

Temporal dynamics of seston: A recurring nighttime peak and seasonal shifts in composition in a stream ecosystem

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Abstract

We measured the baseflow concentration and composition of seston and suspended particulate organic carbon (POC) over a 1-yr period in White Clay Creek, a third-order stream in the southeastern Pennsylvania Piedmont, to assess temporal variability in seston concentration and quality at seasonal and diel timescales. Each month, we sampled stream water under baseflow conditions every 1.5 h over a 24-h period and measured seston and POC concentrations, carbon composition, pigment content, and ¹³C isotopic ratios. Seston and POC concentrations exhibited a strong diel pattern; nighttime concentrations exceeded daytime concentrations by 80% and 43%, respectively. Suspended chlorophyll *a* concentrations did not exhibit a diel pattern. We attribute the diel pattern of seston concentration to bioturbation by the nocturnal stream community, including crayfish, amphibians, eels, and macroinvertebrates. Seasonally, carbon content of seston increased from 9% throughout most of the year to 15% during November, December, and March, while seston $\delta^{13}\text{C}$ was depleted in the late fall and enriched in early spring months relative to the rest of the year. Chlorophyll *a* and pheophytin *a* concentrations in seston peaked during the early spring. Seasonal patterns in seston and POC composition reflect cycles of autumnal leaf litter inputs and vernal algal production. Bioturbation and shifts in organic carbon inputs mediate changes in POC quality and fluxes, which affect the bioavailability of POC and ultimately influence rates of heterotrophic respiration.

Particulate organic carbon (POC) provides energy for microorganisms and macroinvertebrates in headwater streams and, when transported in the suspended load (seston), supports heterotrophic metabolism in downstream reaches and rivers (Wipfli and Gregovich 2002; Mayorga et al. 2005). POC transport represents a longitudinal linkage between upstream autochthonous and allochthonous production and downstream ecosystems, where the magnitude of connection is controlled by the quality, quantity, and timing of POC delivery (Mayorga et al. 2005).

Hydrological and biological dynamics control the timing of seston and POC transport from headwaters. Storms are the most important factor regulating the magnitude of seston and POC fluxes (Golladay et al. 2000). However, because small streams are under baseflow conditions most of the time, temporal POC dynamics under baseflow conditions may disproportionately regulate or reflect stream ecosystem processes such as nutrient cycling or metabolism. For example, White Clay Creek, the third-order eastern Piedmont stream from this study, is at base flow 90% of the time (Newbold et al. 1997), when most heterotrophic respiration occurs. Therefore, we focused on baseflow transport of seston and POC. At base flow, seasonal peaks of POC concentration have been attributed to increased macroinvertebrate fragmentation of leaf litter as stream temperature increases (Molla et al. 2006).

However, diel patterns of seston transport have not been extensively examined. Peaks in seston concentration found in a deciduous European forest stream at midmorning and evening were attributed to diurnal rhythms in algal drift (Pozo et al. 1994), but no diel patterns were found in either boreal (Naiman 1982) or glacier-fed alpine streams (Hieber et al. 2003). Information about temporal patterns can help evaluate the sources of POC (Kendall et al. 2001), quality of the energetic subsidy to downstream biota (Rosi-Marshall 2004), controls on transport (Pozo et al. 1994), and lead to better estimates of baseflow POC fluxes, especially in streams with pulsed inputs of organic matter (Fisher et al. 2004).

Seston is defined as suspended particulate material in natural waters. As such, seston is potentially a mixture of algal and bacterial cells and their remains, leaf or wood fragments in various stages of decomposition, flocculates of dissolved organic carbon, inorganic sand, silt- and clay-sized minerals that typically contain small quantities of adsorbed organic carbon, and stable aggregates of these various materials. Historical observations of seston in streams, primarily rooted in ecology, have focused on organic-based particles of terrestrial origin, such as fragments of leaves and wood created by macroinvertebrate feeding and egestion upstream (Vannote et al. 1980). More recent stable isotope and chlorophyll *a* (Chl *a*) studies have supported the idea that stream POC is primarily terrestrial (Finlay et al. 2002), with minimal contributions from autochthonous production (Angradi 1993). However, many stream ecology studies have ignored the inorganic components of seston, which can be significant even in small streams (Wallace et al. 1982a). On the other hand, studies of seston in rivers, which are largely rooted in geochemistry, have demonstrated with elemental, radioisotope, and microscopic evidence that most seston in rivers is

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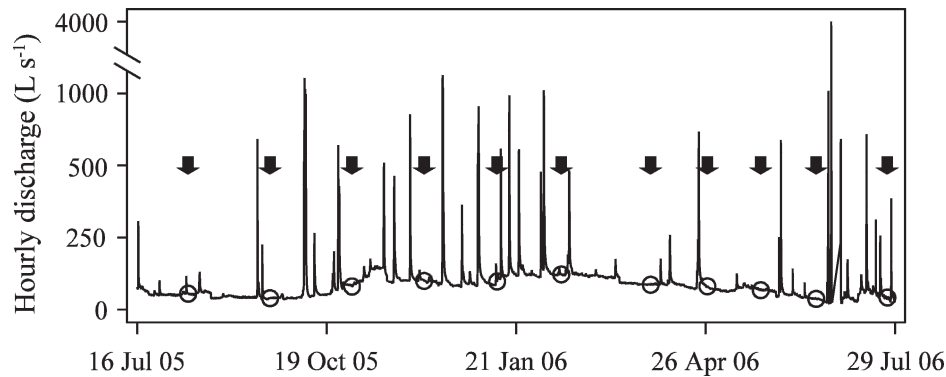


Fig. 1. Hourly discharge of White Clay Creek over the sampling period. Arrows and circles indicate sampling days (11 Aug 05, 21 Sep 05, 01 Nov 05, 07 Dec 05, 12 Jan 06, 24 Feb 06, 31 Mar 06, 27 Apr 06, 24 May 06, 20 Jun 06, 26 Jul 06). Note the break in the y -axis scale to account for one large storm in 28 Jun 06.

composed of small ($<20 \mu\text{m}$), high-mineral-content particles that are low in carbon content (0.5–3% organic carbon), old (50–5000 yr), and have carbon to nitrogen ratios lower than leaves or wood (Meybeck 1982; Mayorga et al. 2005). These perspectives were first reconciled by Meybeck (1982), who showed that seston in the world's rivers spanned the range from high to low carbon content with increasing seston concentration and suggested that these trends represented systematic variation in the contributions of different particle types to seston. We thus consider seston as a mixture of three fundamental particle types: inorganic particles with adsorbed terrestrially derived organic matter (Aufdenkampe et al. 2001), algal cells, and fragmented leaves or woody debris. We used a comprehensive array of measurements to characterize seston, distinguish these particle types, and infer the sources of POC.

