

Relationships between bacterial productivity and organic carbon at a soil–stream interface

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Abstract

Microbial communities at soil–stream interfaces may be particularly important in regulating amounts and forms of nutrients that leave upland soils and enter stream ecosystems. While microbial communities are thought to be responsible for key nutrient transformations within near-stream sediments, there is relatively little mechanistic information on factors that control microbial activities in these areas. In this study, we examine the roles of dissolved organic carbon (DOC) vs. particulate organic carbon (POC) as potential controls on rates of bacterial productivity (measured as incorporation of [³H]thymidine into bacterial DNA) and amounts of bacterial biomass (measured as fatty acid yield) in sediments along a transect perpendicular to a soil–stream interface. We hypothesized that spatial patterns in bacterial productivity would vary in response to strong and persistent patterns in pore-water concentrations of DOC that were observed along a soil–stream transect throughout a 2-year period. Our results did not support the existence of such a link between pore-water DOC and bacterial productivity. In contrast, we found bacterial productivity and biomass were related to small-scale spatial variations in sediment POC on 3 of 4 sample dates. While our results indicate that total bacterial productivity in near-stream sediments is not consistently linked to spatial variations in pore-water DOC, it is likely that DOC and POC are not mutually exclusive and the relative contribution of DOC and POC to sedimentary microbes varies temporally and spatially in different riparian habitats.

Introduction

Microbial processes that occur at the interface between terrestrial and lotic ecosystems can influence both amounts and forms of nutrients that move from upland soils to surface waters (Likens, 1984; Wetzel, 1990; Hedin et al., 1998). For example, denitrifying bacteria at the interface between upland soils and streams can have an important impact on amounts of dissolved inorganic nitrogen that are exported from terrestrial to aquatic ecosystems (Groffman et al., 1992; Hanson et al., 1994; Hedin et al., 1998). Such control by mi-

crobial communities on nutrient flux is thought to be particularly important in regions where nutrients enter streams primarily via subsurface flows of soil-pore water and groundwater (McDowell & Likens, 1988; McClain et al., 1994; Dosskey & Bertsch, 1994).

Despite the potential biogeochemical importance of microbial processes within soil–stream interfaces, we know relatively little about factors that control the activities of microbial communities within these habitats. Other aquatic habitats have in comparison received more attention. In many freshwater and marine sediment habitats bacterial productivity appears to

be primarily controlled by the availability of decomposable organic matter supplied as sediment-bound, particulate organic carbon (POC) (see reviews by Cole et al., 1988; Sander & Kalff, 1993); however additional factors (e.g., temperature, inorganic nutrients, and grazing) can influence production rates (White et al., 1991). In stream and riverine sediments dissolved organic carbon (DOC) (Findlay et al., 1993; Vervier et al., 1993; Jones et al., 1995) and POC (Hedin, 1990; Pusch & Schwoerbel, 1994; Marxsen, 1996) have both been shown to influence the activity of bacteria. DOC has received increased attention in stream and riverine sediments, relative to lentic aquatic habitats, because it frequently dominates the flux of organic matter through lotic ecosystems (Thurman, 1985). However, only a fraction of the DOC transported in streams appears to be readily available for bacterial uptake (Thurman, 1985; Kaplan & Newbold, 1993), and transformations between DOC and POC are known to occur (Metzler & Smock, 1990; Findlay & Sobczak, 1996). Hence, the relative role of DOC vs. POC as sources of carbon for stream bacteria is difficult to resolve.

While several studies have addressed the regulation of microbial activity in stream sediments (Findlay et al., 1993; Hendricks, 1996; Marxsen, 1996), no study has examined the importance of organic matter in controlling patterns and rates of bacterial productivity in near-stream (i.e., riparian) sediments: along hydrologic flow paths from upland soils to stream sediments. In this study we address whether patterns of bacterial productivity and biomass in riparian sediments vary as a function of changes in concentrations of DOC in pore waters or amounts of sediment-bound POC. We took advantage of a strong cline in pore-water DOC concentrations (Figure 1) which consistently occurred across a riparian soil-stream interface for over two years (Hedin et al., 1998). Based on previous suggestions of the importance of DOC in controlling bacterial activity in streams (see Kaplan & Newbold, 1993), we hypothesized that bacterial productivity would decrease in concert with DOC across the riparian interface. In addition, we examined the hypothesis that bacterial productivity was more closely coupled to variations in standing stocks of POC within riparian sediments. We employed an experimental design that aimed to provide variation in DOC and POC along a discreet riparian transect in which physical and chemical conditions were well characterized (Hedin et al., 1998), as opposed to relying on variation in DOC and POC from an array of sites or streams in

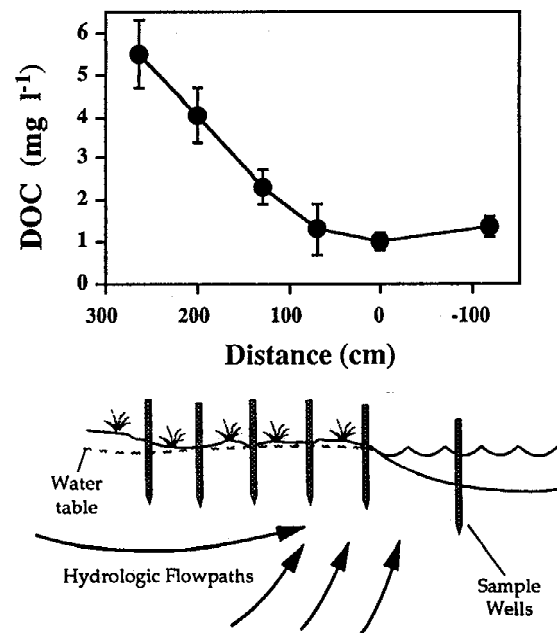


Figure 1. Persistent trend in DOC in pore waters across the soil-stream interface at our study site. Values are means based on 13 sample events. For each sample event we sampled between one to four parallel transects of sample wells. Error bars indicate standard deviations based on $n = 13$ sample events. See Hedin et al. (1998) for additional pore water chemistry at this site.

which physical and chemical conditions vary widely or are poorly characterized. In addition, we employed a novel sampling protocol that allowed us to estimate bacterial productivity in anoxic sediments *in situ*. Because this is, to our knowledge, the first study of bacterial productivity in anoxic sediments along a riparian transect we compare our estimates of bacterial productivity to those reported from other aquatic habitats.

