32.9 ± 7.4	24.9 ± 8.1	35.0 ± 8.9	37.5 ± 10.5	41.6 ± 10.6	68.3 ± 12.5
Leaves	8.9 ± 2.3	24.1 ± 11.8	7.4 ± 1.6	13.7 ± 6.3	12.6 ± 3.8	16.0 ± 6.2	15.9 ± 6.3	40.8 ± 16.0
Wood	9.7 ± 7.8	12.5 ± 4.6	16.0 ± 6.9	4.8 ± 1.8	10.8 ± 5.8	12.2 ± 4.1	12.8 ± 5.0	15.8 ± 10.6
Reproductive	0.7 ± 0.2	0.1 ± 0.1	0.5 ± 0.1	0.1 ± 0.1	1.4 ± 1.1	0.3 ± 0.2	2.5 ± 1.6	0.7 ± 0.6
Misc.	7.8 ± 1.4	8.5 ± 4.1	9.0 ± 1.2	6.2 ± 1.6	10.2 ± 4.3	9.0 ± 1.4	10.5 ± 1.7	11.0 ± 3.4
FPOM	6.3 ± 1.2	4.9 ± 1.8	7.1 ± 1.2	9.4 ± 3.1	8.5 ± 2.2	14.2 ± 2.8	6.3 ± 1.2	7.5 ± 3.4
VFPOM	22.1 ± 5.8	27.3 ± 5.3	22.5 ± 5.3	46.0 ± 13.6	16.8 ± 2.3	20.3 ± 5.8	17.9 ± 3.4	45.1 ± 5.7
Total BOM	55.5 ± 15.7	77.5 ± 24.6	62.6 ± 7.2	80.3 ± 17.4	60.2 ± 8.7	72.0 ± 10.7	65.8 ± 13.5	120.8 ± 9.9
Depositional								
Total CPOM	123.2 ± 58.6	54.4 ± 24.5	169.9 ± 60.2	130.9 ± 96.8	131.2 ± 38.5	67.7 ± 59.9	454.9 ± 138.4	38.7 ± 8.6
Leaves	9.1 ± 3.9	7.3 ± 7.2	10.1 ± 3.2	12.2 ± 6.2	19.2 ± 5.3	7.7 ± 4.3	26.3 ± 12.6	17.3 ± 5.5
Wood	69.0 ± 46.5	19.3 ± 9.9	93.3 ± 53.1	59.2 ± 58.9	53.9 ± 20.8	53.3 ± 59.9	284.5 ± 103.0	4.6 ± 2.9
Reproductive	5.9 ± 2.1	3.7 ± 2.3	13.4 ± 5.5	12.2 ± 10.6	5.6 ± 1.7	0.9 ± 1.0	34.3 ± 20.4	1.8 ± 1.2
Misc.	39.2 ± 13.0	24.1 ± 7.0	53.1 ± 14.3	47.3 ± 23.7	52.6 ± 15.3	5.8 ± 1.7	109.7 ± 21.7	15.0 ± 2.3
FPOM	23.1 ± 3.6	18.6 ± 3.9	27.4 ± 5.1	22.8 ± 6.6	30.7 ± 5.3	15.4 ± 3.4	41.0 ± 5.5	10.9 ± 0.7
VFPOM	84.8 ± 12.8	90.5 ± 12.1	65.9 ± 10.3	119.6 ± 20.5	77.9 ± 38.3	66.5 ± 9.0	100.6 ± 14.0	86.8 ± 17.0
Total BOM	231.1 ± 65.0	163.5 ± 37.8	263.2 ± 58.0	273.3 ± 93.8	239.8 ± 60.8	149.5 ± 63.8	596.5 ± 144.4	136.3 ± 16.3
Habitat weighted								
Total CPOM	52.4 ± 14.9	47.7 ± 15.7	103.9 ± 31.4	79.9 ± 52.6	73.4 ± 18.9	49.6 ± 29.4	112.9 ± 30.8	63.2 ± 10.6
Leaves	9.0 ± 1.6	19.7 ± 8.4	8.8 ± 1.0	12.9 ± 5.8	15.2 ± 3.4	12.7 ± 4.5	17.7 ± 7.0	36.8 ± 12.8
Wood	25.3 ± 12.8	14.3 ± 3.7	56.1 ± 27.9	33.0 ± 31.0	28.0 ± 10.4	28.6 ± 25.6	59.7 ± 19.2	13.9 ± 9.3
Reproductive	2.1 ± 0.6	1.1 ± 0.6	7.2 ± 2.8	6.4 ± 5.5	3.1 ± 0.7	0.6 ± 0.5	8.0 ± 3.7	0.9 ± 0.7
Misc.	16.1 ± 3.2	12.6 ± 3.9	31.9 ± 7.3	27.6 ± 12.3	27.2 ± 7.1	7.7 ± 0.6	27.6 ± 4.2	11.7 ± 3.1
FPOM	10.7 ± 1.1	8.5 ± 2.1	17.6 ± 3.0	16.4 ± 4.5	17.3 ± 2.0	14.7 ± 1.6	12.2 ± 1.4	8.1 ± 3.0
VFPOM	38.6 ± 6.1	44.0 ± 6.4	45.0 ± 7.8	84.2 ± 16.5	41.3 ± 14.5	38.8 ± 7.0	32.1 ± 2.6	52.3 ± 6.8
Total BOM	101.7 ± 16.2	100.1 ± 21.9	166.6 ± 29.0	180.4 ± 52.6	132.0 ± 28.0	103.0 ± 31.1	157.3 ± 33.2	123.5 ± 9.0