We report results from intensive field surveys of seston quantity and quality in a third-order piedmont stream in southeastern Pennsylvania. We measured the concentration and composition of seston through monthly diel sampling regimes over a 1-yr period to assess the temporal variability in seston transport and quality at both seasonal and diel timescales. Here, we report a consistent and repeatable diel pattern of nighttime peaks in seston and POC concentrations that we attribute to bioturbation and seasonal shifts in composition associated with annual cycles of autumnal leaf-fall and vernal algal production prior to canopy closure.

Methods

Site description—The upper east branch of White Clay Creek (WCC: $39^{\circ}51'30''\text{N}$, $75^{\circ}46'60''\text{W}$) is a third-order watershed that drains 7.3 km^2 of eastern Piedmont. In this watershed, 23% of the total area is temperate deciduous forest with a largely intact riparian forest, 52% is pastures or hay fields, and 22% is row crop agriculture (Newbold et al. 1997). The mean daily baseflow discharge averaged 122 L s^{-1} from 2000 to 2006, with a high annual mean discharge of 174 L s^{-1} and low of 59 L s^{-1} . At base flow, WCC has high nutrient concentrations ($3\text{--}5 \text{ mg NO}_3\text{-N}$

L^{-1} ; $4\text{--}33 \mu\text{g PO}_4\text{-P L}^{-1}$) from agricultural land use and dissolved organic carbon (DOC) concentrations of $1.5 \text{ mg DOC L}^{-1}$ (Newbold et al. 1997). Most of the particulate organic matter input (predominantly leaves) occurs from late October to mid-November (R. L. Vannote unpubl.).

Temperature and discharge—Stream water temperature was recorded using automated temperature loggers (Onset Computer Corporation), and stream stage was recorded using an automated pressure transducer (Telog Instruments), both at 15-min intervals. Stream stage was converted to stream discharge using a 10-yr rating curve and was averaged to hourly discharge. We used the discharge record to identify antecedent storm discharges and defined storm flows as greater than two times baseflow discharge because such flows typically result in bed mobilization in WCC (Newbold et al. 1997).

Sampling protocol—Under baseflow conditions, stream water was collected every 1.5 h during one 24-h period every 30 to 40 d from August 2005 to July 2006 (Fig. 1) using an automated water sampler (Teledyne Isco), with the collection tube (9.5 mm inner diameter) at two-thirds depth in the middle of the stream. Sampling days (11 Aug 05, 21 Sep 05, 01 Nov 05, 07 Dec 05, 12 Jan 06, 24 Feb 06, 31 Mar 06, 27 Apr 06, 24 May 06, 20 Jun 06, 26 Jul 06) were not sampled in even intervals; however, we have delineated names based on the sampling month (Aug, Sep, Nov, Dec, Jan, Feb, Mar, Apr, May, Jun, Jul). In August 2006, sampling included three additional sites, all second-order streams within the watershed upstream of the WCC site. Throughout the text, we refer to this sampling effort as spatial sampling. At each of the four locations, three samples were taken at night and three were taken during the day to ascertain whether diel patterns extended upstream within the stream network.

The automated sampler was set to collect four 1-liter samples at each time period. The first sample was considered a rinse of the inflow tubing and discarded, the second was used for pigment analysis, and the final two samples were used for replicate seston and POC analyses. Only the first replicate of seston and POC analysis is

reported; the second replicate was used to calculate the precision of the automated sampling or as a substitute if the first replicate was lost. Grab samples were taken as a check for bias and accuracy in the automated sampling of stream seston. Once or twice each month, three replicate grab samples for seston were taken simultaneously with the automated sampling by submerging 1-liter bottles at two-thirds depth.

Seston—Seston concentration was determined gravimetrically using the dry weight of total suspended solids. Entire 1-liter stream water samples were filtered, after recording the precise volume, through stacked pairs of preweighed and pre-ashed (480°C for 4.5 h), 47-mm glass fiber filters (Millipore AP40 with nominal pore size of 0.7 µm). The sample was filtered through two filters to check analytical accuracy, assess the integrity of the top filter, and ensure even distribution of seston across the filter. The sample was discarded if the bottom filter gained or lost more than 0.2 mg. The filters were dried for 12–18 h at 60°C, reweighed to calculate seston mass on the filter, which was divided by the filtered volume to calculate seston concentration (mg seston L⁻¹).

Pigments—Samples for pigment analysis were filtered onto a glass fiber filter (Millipore AP40), frozen, and processed within 30 d using a hot ethanol extraction method. The samples were heated to 78°C for 10 min in 90% ethanol and then stored frozen for 24 h. Chl *a* and pheophytin *a* (Pheo *a*) concentrations (µg L⁻¹) were calculated using measurements of absorbance on a spectrophotometer (Beckman Coulter DU-640) before and after acidification. Pheo *a*, a degradation product of Chl *a*, suggests dead or senescing algal cells (Peterson and Stevenson 1992).

Elemental and stable isotope analysis—Subsamples of each seston filter were wetted with nanopure water and fumed with hydrochloric acid vapors for 18 h, effectively removing carbonates (A. K. Aufdenkampe unpubl.). Subsamples were analyzed in batches on an Elemental Analyzer (Costech ECS 4010) interfaced with an Isotope Ratio Mass Spectrometer (Thermo DeltaPlus XP). Standard curves for the elemental and isotopic analyses were created for each batch using eight or nine isotopically enriched (+37.63‰) or depleted (−26.39‰) L-glutamic acid standards over a range of carbon masses that bracketed the subsample masses. Stable carbon isotope ratios, reported using δ¹³C notation, were normalized relative to the Vienna Pee Dee Belemnite standard. POC concentration (mg L⁻¹) was calculated from the mass of C analyzed, the fraction of total sample analyzed, and the volume of stream water filtered. Weight percent organic carbon of seston (carbon content) was calculated as the ratio of POC (mg L⁻¹) to seston (mg seston L⁻¹) concentrations, and POC flux (mg s⁻¹) was calculated by multiplying the POC concentration (mg L⁻¹) by the average hourly discharge (L s⁻¹).

End-member analysis—Four species of dried, senesced leaves (American beech: *Fagus grandifolia* Ehrh., northern

red oak: *Quercus rubra* L., red maple: *Acer rubrum* L., and tulip poplar: *Liriodendron tulipifera* L.) were collected from the forest floor, dried, and analyzed for stable carbon isotopes as potential allochthonous sources of POC. In May 2007, epilithon (predominantly *Melosira varians*), collected from six rocks in riffles in WCC and rinsed carefully to remove large sediments and trapped leaf pieces, was analyzed for stable carbon isotopes as potential autochthonous sources of POC.

