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Particulate organic matter dynamics in tropical headwater streams: a comparison of biotic and abiotic factors

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Introduction

Particulate organic matter often constitutes a large proportion of the energy fueling stream food webs (WALLACE et al. 1982, WEBSTER & MEYER 1997). As a consequence, stream ecologists have expended considerable effort in understanding the linkages between organic matter inputs, storage and transport. Detrital dynamics are strongly related to discharge (CUFFNEY & WALLACE 1989, WEBSTER & MEYER 1997, LARNED 2000) and more loosely associated with biotic assemblages. During periods of high discharge, detrital processing is often largely controlled by physical processes, showing little correlation with the biota (WEBSTER et al. 1994, RACTLIFFE et al. 1995). However, during periods of prolonged base flow conditions, detritus is often regulated by macro-shredders and consumers (CROWL et al. 2001). Tropical mountain streams are often characterized by steep gradients and highly variable rainfall, which results in torrential flows. These conditions typically lead to low retention of organic matter, high transport and minimal biotic processing. However, few studies have compared detrital storage, processing and transport across streams of various discharge regimes and biotic community assemblages to determine the relative strengths of physical and biotic processing (SPAIN 1984, PEARSON et al. 1989, SMOCK 1990, JONES & SMOCK 1991, RICHARDSON 1992).

In this study, detrital storage, transport and size fractionation in four first-order, headwater streams that comprise part of long-term ecological research at the Luquillo Experimental Forest, Puerto Rico are described. These streams are located across the forest landscape, resulting in differing elevations, gradients and discharge regimes while having very similar riparian input rates and composition. Moreover, each of these streams has a different macro-benthic community resulting in a range of physical and biotic gradients. These streams have been sampled biannually (during the dry and wet seasons) since 1998. In this paper, hydrologic and biotic features of each sampling site are linked with the amount of detrital material stored, transported and processed. Biotic interactions represent important drivers to the detrital web, even during periods of high and variable flows. During prolonged periods of base flow conditions, the biota represent the main indicator of detrital dynamics.

Methods

Study site

The four streams in the present analysis are first-order streams that begin at approximately 550-m elevations in the mountains of the Luquillo Experimental Forest, northeastern Puerto Rico (18° 18' N, 65° 47' W). Two of the study streams (Bisley 3 and Bisley 5) are first-order tributaries to the Rio Mameyes, a river that exhibits no geomorphic barriers to upstream dispersal of predatory fish. The remaining two study streams (Toronja and Prieta) are first-order tributaries to the Rio Espiritu Santo, and are situated upstream of a large main-channel waterfall (>10 m) which acts as a barrier to the upstream migration of predatory fish. The riparian forest is dominated by sierra palms (*Prestoa montana*) and tabonuco (*Dacryodes excelsa*) with 20 other species being common (LUGO & SCATENA 1995). The steeply sloped stream channels are cobble and boulder-lined. Mean annual precipitation is 360 cm/year and is seasonal, with more rainfall occurring from May to December and less from January to April. Stream flow, calculated from gage measurements (U.S. Geological Survey), is highly variable and rapidly responsive to rainfall events, especially during the wet season. The sites are within the areas under intensive study by the National Science Foundation's Long-term Ecological Research Program (see SCATENA 1989, LUGO & SCATENA 1995, COVICH et al. 1996 and CROWL et al. 2001, for further description).

The decapod fauna of these headwater streams consists of three families of shrimps (Atyidae, Palaemonidae, and Xiphocarididae), represented by 10 species, and one endemic freshwater crab (*Epilob-*

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ocera sinuatifrons: Pseudothelphusidae). Predatory fish include the freshwater mullet (*Agonostomus monticolus*: Mugilidae), the freshwater eel (*Anguilla rostrata*: Anguillidae), and three species of omnivorous gobies (*Awaous taiasica, Bathygobius soporator,* and *Gobiomorus dormitor*: Gobiidae). At high elevations, the only fish species present is the algivorous goby *Sycidium plumieri* (Gobiidae), which can negotiate waterfalls and rapids with its modified pelvic fins. The insect community of these headwater streams has been described by COVICH (1988), MASTELLER & BUZBY (1993), CROWL & COVICH (1994) & COVICH & MCDOWELL (1996).