CPOM = coarse particulate organic matter (>1 mm); FPOM = fine particulate organic matter (<1 mm > 250 μm); VFPOM = very fine particulate organic matter (<250 μm > 1.6 μm). Values are g ash-free dry mass (AFDM) m^{-2} ± 1 SE. Reproductive materials = seeds, fruits, nuts, and flowers; miscellaneous = moss, roots, herbaceous plants, and unidentified small detritus particles

except for Fortuna 2 stream, where total BOM standing stocks were more similar in erosional and depositional habitats. Total habitat-weighted organic matter standing stocks ranged from 50–66% CPOM, 7–13% FPOM, and 27–40% VFPOM across sites. Leaves were the dominant contributor to CPOM stocks (31–48%) in erosional habitats, except for El Copé 2, where wood was the dominant contributor (41% of total). Small woody debris composed over half of the annual average CPOM stocks (50–59%) in depositional habitats at all sites.

Habitat-weighted BOM values in El Copé streams did not change appreciably with season, but BOM stocks in Fortuna streams decreased by 21–22%

during the dry season, mostly due to decreases in CPOM (Table 3). Leaves showed a pattern of increase during the dry season in all reaches except for Fortuna 1, where values remained similar throughout the year (Table 3). Habitat-weighted FPOM values did not vary appreciably with season. Habitat-weighted VFPOM values increased during the dry season at Fortuna 2 and El Copé 2 (38–47%, respectively), and CPOM decreased during the dry season at Fortuna 2 (44%). During the wet season, small wood was the main contributor to CPOM in erosional habitats in El Copé streams, while leaves dominated CPOM in Fortuna streams. During the dry season, leaves dominated CPOM in erosional habitats

across all sites. In depositional areas, small wood was the main contributor to CPOM at all sites during the wet season, except for Fortuna 1, where wood and miscellaneous materials contributed equally. Small wood remained the main contributor to CPOM in depositional habitats during the dry season at El Copé 2 and Fortuna 1, whereas miscellaneous materials and leaves were the largest contributors to dry season CPOM standing stocks in El Copé 1 and Fortuna 2, respectively (Table 3).

Organic seston

Seston concentrations, including both fine and very fine fractions, were consistently higher in Fortuna streams than El Copé. There were no distinct seasonal trends in seston concentrations, except Fortuna 2 stream, where total seston concentrations increased by $\sim 1.5\times$ in the dry season, mostly due to an increase in concentrations of very fine particles (Table 4). Very fine particles accounted for 85%–92% of organic seston concentrations at all sites (Table 4).