Mixing model—We modeled seston composition as a mixture of two distinct particle types: organic-based particles composed of algal cells, leaf fragments, and bacterial cells (carbon content for mixture = 45%); and mineral-core particles with adsorbed organic carbon and bacterial cells (carbon content = 1.5%) (Meybeck 1982; Hedges et al. 1986). For each sample, we simultaneously solved Eqs. 1 and 2

$$S = P_o + P_m \quad (1)$$

$$\text{POC} = 0.45 \times P_o + 0.015 \times P_m \quad (2)$$

using measured seston (*S*) and POC concentrations to determine the concentration of organic-based (*P_o*) and mineral-core (*P_m*) particles in seston and the concentration of organic-based (0.45 × *P_o*) and mineral-core (0.015 × *P_m*) particles in POC. Mixing model results are reported as the fraction of total concentration by particle type (e.g., *P_o*/*S* as the organic-based particle fraction of seston by weight). Modeling results were split post-hoc into two groups: months with increased organic inputs from allochthonous (Nov, Dec) and autochthonous sources (Mar) and lower organic inputs (all other months).

Environmental scanning electron microscopy (ESEM)—Seston was collected on 16 January 2006 from WCC, and images of particles in stream water were captured at ×1300 to ×14,500 magnification using an environmental scanning electron microscope (Electro Scan) with an accelerating voltage of 28 kV.

Statistical analyses—All statistical analyses were conducted using SAS v9.1 Level 1M3 (2007, SAS Institute). We performed two-way ANOVAs (PROC MIXED) for seston, POC, Chl *a* and Pheo *a* concentrations, POC flux, percent carbon of seston, and δ¹³C data with month and day-or-night as treatments. For the spatial sampling, we performed two-way ANOVAs for seston, POC and Chl *a* with station and day-or-night as treatments. To ensure homogeneity of variances, several variables (seston, POC) were log-transformed; these are reported as back-transformed geometric means. Following each ANOVA, we made multiple mean comparisons using Tukey's test. Tests of auto-correlation (Durbin-Watson) revealed a violation of ANOVA assumptions of independence of residuals for seston, POC, carbon content, POC flux, and stable isotopes within each month. Therefore, to achieve a conservative test of the overall diel effect for each of these parameters, we used a paired *t*-test based on the monthly pairs of day

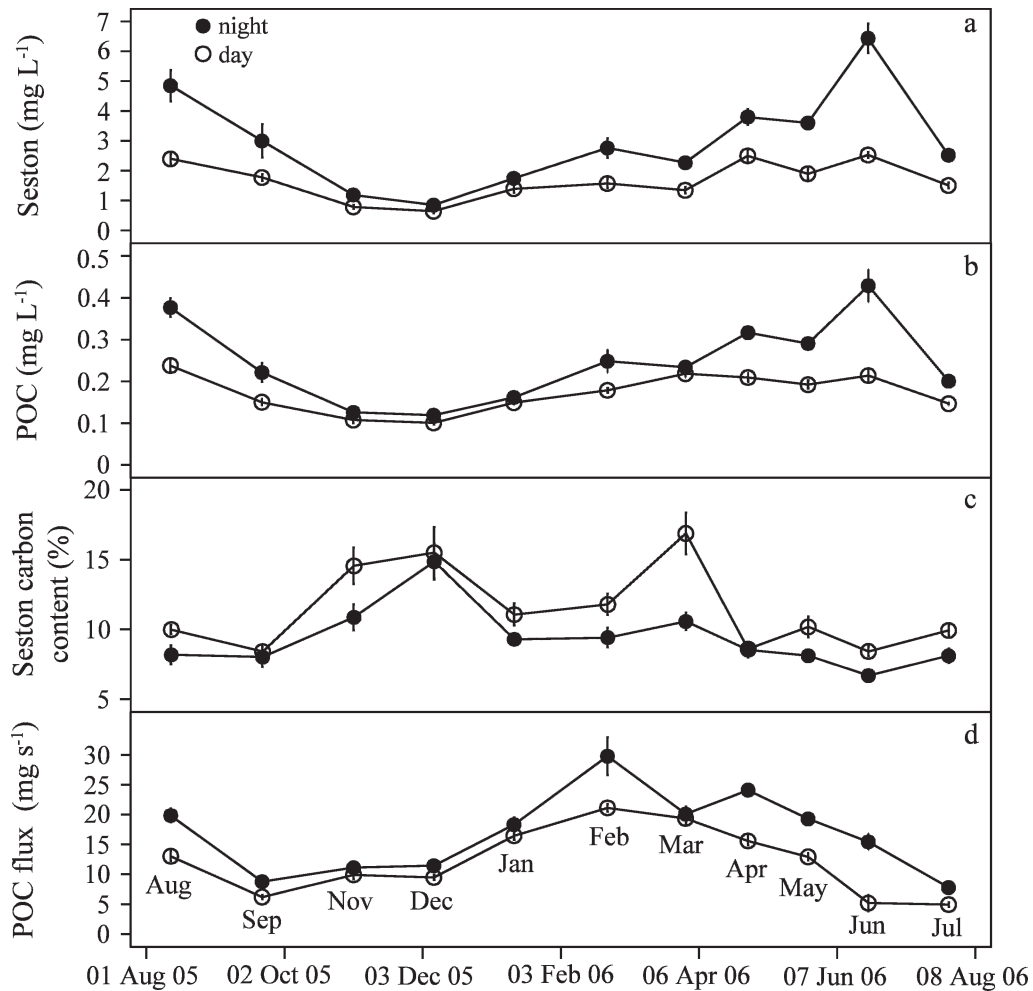


Fig. 2. Seasonal changes in (a) seston concentration, (b) particulate organic carbon concentration, (c) seston carbon content, and (d) particulate organic carbon flux for day and night samples. The means were plotted against Julian day because of uneven intervals between sampling periods but are identified as the month in which they were sampled. Error bars are standard errors; some cannot be seen when smaller than the symbol.

and night means, rather than the ANOVA main effect, reducing the error-degrees of freedom from 163 to 10. We did, however, use the within-month mean squared error in conjunction with Tukey's test to identify specific months in which the diel effect was observed, reasoning that most or all of the serial auto-correlation reflected real (mechanistic) trends over the course of the day or night, rather than oversampling of the random error.

Linear correlation (PROC REG) was used to identify relationships among dependent and explanatory variables of interest, including temperature, discharge, and antecedent storm timing and magnitude. Outliers were identified (PROC ROBUSTREG) using a prespecified residual value (3.0). For quality control, we analyzed the correlation between the automated sampler and grab samples and compared the slope and intercept to the 1:1 line using *t*-tests (PROC TTEST). For the mixing model results, fractions of seston and POC as mineral-core and organic-based particles were compared among the grouped months using paired *t*-tests (PROC TTEST).