Sampling

Distributions and abundances of shrimp in pools along each of the stream channels have been sampled biannually using baited wire traps. On each sampling date, pools were measured to determine surface area, volume, and maximum depth under different rainfall conditions (COVICH et al. 1991). Pool cross-sections were surveyed to determine bank widths, bank morphology, and locations of riparian tree species. In addition to shrimp abundances and physical habitat, organic matter size fractions (coarse >1 mm; fine <1 mm) were collected using benthic and drift nets. Replicate benthic organic matter samples were taken at each site by placing a 0.09-m^2 net over the substrate, washing the substrate into the net and then rinsing the net contents with alcohol into a sample cup. Replicate drift nets were set for approximately 24 h at each site, with exact times of setting and retrieving as well as velocity through each net recorded. Net contents were rinsed into sample cups using alcohol. Once in the laboratory, sample contents were rinsed through a 1-mm sieve to separate coarse and fine organic matter. Organic size fractions were then dried in a drying oven at 55 °C for 24 h and then ashed at 600 °C overnight. Ash-free dry weights (AFDW) were then recorded for each sample.

Statistical analyses

To determine how discharge versus biotic variables influenced organic matter storage, transport and processing, a series of hierarchical analyses were performed. In the first analysis, fine and coarse organic matter from the benthos (stored) and from the drift between wet and dry seasons pooled across streams and sites were compared using a one-way analysis of variance. In the second analysis, the same dependent variables in the wet and dry season were compared, but for each stream independently. Finally, stepwise linear regression models were used to determine which physical and biotic variables best explained the observed variance in organic matter processing. All analyses were performed using the SAS statistical package for micro-computers.

Results and discussion

If organic matter transport (FPOM and CPOM in the drift) and storage (FPOM and CPOM from the substrate) were strongly controlled by abiotic factors such as discharge magnitude and variability, large differences in those variables between dry-season samples, which represent prolonged base-flow conditions, and wet-season samples (periods of high and fluctuating flows) independent of stream or site would be expected. Rather, no significant differences were observed for these variables when all samples were pooled by hydroperiod (Fig. 1). Neither CPOM ($F = 0.02$, $P = 0.9010$, df = 1,47) or FPOM ($F = 0.17$, $P = 0.6792$, df = 1,47) from the drift showed significant differences between seasons. Similarly, CPOM stored in the substrates was not different among seasons ($F = 0.93$, $P = 0.3400$, df = 1,48). Only FPOM sampled from the substrate showed weak differences between seasons ($F = 4.78$, $P = 0.0330$, df = 1,48), with more fine particles being stored during the wet season (Fig. 1).

Because considerable variation occurs among the streams in terms of hydrology, physical variables and macro-biota, values for the same four organic matter variables were compared between wet and dry seasons for each stream separately. When data were analyzed in this fashion, numerous significant differences were observed (Fig. 2). However, little consistency was observed among the streams, again suggesting that simple differences in hydrograph could not explain the dynamics of organic matter storage, transport or processing. For example, CPOM in the drift was significantly higher during the dry season in the Prieta and Bisley 3 as compared to the wet season, but the opposite pattern was observed for the Toronja and Bisley 5. Fine particles drifted more in the Prieta and Toronja during the wet season relative to the dry season, but the opposite pattern was observed in Bisley 3 and 5. Similar inconsistencies were found for CPOM stored in the substrate. Fine particles stored in the substrates

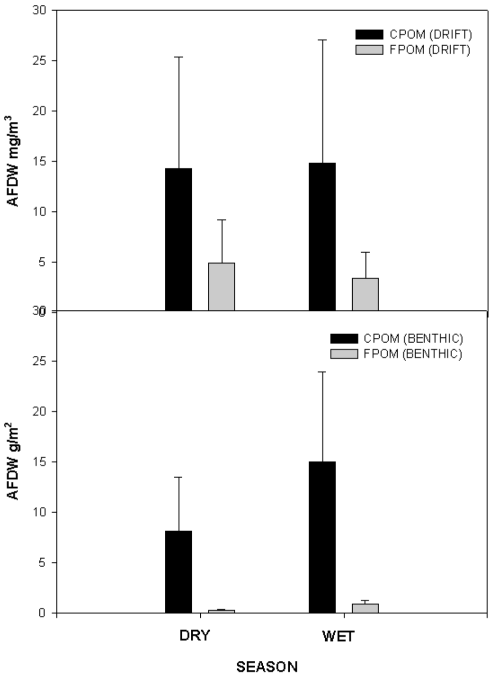

Fig. 1. Biomass of coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM) in transport (drift) and storage (benthic) for all sites and streams pooled during the dry and wet seasons. All weights are ash-free dry mass.

showed no differences for any streams between wet and dry seasons (Fig. 2).