Slopes of relationships of Nitrogen per unit carbon of fine seston particles were similar between El Copé and Fortuna sites ($F_{1, 50} = 1.87$, $P = 0.18$), and Nitrogen per unit Carbon was significantly higher in El Copé sites compared to Fortuna sites ($F_{1, 50} = 9.88$, $P = 0.0028$, Fig. 1a); average C/N of fine organic seston in El Copé reaches was 7.6 ± 0.08

Table 4 Mean annual and seasonal concentrations of organic seston (mg AFDM $l^{-1} \pm 1$ SE) in the four study streams

	El Copé 1	El Copé 2	Fortuna 1	Fortuna 2
Fine seston				
Annual	0.2 ± 0.0	0.1 ± 0.0	0.6 ± 0.1	0.6 ± 0.1
Wet season	0.2 ± 0.1	0.1 ± 0.1	0.5 ± 0.1	0.6 ± 0.1
Dry season	0.1 ± 0.0	0.2 ± 0.0	1.1 ± 0.2	0.8 ± 0.2
Very fine seston				
Annual	2.4 ± 0.4	2.0 ± 0.3	3.5 ± 0.6	4.7 ± 0.7
Wet season	2.3 ± 0.5	2.2 ± 0.4	3.5 ± 0.6	4.3 ± 0.8
Dry season	2.8 ± 0.6	1.8 ± 0.3	3.0 ± 0.9	6.8 ± 1.1
Total seston				
Annual	2.6 ± 0.4	2.2 ± 0.3	4.1 ± 0.6	5.4 ± 0.8
Wet season	2.5 ± 0.6	2.3 ± 0.4	4.1 ± 0.7	4.9 ± 0.9
Dry season	2.9 ± 0.6	2.0 ± 0.3	4.1 ± 0.1	7.6 ± 1.2

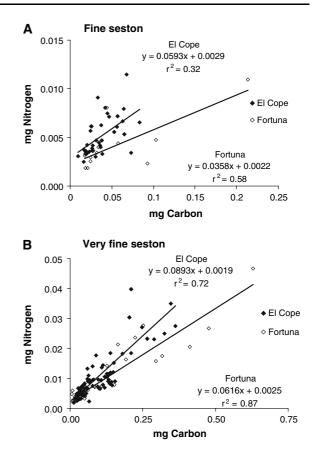Fine seston = 250–754 μm, very fine = 1.6–250 μm

Fig. 1 Nitrogen per unit carbon (C/N) of (**A**) fine particles (250–754 μm) and (**B**) very fine particles (1.6–250 μm) from El Copé and Fortuna study reaches. For fine particles, slopes were similar ($F_{1, 50} = 1.87$, $P = 0.18$) and N per unit C was significantly higher (higher elevation) at El Copé sites compared to Fortuna ($F_{1, 50} = 9.88$, $P = 0.0028$). Slopes of the relationships for very fine particles differed ($F_{1, 122} = 12.75$, $P = 0.0005$) and therefore differences in elevation were not tested for

(mean $\pm$ 1 standard error) compared to 12.6 ± 0.70 at Fortuna. Slopes of C/N relationships for very fine seston differed between El Copé and Fortuna sites ($F_{1, 122} = 12.75$, $P = 0.0005$), and C/N values of very fine particles from each site were similar (mean = 9.4 ± 0.05 at El Copé and 9.8 ± 0.13 at Fortuna, Fig. 1b).

Discussion

Litter inputs

The magnitude of litter inputs measured during our study suggests that allochthonous energy sources are

significant in these neotropical headwaters, as they exceed those of many other forested headwater systems in other regions that are considered heterotrophic (see Webster & Meyer, 1997). Although total inputs were generally higher during the longer wet season, input rates were greater during the dry season at both sites for most categories of inputs. We initially expected higher rates of litter inputs in the wet season because of more frequent storm events. However, during the dry season winds are generally higher and many trees in this region drop leaves at this time, two important factors contributing to allochthonous litter inputs. The trend of higher-input rates in the dry season that we observed is also consistent with suggested patterns of leaf fall in similar upland streams in Costa Rica (Jackson & Sweeney, 1995), where a substantial increase in leaf fall occurs during the dry season, when only 12% of rainfall occurs (Newbold et al., 1995). Haines & Foster (1977) suggested that similar seasonal trends in leaf fall on Barro Colorado Island, Panamá, are likely an evolutionary strategy for reducing loss of water from trees while also increasing exposure of the flowers and fruit to animals. Patterns in the relative contributions of direct and lateral litter inputs that we observed were also consistent with the few other studies that have examined both, and suggest that direct inputs are generally greater than lateral inputs in forested systems (Cillero et al., 1999; Crowl et al., 2006).