Results

Over the year, 183 samples were taken during baseflow conditions on 11 monthly sampling days over 24 h to 25.5 h (Fig. 1). Mean water temperatures ranged from 2°C in December to 20°C in August and July, while mean daytime temperature exceeded nighttime temperatures by at least 0.15°C (November) and as much as 1.5°C (April). WCC discharges during sampling ranged from 23 L s⁻¹ in June to 120 L s⁻¹ in February (Fig. 1), with minimum discharge in late summer and maximum discharge in winter. Daytime discharge did not differ from nighttime discharge ($t = 0.96$, $df = 10$, $p = 0.35$). A series of storms occurred during the winter; one large summer storm, on 28 June 2006, reached twice the maximum discharge of any other storm (Fig. 1).

Seston and POC—Over the year, nighttime seston and POC concentrations exceeded daytime concentrations by 80% and 43%, respectively (Fig. 2a, 2b, Table 1). While

Table 1. Day and night averages of seston and POC concentrations (mean \pm SE), percentage increase from day to night (diel increase), and statistical results from the day and night differences (diel effect), month effect, and interaction effect (diel \times month) for all 11 sampling months and the sampling month with the greatest diel increase (June 2006).

Time period	Parameter	Night	Day	Diel increase	ANOVA results		
					Diel effect	Month effect	Interaction effect
All 11 months	seston (mg L ⁻¹)	3.0 \pm 0.07	1.7 \pm 0.07	80%	$t=8.7$, $df=10$, $p<0.001$	$F_{10,163}=67$, $p<0.001$	$F_{10,163}=2.4$, $p=0.01$
	POC (mg C L ⁻¹)	0.24 \pm 0.005	0.17 \pm 0.005	43%	$t=3.9$, $df=10$, $p=0.003$	$F_{10,156}=42$, $p<0.001$	$F_{10,156}=8.6$, $p<0.001$
June 2006	seston (mg L ⁻¹)	6.4 \pm 0.43	2.5 \pm 0.21	155%	$t=7.1$, $df=1$, $p=0.04$		
	POC (mg C L ⁻¹)	0.43 \pm 0.017	0.21 \pm 0.013	105%	$t=9.9$, $df=1$, $p=0.03$		

mean nighttime concentrations were always greater than daytime concentrations, the difference was suppressed during winter months (Fig. 2a,b; Table 1). Seasonally, seston and POC concentrations were lowest during the late fall and winter months and highest in the summer (Fig. 2a,b; Table 1). We observed the largest diel variation of seston and POC in June, when the nighttime seston and POC concentrations exceeded daytime concentrations by 155% and 105%, respectively (Fig. 3; Table 1).

Neither seston nor POC concentrations, averaged by month, were correlated with stream discharge or with time since antecedent storm ($p > 0.05$). However, seston concentration was correlated with other physical changes in the stream. Water temperature was positively correlated with both day (Fig. 4; $n = 11$, $p = 0.02$, $r^2 = 0.45$) and night (Fig. 4; $n = 11$, $p = 0.02$, $r^2 = 0.45$) seston concentrations. The slopes for day (0.07 ± 0.03 : mean \pm SE) and night (0.18 ± 0.07 : mean \pm SE) regression fits were not statistically different from each other (Fig. 4; $t = 1.55$, $df = 18$, $p = 0.13$). Mean nighttime POC concentrations were also positively correlated with water temperature ($n = 11$, $p = 0.05$, $r^2 = 0.37$), but daytime concentrations were not ($n = 11$, $p > 0.05$, $r^2 = 0.26$). The maximum discharge from the antecedent storm was negatively correlated with nighttime seston ($n = 11$, $p = 0.04$, $r^2 = 0.39$) and POC ($n = 11$, $p = 0.04$, $r^2 = 0.38$) concentrations but not with

daytime concentrations ($p > 0.05$). The maximum discharge from the antecedent storm was negatively correlated with the percentage increase of seston from day to night (Fig. 5; $n = 11$, $p = 0.005$, $r^2 = 0.61$). However, the antecedent storm discharge did not explain diel differences in POC concentrations ($n = 11$, $p = 0.09$, $r^2 = 0.28$).

Carbon content—The daytime carbon content ($11.4\% \pm 0.2\%$: mean \pm SE) exceeded the nighttime carbon content ($9.3\% \pm 0.2\%$: mean \pm SE) by 2.1% (Fig. 2c; $t = 3.9$, $df = 10$, $p = 0.003$). Although the mean carbon content was higher in the daytime than in the nighttime each month, the difference was significant only for November and March. The percent carbon varied seasonally; the highest values occurred in November, December, and March ($F_{10,156} = 18$, $p < 0.001$).

Baseflow POC flux—The downstream flux of POC had both diel and seasonal trends. The nighttime POC fluxes (Fig. 2d; $17.3 \text{ mg s}^{-1} \pm 0.9$: mean \pm SE) were 45% greater than daytime fluxes ($11.9 \text{ mg s}^{-1} \pm 0.6$: mean \pm SE; $t = 4.5$, $df = 10$, $p = 0.001$). The magnitude of this effect was buffered in the winter, when both the day-night differences in POC concentration were lower and the stream discharge

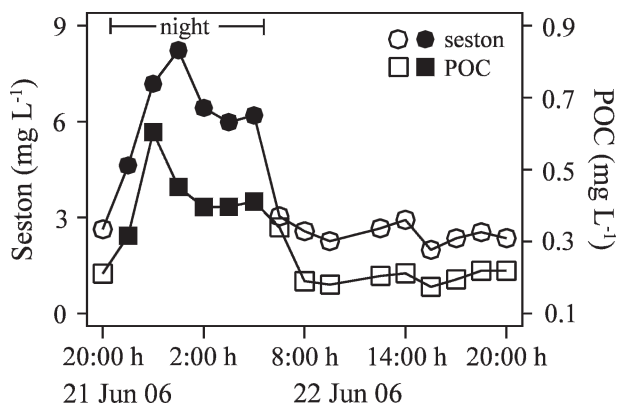


Fig. 3. Example diel curve of seston concentration (left vertical axis) and particulate organic carbon (POC) concentration (right vertical axis).