When all the information on discharge, physical characteristics and decapod assemblage and densities was combined, it explained between 32 and 62% of the variation in organic matter storage and transport (Table 1). In almost all cases, the density and species composition of the shrimp explained the highest amount of variation, with physical variables rarely being important. This analysis suggests that biotic processing by decapods is the most important driving variable for organic matter processing, at least in these small, headwater streams.

In previous work, important biotic effects of decapods on overall community dynamics (Crowl & Covich 1994, Crowl et al. 2001a) and organic matter transport (Crowl et al. 2001b) were seen in small pool experiments.

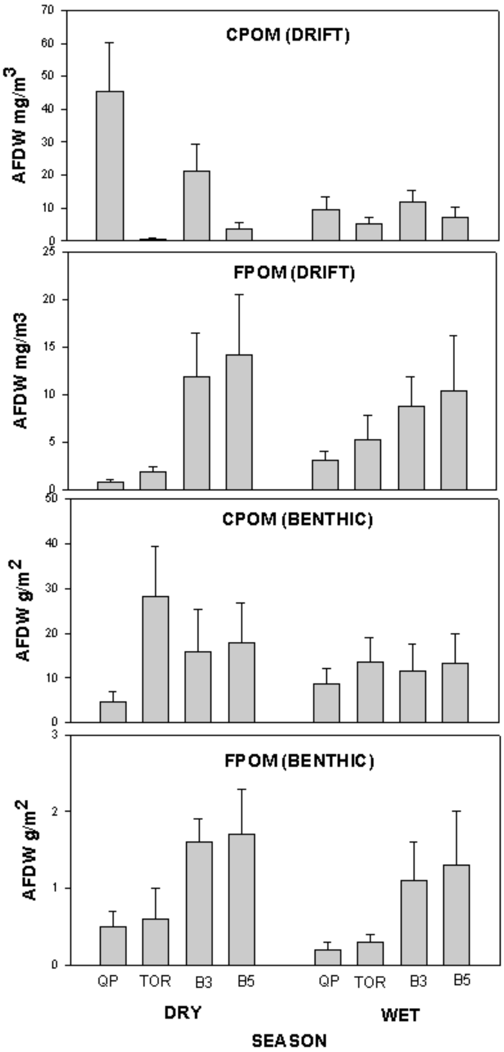

Fig. 2. Biomass of coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM) in transport (drift) and storage (benthic) for each stream during the dry and wet seasons separately. All weights are ash-free dry mass.

These analyses suggest that biotic interactions occur at a larger scale and over a wider range of hydrologic conditions than previously noted. The role of macro-biota in processing leaf litter is certainly not a new finding (Anderson & Sedell 1979, Benstead 1996); however, the spatial and temporal extent of these findings

Table 1. Stepwise regression results for each site analyzed separately.

Response variable	Predictor	R-square	F	P
CPOM (drift)	*Xiphocaris* density	61.4	24.2	<0.0001
FPOM (drift)	*Atya* density	20.2	5.3	0.0313
	Xiphocaris density	10.1	3.9	0.0587
CPOM (benthic)	*Xiphocaris* density	22.5	8.0	0.0181
	Discharge	9.3	3.3	0.0951
FPOM (benthic)	*Atya* density	22.8	8.7	0.0098
	Pool depth	6.1	2.8	0.1013

differed. Many other studies have suggested a more modest role for biotic processing, with much more importance put on riparian inputs and physical variables affecting storage and transport (GRAY 1997, MARXSEN et al. 1997). These preliminary analyses and results provide a template to carry out larger scale manipulations of both decapod assemblage structures and riparian inputs to determine how organic matter is processed and cycled in these tropical headwater streams.

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