It is difficult to compare our findings with other Neotropical headwater streams because few studies have quantified organic matter pools in these systems. Variable sampling methods across studies (e.g., not accounting for lateral inputs, short sampling periods) further impede comparisons. Wantzen & Wagner (2006) observed direct litterfall inputs that were comparable to our sites (820 g DM $m^{-2} y^{-1}$) in Córrego Tenente Amaral, a 2nd order highland stream in Mato Grosso, Brazil, but they did not measure lateral inputs. Crowl et al. (2006) estimated daily direct litterfall inputs of 13.0 g DM m^{-2} and daily lateral inputs of 1.0 g DM m^{-2} in Quebrada Prieta, a 2nd order stream in northeast Puerto Rico. Although Crowl et al. (2006) did account for both direct and lateral inputs, their daily input measurements are difficult to compare with our estimates because their values do not account for seasonal variation, storm events, and other factors that are integrated into longer-term studies.

Although comparisons to other tropical headwaters are difficult, we can make comparisons to forested headwater systems in other regions where similar sampling methods were used over similar study durations. Comparisons with seven other forested headwater systems in North America and Europe, where comprehensive studies of litter inputs and in-stream organic matter standing stocks have occurred, indicate that our study streams have relatively high annual litter inputs, but low in-stream storage (Fig. 2). Whereas high inputs are related to the presence of a productive and extensive forest canopy, low in-stream storage is likely linked to high rainfall and frequent scouring events that characterize these neotropical headwaters. Despite high channel sinuosity and the prevalence of coarse substrates and occasional debris dams that normally facilitate retention (Jones, 1997), frequent high-discharge events in our study streams, particularly during the wet season, apparently reduce in-stream storage of organic materials. Unlike hydrologic pulses in lower gradient headwater streams of the Amazon, where backflooding into tributaries facilitates retention of materials (Rueda-Delgado et al., 2006), our study sites are all high-gradient headwaters that rapidly drain during peak flows.

Whereas most studies report litter inputs in AFDM, we measured inputs in dry mass because of
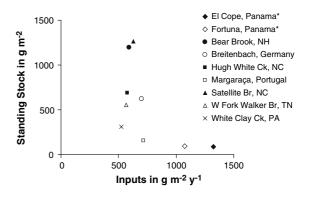

Fig. 2 Annual total litter inputs (includes direct and lateral inputs, except for White Clay Creek, PA and Margaraça, Portugal sites, which did not include lateral inputs) compared to annual mean BOM standing stocks in forested headwater streams from different regions. * Inputs for El Copé and Fortuna are g DM measured in one stream at each site; all other values for El Copé and Fortuna are AFDM and are averages of two study reaches at each site. Data from individual sites other than Panamá are from Webster & Meyer (1997), except Margaraça, Portugal, which are from Abelho & Graça (1998)

the constraints of working in remote locations where a high-temperature furnace was not available. Hence, our litter estimates are slight overestimates compared to other studies. Post-abscission leaves that enter our study streams are generally 5–10% ash (Whiles et al., unpublished data), and thus for more accurate comparison with other studies our values could be corrected by a factor of 0.9. However, even with this conservative correction applied, the streams we studied still have higher inputs compared to streams from other regions where similar studies have been performed (Fig. 2).

Benthic organic matter standing stocks

Jones (1997) compared organic matter storage in streams across the U.S. and Canada and found BOM stocks were higher in streams with higher gradients. Jones (1997) also found a relationship between BOM storage and precipitation, whereby regions in the northwestern U.S. with higher precipitation stored greater amounts of BOM than regions in dryer western and Midwestern states. Our neotropical study streams do not appear to fit these relationships (e.g., high gradient, high precipitation, but low BOM storage), and this is likely related to amounts of coarse woody debris in stream channels. The relationship between gradient and BOM observed by Jones (1997) was confounded with the presence of wood, whereby large amounts of wood (>25,000 g wood/m^2) were present in some of the high-gradient headwater sites included in analyses (e.g., headwater streams in Oregon draining mature conifer forests). Along with directly contributing to organic matter pools, coarse woody debris is also a very important mechanism for retention of BOM in stream reaches (Bilby & Likens, 1980; Wallace et al., 1996). We did not measure large wood in our study sites, but our field observations indicate large wood is nowhere near as abundant in our systems as in some of the headwater systems examined by Jones (1997). This is likely a result of frequent removal of this material during scouring floods; we witnessed floods that removed entire large snags (e.g., dead trees >4 m long with trunks >50 cm in diameter) from our study reaches during the course of this study. Further, inputs of large woody debris are likely low in our streams compared to some of the headwaters

examined by Jones (1997) that drain mature conifer forests. Our study streams drain secondary growth deciduous forests, which should contribute less large woody debris to streams than more mature forest, particularly mature conifer forests (e.g., Harmon et al., 1986; Harmon & Hua, 1991).