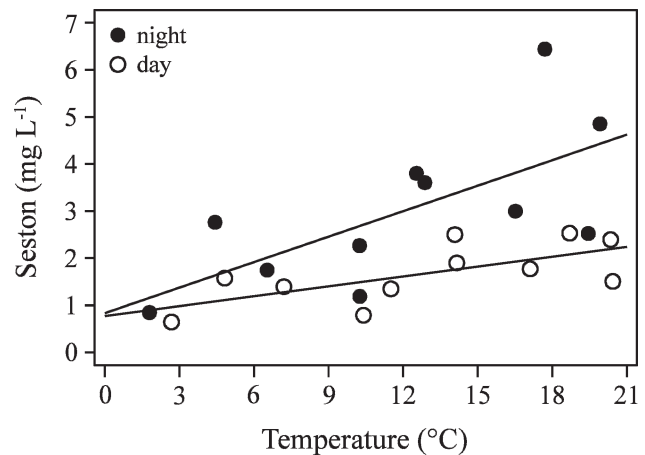


Fig. 4. Least-squares linear regressions between temperature and seston concentration for both day (seston = $0.07[\text{temperature}] + 0.78$, $r^2 = 0.45$, $p = 0.02$) and night (seston = $0.18[\text{temperature}] + 0.83$, $r^2 = 0.45$, $p = 0.02$) samples.

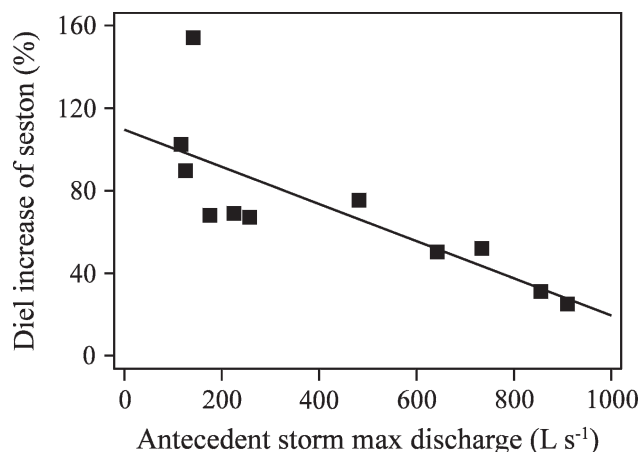


Fig. 5. Least-squares linear regressions between the maximum discharge of the antecedent storm and the increase of total seston concentration from day to night for each sampling month ($\% \text{ increase} = -0.09[\text{max discharge}] + 119$, $r^2 = 0.61$, $p = 0.005$).

was higher (interaction effect: $F_{10,155} = 3.7$, $p < 0.001$). POC flux varied seasonally, peaking during the late winter and early spring ($F_{10,155} = 45$, $p < 0.001$).

Pigments—Chl *a* concentration ($1.26 \mu\text{g L}^{-1} \pm 0.8$: mean \pm SE) was less variable than seston or POC concentrations. Chl *a* varied by month (Fig. 6a; $F_{10,165} = 5.32$, $p < 0.001$), but there were neither diel ($t = 0.2$, $df = 10$, $p = 0.77$) nor interaction effects ($F_{10,165} = 1.33$, $p = 0.22$). The mean Chl *a* concentrations for March were significantly greater than all other months ($p < 0.05$). Pheo *a*, unlike Chl *a*, showed a diel difference (Fig. 6b; $t = 5.3$, $df = 10$, $p < 0.001$), where nighttime Pheo *a* concentrations ($2.10 \mu\text{g L}^{-1} \pm 0.07$: mean \pm SE) were greater than daytime concentrations ($1.56 \mu\text{g L}^{-1} \pm 0.07$: mean \pm SE).

Pheo *a* concentrations also varied by month ($F_{10,165} = 122$, $p < 0.001$) and could be divided into three groups: highest concentrations during February and March, intermediate concentrations during late spring and summer, and lowest concentrations during the late fall and early winter. Pheo *a* concentrations were more variable than Chl *a* and included monthly means both lower than and double the average Chl *a* concentration (Fig. 6a,b).

Stable carbon isotopes—The highest $\delta^{13}\text{C}$ value of POC occurred during March, while the lowest values occurred during December and January (Fig. 7; $F_{10,142} = 28$, $p < 0.001$). For potential allochthonous end members, all four species of leaves had similar $\delta^{13}\text{C}$ values (Fig. 7, box b; $-28.2\text{‰} \pm 0.6$: overall mean \pm SD) that were more depleted than the autochthonous epilithic algae (Fig. 7, box a; $p = 0.03$, $-26.5\text{‰} \pm 1.6$: overall mean \pm SD). The $\delta^{13}\text{C}$ value was positively correlated with mean pigment (Chl *a* + Pheo *a*) concentrations (Fig. 8; $n = 11$, $p = 0.016$, $r^2 = 0.49$); this trend was driven by the February and March peaks in pigment concentrations. The $\delta^{13}\text{C}$ of March samples (-25.7 ± 0.24 : mean \pm SE) was greater than the end member for epilithic algae, but it was within one standard deviation of the end-member mean. The $\delta^{13}\text{C}$ value of POC showed neither diel ($t = 0.66$, $df = 10$, $p = 0.52$) nor interaction effects ($F_{10,142} = 1.48$, $p = 0.15$).

Mixing model—Throughout the year, mineral-core particles contributed to $>70\%$ of seston concentration, and organic-based particles contributed $<30\%$ of seston concentration by weight. However, organic-based particles consistently contributed the majority of POC concentration by weight (Table 2). The contribution of organic-based particles to both seston and POC increased during periods of increased carbon influx (November, December, and

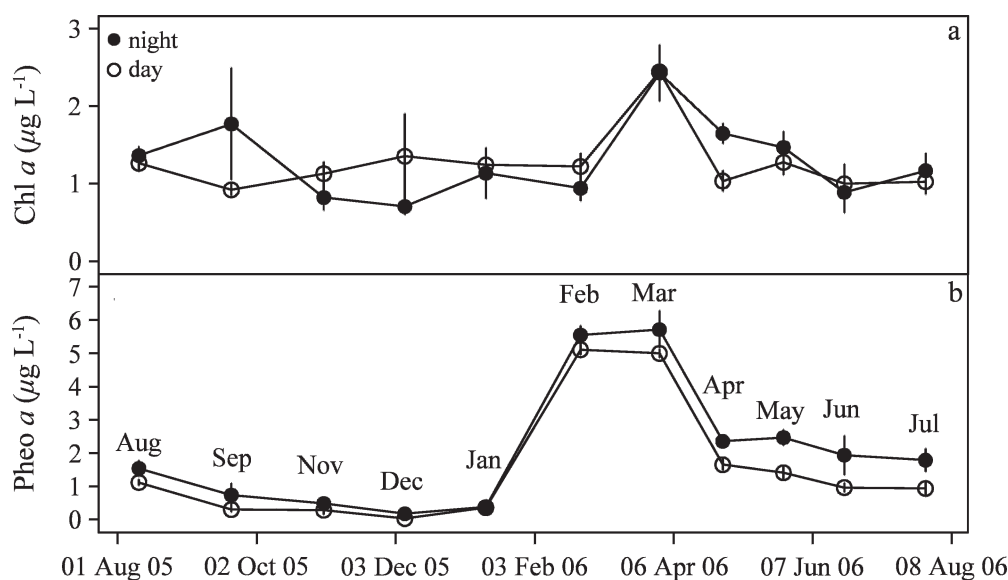


Fig. 6. Seasonal changes in (a) Chl *a* and (b) Pheo *a* concentrations for day and night samples. The means were plotted against Julian day because of uneven intervals between sampling periods but were identified as the month in which they were sampled. Error bars are standard errors; some cannot be seen when smaller than the symbol.