Our BOM standing stock values include estimates of VFPOM, which most studies do not account for, but which can constitute a large portion of organic matter standing stocks in stream sediments. In our study, VFPOM constituted ∼1/3 of total BOM standing stocks. Hence, storage in our study systems is even lower compared to similar-sized forested streams in other regions (see Fig. 2), as most sites that we could make comparisons with did not account for VFPOM, which would greatly increase their BOM estimates. On the other hand, our BOM estimates do not include large wood, which is included in some estimates from other sites (e.g., Bear Brook, NH; White Clay Creek, PA; Satellite Branch, NC; Hugh White Creek, NC). Although inclusion of large wood would increase our estimates somewhat, as noted above, large wood does not appear to be a dominant feature in these streams and likely would not change the general relationship with other sites, particularly if VFPOM was accounted for at other sites.

We did not directly measure litter decomposition, but gross system-level estimates (average daily input rates/average in-stream CPOM standing stocks [e.g., Chadwick & Huryn, 2003]) suggest that CPOM decomposition in our study streams, which ranged from 0.038 day^{-1} in Fortuna 1 in the wet season to 0.115 in El Copé 1 in the wet season, is in the intermediate to fast range for litter decomposition (Petersen & Cummins, 1974). A leaf-litter decomposition study from a 1st order stream in the Amazonian floodplain also found intermediate decomposition rates ranging from 0.010 day^{-1} to 0.031 day^{-1} during a period of flashy discharge (Rueda-Delgado et al., 2006). Crowl et al. (2006) measured decomposition rates that are among the highest published, ranging from 0.12 day^{-1} to 0.26 day^{-1}, in the presence of shrimps in a headwater stream in Puerto Rico. Based on these studies, decomposition rates in our study streams are within the range reported for other tropical headwaters. However, these gross estimates for our study steams do not account for downstream loss of CPOM before decomposition,

and based on our observations a substantial fraction of CPOM is transported downstream during storm events before decomposition occurs. Hence, these estimates represent the upper range of decomposition rates we would expect for our study streams.

Low BOM storage in these headwater channels likely limits populations of detritivores such as leaf-shredding invertebrates (e.g., Richardson, 1991). In a concurrent study in these same stream reaches, we found very low densities and biomass of shredder invertebrates (Colón-Gaud, unpublished data), and others have observed a paucity of shredding invertebrates in neotropical streams compared to forested systems in other regions (Rosemond et al., 1998; Rueda-Delgado et al., 2006). Low in-stream retention of BOM, as observed in our study sites, may be an important contributing factor to this enigmatic pattern of low shredder populations in streams draining productive tropical forests.

Organic seston

Our seasonal seston concentration values represent baseflow or near-baseflow conditions for these streams, and thus do not account for periods of high discharge that can result in greatly elevated seston concentrations and most of the annual seston export from streams (Wallace et al., 1991; Wallace et al., 2006). While there was a trend of higher seston concentrations in the dry season, this pattern was not consistent across sites or particularly pronounced within most sites. Given the pervasive influence of high-discharge events on seston concentrations, the lack of strong seasonal patterns in our baseflow datasets is not surprising, as our sampling regime did not account for periods with highest concentrations. Generally higher seston concentrations in Fortuna 2 were likely because it has the highest gradient and lowest proportion of depositional habitats of the sites we examined. Baseflow concentrations that we measured are on the low end of values reported for a variety of stream and catchment types in other regions (Whiles & Dodds, 2002; Dodds & Whiles, 2004), but within the range for undisturbed forested catchments (Golladay, 1997; Dodds & Whiles, 2004).