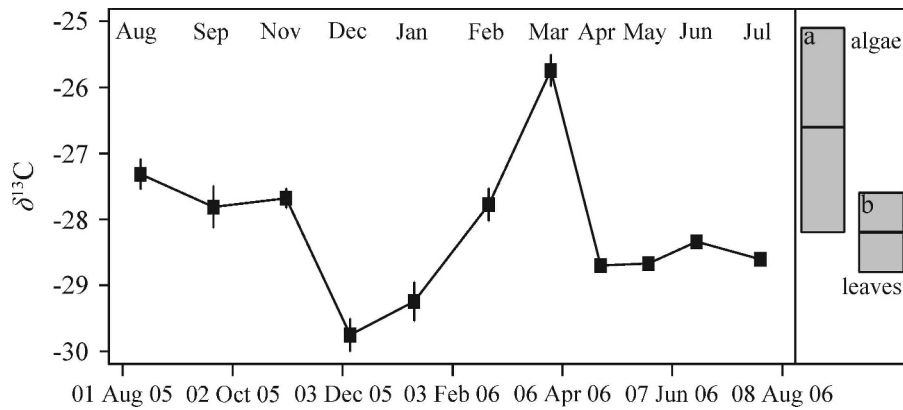


Fig. 7. Seasonal changes in δ¹³C of POC averaged across day and night samples. The means were plotted against Julian day because of uneven intervals between sampling periods but were identified as the month in which they were sampled. Error bars are standard errors; some cannot be seen when smaller than the symbol. Boxes (mean ± 1 SD) represent the range of δ¹³C of (a) epilithic algae as autochthonous and (b) four species of senesced leaf species as allochthonous end members.

March) due to leaf fall, blow in of leaf litter from the forest floor, or vernal algal blooms compared to other months (Table 2).

Spatial sampling—In all four streams sampled within the WCC watershed in August, nighttime concentrations of seston (9.0 mg L⁻¹ ± 5.5: mean ± SE) and POC (0.64 mg L⁻¹ ± 0.37: mean ± SE) were greater than daytime concentrations of seston (2.2 mg L⁻¹ ± 0.4: mean ± SE, *p* < 0.05) and POC (0.19 mg L⁻¹ ± 0.02: mean ± SE, *p* < 0.05). There were no differences across the streams. However, mean day and night seston and POC concentrations across the four streams exceeded annual day and night averages for WCC (Table 1). Suspended Chl *a* concentrations were low in all four streams, and there were neither diel nor spatial differences among streams.

ESEM—Seston, collected on 16 January 2006 from WCC, was qualitatively analyzed using ESEM (Fig. 9). Seston was

mostly amorphous clay and silt particles (Fig. 9a) with occasional clearly recognizable diatoms (Fig. 9b). Light microscopy results from several other dates were consistent with this pattern (D. C. Richardson unpubl.).

Precision and accuracy of automated sampler—All automated samples were within ±10% of grab samples, and there was a positive correlation in seston concentrations between grab and automated samples that explained 90% of the variance (*r*² = 0.88, *F*_{1,13} = 106.5, *p* < 0.001, *n* = 14). One observation was excluded from the regression because it was identified as an outlier with a standardized robust residual (6.3) greater than the prespecified value (3.0). The regression line was statistically identical to the 1:1 line, (intercept = 0, *p* = 0.68; slope = 1, *p* = 0.68). Duplicate automated samples revealed a high degree of relative precision expressed as coefficients of variation for seston (6.5% ± 6.5: mean ± SD, *n* = 183 pairs) and POC samples (8.8% ± 9.8: mean ± SD, *n* = 104 pairs).

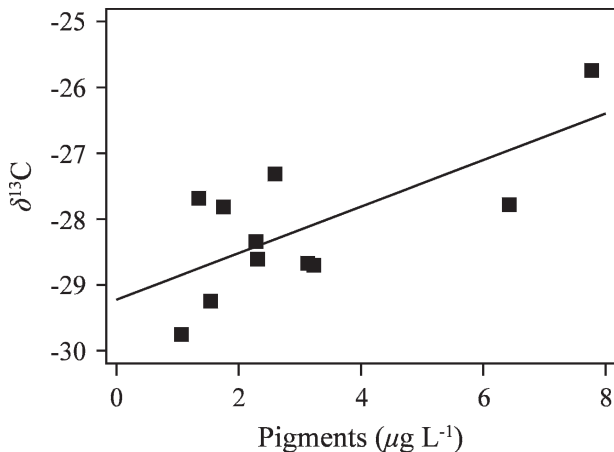


Fig. 8. Least-squares linear regressions between total pigment concentrations (Chl *a* + Pheo *a*) and δ¹³C of POC (δ¹³C = 0.35[pigments] - 29.2, *r*² = 0.49, *p* = 0.015).

Discussion

Diel patterns—Mechanisms for the consistent nighttime increases in seston and POC concentrations (Fig. 2a,b)

Table 2. Mixing model results presented as the percent of seston and POC concentration by mass (mean ± SE), where ‘m’ represents mineral-core, ‘o’ represents organic-based particles, and *p* < 0.05 indicates significant difference between high-organic-matter input months (Nov, Dec, Mar) and the rest of the year from paired *t*-tests (df = 75 for each test).

Analyte	Type of particle	% of mass		<i>t</i> -test <i>p</i> value
		Nov, Dec, Mar	Other months	
seston	m	70 ± 1.4	81 ± 0.4	<0.001
seston	o	29 ± 1.4	18 ± 0.4	<0.001
POC	m	5 ± 0.4	9 ± 0.2	<0.001
POC	o	94 ± 0.4	90 ± 0.2	<0.001

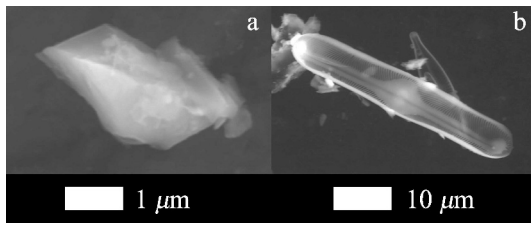


Fig. 9. Environmental scanning electron microscope images of seston. (a) Most particles were small angular clays and silts with adsorbed bacteria or organic matter, while (b) other particles were recognizable as diatom cell (e.g., *Pinnularia*).

could include diel cycles in stream flow, primary production, and feeding-related particle processing (e.g., shredding, suspension of noningested food particles, egestion), but we argue that bioturbation by nocturnal animals is most consistent with our data. Stream flow can be higher at night due to decreases in evapotranspiration in deciduous forests. In WCC, nighttime base flow is <5% greater than daytime base flow, but only during the growing season (J. D. Newbold unpubl.); we observed diel seston and POC patterns in all seasons. Primary production in WCC causes diurnal increases in dissolved organic matter concentrations (Kaplan and Bott 1982) and could be expected to cause similar diurnal increases in the Chl *a* portion of seston due to algal drift (Pozo et al. 1994; Peterson 1996). However, we observed the opposite pattern, with nocturnal increases in seston concentration, and we saw no diel variations in Chl *a* in any of the sampling months (Fig. 6a) or across the watershed. Feeding-related particle processing should increase at night (Wagner 1991), and it could contribute to seston through particle shredding, suspension of noningested food particles (“sloppy feeding”), or suspension of egested particles (Wallace et al. 1982b). We would expect, however, that all of these processes would preferentially contribute carbon-rich particles to seston, whereas the carbon content of seston actually declined at night (Fig. 2c). Thus, none of these explanations proves satisfactory. In contrast, bioturbation, activity that suspends streambed particles during nest digging, foraging, and movement (Moore 2006), is consistent with our findings.

Although we did not explicitly measure bioturbation, several lines of evidence support our contention that bioturbation was the causal mechanism for the diel pattern. The diel pattern appears to be biologically driven because rising water temperatures, and subsequent increases in organism activity (Wallace et al. 1991), resulted in greater nighttime suspension (Fig. 4). Furthermore, in our study, seston and POC concentrations increased after twilight without a lag (Fig. 3), which matches the activity patterns of nocturnal aquatic organisms (Schloss and Haney 2006). For example, stream macroinvertebrates are most active during the night to minimize risk of fish predation (Cowan and Peckarsky 1994). While we cannot exclude the activities of aquatic or terrestrial mammals, such as muskrat, deer, or raccoons, as a mechanism for the diel patterns, we suspect that those organisms would generate intermittent pulses of seston resulting from isolated

movements, such as fishing for food, drinking, or crossing the stream. Rather than intermittent pulses, we saw nighttime increases of seston and POC concentrations that were maintained throughout the night (e.g., Fig. 3). Pheo *a* concentrations, which indicate dead or senescing algae, increased during the nighttime (Fig. 6b); it is feasible that these algae are more susceptible to bioturbation and nighttime sloughing. We did not see concomitant increases in suspended Chl *a*, which would have been evidence for excess production or grazing. Bioturbation is known to affect ecosystem function in marine ecosystems, but, recently, it has received attention in stream and river ecosystems (Moore 2006). Studies of freshwater aquatic ecosystems in various biomes have identified nocturnal species of macroinvertebrates and amphibians as drivers of bioturbation (Zanetell and Peckarsky 1996; Statzner et al. 2000). Predaceous stoneflies increase sediment suspension from the streambed while searching the rocks and sediments for prey (Zanetell and Peckarsky 1996). Crayfish and amphibians, such as tadpoles, suspend particles through predator avoidance, conspecific aggression, and feeding at night (Ranvestel et al. 2004; Usio and Townsend 2004) but spend much of the day in burrows or under rocks and other refugia (Statzner et al. 2000). Key fish species, in both tropical and Alaskan streams, cause appreciable sediment and POC suspension and downstream export through movement, migration, spawning, feeding, and egestion (Moore 2006; Taylor et al. 2006).

In WCC, the nocturnal community, including crayfish, amphibians, eels, and macroinvertebrates, likely drives diel patterns of seston transport. The stream community in WCC includes 104 species of mayflies (Ephemeroptera), 45 species of stoneflies (Plecoptera) (J. K. Jackson unpubl.), two species of crayfish (D. A. Lieb pers. comm.), and three species of salamanders (E. H. Grant unpubl.). Fish probably do not drive the diel pattern because, of all 20 fish species in WCC, only eels are nocturnal (R. J. Horwitz pers. comm.). Furthermore, the diel patterns occurred throughout the watershed, including several second-order streams (<10 cm deep) that would exclude large eels and fish such as trout or sunfish.

Seasonal patterns—Warm season peaks of POC and seston concentrations have been attributed to increased macroinvertebrate fragmentation of leaf litter in streams in North Carolina (Wallace et al. 1991) and Spain (Molla et al. 2006). Similarly, we observed peak concentrations during the warm seasons in addition to the consistently observed diel patterns (Fig. 2a,b). The peaks, in spring and summer, can be explained by stream organism activity, such as feeding and bioturbation, because maximum macroinvertebrate activity and biomass occur during these warm seasons (Wallace et al. 1991). Bioturbation likely helps to control seasonal patterns because the organic content of seston decreased during the warm months (Fig. 2c), indicative of bioturbation rather than feeding behaviors (sloppy feeding, egestion). Filter-feeding macroinvertebrates could selectively feed on high-carbon-content particles (Parkes et al. 2004) but are likely not responsible for ecosystem-level decreases in POC content. Monaghan

et al. (2001) showed that filter feeders are responsible for only 11% of particulate organic matter removal from the water column in an Idaho stream.

Seasonal changes within the deciduous riparian vegetation appeared to drive seasonal patterns of seston quality. In late October and early November, WCC receives 40–50% of annual organic matter fall-in ($313 \text{ g m}^{-2} \text{ yr}^{-1}$; Newbold et al. 1997), while in late winter and early spring, the open canopy, increasing hours of daylight, and warming temperatures are conducive to the growth of long algal filaments on rocks and sediments (Kaplan and Bott 1982). The two seasonal peaks in carbon content coincide with autumnal leaf-litter inputs and vernal algal blooms (Fig. 2c). Despite the seasonal changes in quality, the overall carbon content (9% to 15%) was still low compared to organic-based matter like leaves, wood, or algae (~45%) but higher than seston in large rivers with high sediment loads (~1–3%; Hedges et al. 1986). Seston is likely a mixture of these two types of particles (organic-based and mineral-core; Meybeck 1982), with peaks in organic-based particles occurring in autumn and spring (Table 2). Mineral-core particles comprised most of total seston mass (Table 2). Similarly, microscopic analyses showed that most seston particles are clays or empty diatom frustules (Fig. 9). However, organic-based particles, despite being a relatively small fraction of total seston mass and rarely seen in microscopic analyses (Fig. 9), actually represented a large fraction of carbon flux because of their high carbon content (Table 2).