Differences in the quality of organic seston between pre-amphibian decline (El Copé) and post-decline (Fortuna) sites suggest that amphibian

extirpations in this region may have important ecological consequences. While we predicted that tadpoles would increase concentrations of fine particles through their feeding, egestion, and bioturbation, this pattern was not evident in our study, and was likely because we did not sample during storm events when most particles produced by tadpoles and other processes would be suspended in the water column as seston (e.g., Wallace et al., 1991, 2006). However, we did find a significant difference in baseflow seston quality (as measured as C/N), which has implications for filter-feeders in these streams as well as downstream food-webs. Filter-feeding organisms in streams can be limited by seston quality (Richardson, 1984; Fuller et al., 1988; Schneider et al., 1998) and seston represents an important export of materials and energy from headwaters to downstream reaches (Vannote et al., 1980; Minshall et al., 1985). While we cannot strictly attribute differences in C/N to tadpoles, these results provide intriguing circumstantial evidence for one of the potentially myriad ecological consequence of amphibian declines, and are intuitive considering that tadpoles grazing on periphyton and biofilms likely produce fecal particles that are relatively high in quality compared to other detrital particles in seston (e.g., refractory remnants of leaf detritus). Further, we only found significant differences in seston quality for fine seston particles (>250 μm), which encompasses the size range of most fecal materials produced by tadpoles in these streams (Whiles, unpublished data).

Our study was limited because of the low number of sites we examined. However, we performed comprehensive, year-round sampling on these remote, poorly studied systems, and these datasets can eventually be used to assess conditions before and after declines in the same systems. Given that catastrophic amphibian declines are ongoing in many regions of the planet (Stuart et al. 2004), particularly in the tropics (Lips et al. 2006), further studies are needed to fully assess the ecological consequences of these losses.

References

Abelho, M. & M. A. S. Graca, 1998. Litter in a first-order stream of a temperate deciduous forest (Margaraca Forest, central Portugal). Hydrobiologia 386: 147–152.

Addames, A. J., 1977. Evaluación ambiental y efectos del proyecto hidroelectrico Fortuna. Revista Loteria 254–255: 1–538.

Andrada, J., 2000. Panama National Parks. Ediciones Balboa, Panamá, Panamá.

Araujo-Lima, C. A. R. M., B. R. Forsberg, R. Victoria & L. Martinelli, 1986. Energy sources for detrivorous fishes in the Amazon. Science 234: 1256–1258.

Benfield, E. F., 2006. Decomposition of leaf material. In F. R. Hauer & G. A. Lamberti (eds), Methods in Stream Ecology, 2nd ed. Academic Press, San Diego California, USA: 711–720.

Benstead, J. P., 1996. Macroinvertebrates and the processing of leaf litter in a tropical stream. Biotropica 28: 367–375.

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

Bray, J. R. & E. Gorham, 1964. Litter production in forests of the world. Advances in Ecological Research 32: 101–157.

Brokaw, N. V. L., 1982. Treefalls: frequency, timing, and consequences. In E. G. Leigh Jr., A. S. Rand & D. M. Windsor (eds), The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes. The Smithsonian Institution Press, Washington D.C., USA: 101–108.

Chadwick, M. A. & A. D. Huryn, 2003. Effect of a whole-catchment N addition on stream detritus processing. Journal of the North American Benthological Society 22: 194–206.

Cillero, C., I. Pardo & E. S. Lopez, 1999. Comparisons of riparian vs. over stream trap location in the estimation of vertical litterfall inputs. Hydrobiologia 416: 171–179.

Covich, A. P., 1988. Geographical and historical comparisons of neotropical streams: biotic diversity and detrital processing in highly variable habitats. Journal of the North American Benthological Society 7: 361–386.

Crowl, T. A., V. Welsh, T. Heartsill-Scalley & A. P. Covich, 2006. Effects of different types of conditioning on rates of leaf-litter shredding by Xyphocaris elongate, a Neotropical freshwater shrimp. Journal of the North American Benthological Society 25: 198–208.

de Sousa, F., 1999. Fortuna Reserva Biologica. Editorial Universitaria, Panamá.

Dodds, W. K. & M. R. Whiles, 2004. Quality and quantity of suspended particles in rivers: continent-scale patterns in the United States. Environmental Management 33: 355–367.

Fittkau, E. J. & H. Klinge, 1973. On biomass and trophic structure of the central Amazonian rain forest ecosystem. Biotropica 5: 2–14.

Fuller, R. L., T. J. Fry & J. A. Roelofs, 1988. Influence of different food types on the growth of Simulium vittatum (Diptera) and Hydropsyche betteni (Trichoptera). Journal of the North American Benthological Society 7: 197–204.

Golladay, S. W., 1997. Suspended particulate organic matter concentration and export in streams. In J. R. Webster & J. L. Meyer (eds), Stream Organic Matter Budgets.

Journal of the North American Benthological Society 16: 122–131.