Autochthonous sources provide a fraction of organic-based particles in seston; it is necessary to convert pigment concentration to algal carbon to determine the proportion of POC from autochthonous carbon. If we assume a fixed C:Chl *a* ratio of 30 (Smith 1980), algal carbon would vary between 70% of POC during early spring and 30% during the summer. However, C:Chl *a* ratios vary with growth rate, irradiance, temperature, and nutrient concentration (Cloern et al. 1995), and pheopigments, degradation products of Chl *a* including Pheo *a*, are not included in these calculations. This is problematic because pheopigments represent algal-derived carbon from old, dying cells sloughed from epilithon (Peterson and Stevenson 1992) or otherwise suspended by stream organism activity including bioturbation, herbivory, and filter-feeding egestion (Downs and Lorenzen 1985). Microscopic examination of WCC seston revealed that, of the few particles that were algal cells, most were individual diatoms, and relatively few of these had retained their chloroplasts (Fig. 9). Thus, two types of algal cells appear to exist in the suspended load: fresh algal cells or older, senesced and grazed cells, which likely have different algal carbon:pigment ratios (Downs and Lorenzen 1985). Therefore, algal contributions to POC may exceed our preliminary estimate of 30–70%. More work is needed to accurately estimate the contribution of algal carbon to downstream POC transport by determining the temporal variation of C:pigment ratios in seston and epilithon on the streambed.

Studies from large rivers (Kendall et al. 2001) and streams (Walters et al. 2007) are consistent with our observations that suspended POC is isotopically enriched

in spring and depleted in the late fall months (Fig. 7). Autumnal POC- $\delta^{13}\text{C}$ was depleted even relative to whole deciduous leaves (-28.2‰ ; Fig. 7), suggesting that there was a selective preservation of lignin ($\sim -30\text{‰}$) relative to proteins and cellulose ($\sim -27\text{‰}$) (Benner et al. 1987). As much as 25% of leaf carbon leaches within the initial 24 h of wetting (Lush and Hynes 1973), and lignin remains a considerable portion of leaf carbon available for physical and biological fragmentation (Benner et al. 1987). The spring peak in $\delta^{13}\text{C}$ was consistent with a greater algal signal (Fig. 7), and it coincided with the spring peak in Chl *a* (Fig. 6), suggesting an increase in suspended algal carbon. The peak POC- $\delta^{13}\text{C}$ exceeded the mean algal $\delta^{13}\text{C}$ (Fig. 7). The algal $\delta^{13}\text{C}$ (Fig. 7, box a) could have been lowered toward the deciduous tree leaf signal because epilithon may have included carbon with an allochthonous signal (small leaf fragments, bacteria that derived carbon from allochthonous DOC) that was not separated from the algal cells during the rinsing procedure in this study. Isolation of algal $\delta^{13}\text{C}$, and subsequent reduction in $\delta^{13}\text{C}$ variability, requires separation of algal cells from the rest of the epilithon, perhaps using a density fractionation method (McCutchan and Lewis 2002). Furthermore, algal $\delta^{13}\text{C}$ is known to vary spatially as a function of the concentration of dissolved free CO_2 , the $\delta^{13}\text{C}$ of dissolved inorganic carbon, water-velocity effects on cell-wall CO_2 gradients, and primary production rates, which in turn depend on position within the watershed relative to carbonate lithologies and on reach morphology (Finlay et al. 2002; Walters et al. 2007). In this study, we sampled an autochthonous source only from one riffle at one time. Temporally and spatially explicit samples of epilithon are necessary to determine the algal $\delta^{13}\text{C}$ contributions throughout the WCC watershed.

Hydrologic patterns—Most POC and seston export from WCC occurs during storms (Newbold et al. 1997), as is typical of small streams (Golladay et al. 2000). However, during storms, seston is transported long distances downstream, and carbon content decreases, lowering POC quantity and quality available for local biological use. Baseflow transport, though comprising a smaller proportion of the total load, delivers upstream POC to relatively close reaches downstream (Thomas et al. 2001). From measurements of particle deposition velocities (0.1 to 0.4 mm s^{-1} ; Thomas et al. 2001), WCC mean baseflow water velocity (0.12 m s^{-1}), and depth (0.10 m), we can calculate that particles travel between 31 to 124 m on average before they are deposited on the streambed. The short travel distance emphasizes the importance of local reach-scale dynamics on baseflow particle transport.

Hydrology can still influence the quantity of particles available for suspension from the streambed. A large storm or series of successive storms can remove readily suspended particles from the streambed and decrease epilithon biomass on stream sediments (Van Sickle and Beschta 1983). As a result, suspended POC concentrations are higher during extended periods of base flow interrupted by infrequent storms compared to periods with frequent scouring floods because of the decreased amount of

particles available for suspension from the bed (Pozo et al. 1994). In this study, the time since the antecedent storm could not adequately explain the baseflow concentrations or characteristics of seston. However, higher antecedent storm maximum discharge decreased the diel variation in seston, suggesting that large antecedent storms reduced the amount of fine bed sediments available for nighttime increases in seston in the days following the storm (Fig. 5) through the redistribution of particles to stream banks or burial beneath bed sediments (Van Sickle and Beschta 1983).

Implications for energy flow—In a tropical stream, bioturbation increased downstream POC flux by 60% (Taylor et al. 2006), similar to our observation of 45% increases in nighttime POC fluxes in WCC (Fig. 2d). For extrapolation to annual POC fluxes, many studies typically use flow-weighted concentrations or rating curves derived from baseflow samples. However, we demonstrate here that this approach is inappropriate for estimating temporal dynamics or magnitudes of POC fluxes at base flow. For example, using only daytime POC concentrations in WCC, the annual baseflow POC transport fluxes for our sampling period would be 337 kg POC yr⁻¹; however, integrating over day and night concentrations, the annual baseflow POC transport flux is 414 kg POC yr⁻¹. Without consideration of nighttime differences in POC concentration, we would underestimate annual baseflow POC flux by 23%.

Our quantitative and qualitative geochemical analyses of particles in transport suggest that temporal patterns in seston and POC concentration and composition were generated by nocturnal bioturbation and seasonal cycles of leaf fall and algal production. These results argue that the traditional ecological perspective of POC as fragmented and egested leaf litter (Vannote et al. 1980) requires modification to include mineral-core and algal-derived particles as components of the suspended load. Furthermore, our results detail variability in POC fluxes and quality (i.e., carbon content of seston), which control carbon bioavailability (Baisden et al. 2002) and should ultimately influence rates of heterotrophic respiration in downstream rivers (Mayorga et al. 2005). Future work is needed to advance the understanding of the role of river networks in controlling the transformations of allochthonous and autochthonous POC transported from inland waters to the oceans.

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