Graca, M. A. S., C. Cressa, M. O. Gessner, M. J. Feio, K. A. Callies & C. Barrios, 2001. Food quality, feeding preferences, survival and growth of shredders from temperate and tropical streams. Freshwater Biology 46: 947–957.

Grafius, E. & N. H. Anderson, 1979. Population dynamics, bioenergetics, and the role of Lepidostoma quercina Ross (Trichoptera: Lepidostomatidae) in an Oregon woodland stream. Ecology 60: 433–441.

Guerra, C. P. & I. A. Valdespino, 2002. Guide to Division General Omar Torrijos Herrera National Park. ANAM, Panamá.

Haines, B. & R. B. Foster, 1977. Energy flow through litter in a Panamanian forest. Journal of Ecology 65: 147–155.

Harmon, M. E., J. F. Franklin, F. J. Swanson, P. Sollins, S. V. Gregory, J. D. Lattin, N. H. Anderson, S. P. Cline, N. G. Aumen, J. R. Sedell, G. W. Lienkaemper, K. Cromack Jr. & K. W. Cummins, 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15: 133–302.

Harmon, M. E. & C. Hua, 1991. Coarse woody debris dynamics in two old-growth ecosystems—comparing a deciduous forest in China and a conifer forest in Oregon. Bioscience 41: 604–610.

Henderson, P. A. & I. Walker, 1986. On the leaf litter community of the Amazonian black water stream Tarumazinho. Journal of Tropical Ecology 2: 1–6.

Jackson, J. K. & B. W. Sweeney, 1995. Egg and larval development times for 35 species of tropical stream insects from Costa Rica. Journal of the North American Benthological Society 14: 115–130.

Jones, J. B., 1997. Benthic organic matter storage in streams: influence of detrital import and export, retention mechanisms, and climate. In J. R. Webster & J. L. Meyer (eds), Stream organic matter budgets. Journal of the North American Benthological Society 16: 109–119.

Lamberti, G. A. & S. V. Gregory. 2006. CPOM transport, retention, and measurement. In F. R. Hauer & G. A. Lamberti (eds), Methods in Stream Ecology, 2nd ed. Academic Press, San Diego, California, USA: 273–292.

Leigh, E. G., Jr. & D. M. Windsor, 1982. Forest production and regulation of primary consumers on Barro Colorado Island. In E. G. Leigh Jr., A. S. Rand & D. M. Windsor (eds), The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes. The Smithsonian Institution Press, Washington D.C., USA: 111–122.

Lips, K. R., 1999. Mass mortality and population declines of anurans at an upland site in western Panama. Conservation Biology 13: 117–125.

Lips, K. R., F. Brem, R. Brenes, J. D. Reeve, R. A. Alford, J. Voyles, C. Carey, L. Livo, A. P. Pessier & J. P. Collins, 2006. Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. Proceedings of the National Academy of Sciences 103: 3165–3170.

March, J. G. & C. M. Pringle, 2003. Food web structure and basal resource utilization along a tropical stream continuum, Puerto Rico. Biotropica 35: 84–93.

Meentemeyer, V., E. O. Box & R. Thompson, 1982. World patterns and amounts of terrestrial plant litter production. Bioscience 32: 125–128.

Minshall, G. W., K. W. Cummins, R. C. Peterson, C. E. Cushing, D. A. Bruns, J. R. Sedell & R. L. Vannote, 1985. Developments in stream ecosystem theory. Canadian Journal of Fisheries and Aquatic Sciences 42: 1045–1055.

Mosisch, T. D., S. E. Bunn & P. M. Davies, 2001. The relative importance of shading and nutrients on algal production in subtropical streams. Freshwater Biology 46: 1269–1278.

Newbold, J. D., B. W. Sweeney, J. K. Jackson & L. A. Kaplan, 1995. Concentrations and export of solutes from six mountain streams in northwestern Costa Rica. Journal of the North American Benthological Society 14: 21–37.

Padget, D. E., 1976. Leaf decomposition by fungi in a tropical rainforest stream. Biotropica 8: 166–178.

Petersen, R. C. & K. W. Cummins, 1974. Leaf processing in a woodland stream ecosystem. Freshwater Biology 4: 343–368.

Ranvestel, A. W., 2002. The influence of grazing tadpoles on algal biovolume, sediment dynamics, and aquatic insects in a tropical stream. M. S. Thesis, Southern Illinois University, Carbondale, Illinois, USA.

Ranvestel, A. W., K. R. Lips, C. M. Pringle, M. R. Whiles & R. J. Bixby, 2004. Neotropical tadpoles influence stream benthos: evidence for the ecological consequences of decline in amphibian populations. Freshwater Biology 49: 274–285.

Richardson, J. S., 1984. Effect of seston quality on the growth of a lake-outlet filter feeder. Oikos 43: 386–390.

Richardson, J. S., 1991. Seasonal food limitation of detritivores in a montane stream: an experimental test. Ecology 72: 873–887.

Rosemond, A. D., C. M. Pringle & A. Ramirez, 1998. Macroconsumer effects on insect detritivores and detritus processing in a tropical stream. Freshwater Biology 39: 515–523.

Rueda-Delgado, G., K. M. Wantzen & M. B. Tolosa, 2006. Leaf-litter decomposition in an Amazonian floodplain stream: effects of seasonal hydrological changes. Journal of the North American Benthological Society 25: 233–249.

Schneider, D. W., S. P. Madon, J. A. Stoeckel & R. E. Sparks, 1998. Seston quality controls zebra mussel (*Dreissena polymorpha*) energetics in turbid rivers. Oecologia 117: 331–341.

Stuart, S. N., J. S. Chanson, N. A. Cox, B. E. Young, A. S. L. Rodrigues, D. L. Fischman & R. W. Waller, 2004. Status and trends of amphibian declines and extinctions worldwide. Science 306: 1783–1786.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37: 130–137.

Wallace, J. B. & R. W. Merritt, 1980. Filter-feeding ecology of aquatic insects. Annual Review of Entomology 25: 103–132.

Wallace, J. B. & J. R. Webster, 1996. The role of macroinvertebrates in stream ecosystem function. Annual Review of Entomology 41: 115–139.

Wallace, J. B., T. F. Cuffney, J. R. Webster, G. J. Lugthart, K. Chung & B. S. Goldowitz, 1991. Export of fine organic particles from headwater streams: effects of season, extreme discharges, and invertebrate manipulation. Limnology and Oceanography 36: 670–682.

Wallace, J. B., M. R. Whiles, S. Eggert, T. F. Cuffney, G. H. Lugthart & K. Chung, 1995. Long-term dynamics of coarse particulate organic-matter in 3 Appalachian Mountain streams. Journal of the North American Benthological Society 14: 217–232.

Wallace, J. B., J. W. Grubaugh & M. R. Whiles, 1996. The influence of coarse woody debris on stream habitats and invertebrate biodiversity. In McMinn, J. W. & A. Crossley Jr. (eds), Biodiversity and Coarse Woody Debris in Southern Forests. General Technical Report SE-94. USDA Forest Service, Southeastern Forest Experiment Station, Ashville, North Carolina, USA: 119–129.

Wallace, J. B., S. L. Eggert, J. L. Meyer & J. R. Webster, 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277: 102–104.

Wallace, J. B., J. J. Hutchens Jr. & J. W. Grubaugh, 2006. Transport and storage of FPOM. In F. R. Hauer & G. A. Lamberti (eds), Methods in Stream Ecology, 2nd ed. Academic Press, San Diego, California, USA: 249–272.

Wantzen, K. M. & R. Wagner, 2006. Detritus processing by invertebrate shredders: a neotropical-temperate comparison. Journal of the North American Benthological Society 25: 216–232.

Webster, J. R. & J. L. Meyer (eds), 1997. Stream organic matter budgets. Journal of the North American Benthological Society 16: 3–161.

Webster, J. R., E. F. Benfield, T. P. Ehrman, M. A. Schaeffer, J. L. Tank, J. J. Hutchens & D. J. D'Angelo, 1999. What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta. Freshwater Biology 41: 687–705.

Whiles, M. R. & W. K. Dodds, 2002. Relationships between stream size, suspended particles, and filter-feeding macroinvertebrates in a Great Plains drainage network. Journal of Environmental Quality 31: 1589–1600.

Whiles, M. R., K. R. Lips, C. M. Pringle, S. S. Kilham, R. J. Bixby, R. Brenes, S. Connelly, J. C. Colón-Gaud, M. Hunte-Brown, A. D. Huryn, C. Montgomery & S. Peterson, 2006. The effects of amphibian population declines on the structure and function of Neotropical stream ecosystems. Frontiers in Ecology and the Environment 4: 27–34.

Wotton, R. S., 1990. Biology of particles in aquatic systems. CRC Press, Boca Raton, FL.