Study site

We conducted this study along a forested section of Smith Creek, a first-order stream within the Augusta Creek drainage basin in southwestern Michigan (Hedin et al., 1998). Near-stream soils consist of three distinct layers: a highly organic upper horizon (ca. 0–5 cm), a mixed inorganic-organic horizon dominated by sand (ca. 5–60 cm), and a tightly packed inorganic sand horizon (below ca. 60 cm). The Smith Creek drainage basin and water chemistry have been described elsewhere (Wetzel & Manny, 1977; Hedin & Brown, 1994; Hedin et al., 1998).

We focused on a riparian area that was part of a more extensive study on biogeochemical processes that occur within soil–stream interfaces (Hedin et al., 1998). We sampled sediments that were located immediately downstream of a field of 24 wells that were positioned in four rows along an ca. 3 m transect across the soil–stream interface. These wells were used to monitor pore-water chemistry and hydraulic heads. Individual wells were constructed from 19 mm (inner diameter) polyvinyl pipes with a 10 cm deep sample port located 40 cm below the soil surface (Hedin et al., 1998). Sediments were continually inundated with water. Flow paths of pore waters through the soil–stream interface were characterized by measuring hydraulic potentials by using the sampling wells as piezometers, and by following the movement of additions of a conservative tracer (Br^- as NaBr) (Hedin et al., 1998). Additions of inert tracers showed that pore water moved from upland wells towards the stream at velocities ca. $0.4\text{--}0.9\text{ cm hr}^{-1}$ and that rates of vertical movement of pore waters (upwelling) increased with proximity to the stream (Hedin et al., 1998). DOC in shallow pore waters consistently decreased along the flow path (Figure 1). Concentrations of electron acceptors (e.g., O_2 , NO_3^- , SO_4^{2-}) varied in a thermodynamically predictable pattern as pore water moves from anoxic upland soils to oxic stream-surface sediments (Hedin et al., 1998). Sampling and analysis of pore water chemistry is described in Hedin et al. (1998). Briefly, water samples were withdrawn using polypropylene syringes and tygon tubing, filtered immediately through pre-rinsed Gelman A/E glass fiber filters ($<1\ \mu\text{m}$ nominal pore size), stored in polyethylene bottles, and kept on ice until refrigerated (Hedin et al. 1998). Dissolved O_2 was measured using a modified micro-Winkler technique, DOC was analyzed by Ionics high temperature platinum catalyst combustion, and NO_3^- , SO_4^{2-} , and Br^- were analyzed on a Dionex Ion Chromatograph (Hedin et al., 1998).

Materials and methods

Sampling regime

We sampled sediments along two replicate transects (ca. 0.5 m apart) on 4 dates in 1993 (June 16, July 21, July 29 and August 6). The first sample date (i.e., June 16) was during a period of high stream-discharge regionally, while the three latter dates were during a period of low stream-discharge regionally

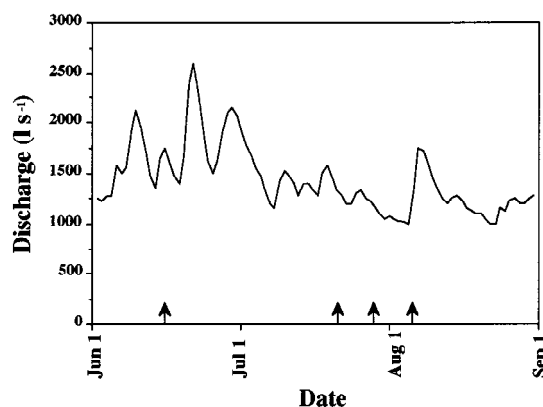


Figure 2. Discharge during 1 June 1993 to 1 September 1993 at the USGS gauging station located on Augusta Creek, MI, USA. Smith Creek is a tributary of Augusta Creek. Arrows indicate sample dates.

(i.e., summer base-flow) (Figure 2). Each of the 2 transects consisted of 5 sampling sites (i.e., coring sites) within a 3 m distance from the stream (Figure 1). We shifted coring transects within a 1 m area between sample dates in order to ensure that a given sample site was previously undisturbed and to minimize potential autocorrelation within the data set. Hence, we examined 40 independent sediment samples. We used a one inch soil corer with plastic sleeve to sample sediments. To prevent O_2 intrusion into anoxic sediments we immediately capped the plastic sleeves with rubber stoppers and positioned them in deoxygenated water before returning to the laboratory. Cores were manipulated in an anaerobic chamber in the laboratory. From each core we removed a portion of sediment between 0.3–0.5 m depth, which coincides with the approximate depth of the inlet ports on our wells. These sections were then homogenized in O_2 -evacuated flasks. To provide representative chemistry during incubations, we added pore water from adjacent wells that had been deoxygenated by sparging with N_2 .

Bacterial productivity

Bacterial productivity was determined by measuring the rate of incorporation of [^3H]thymidine ([^3H]TdR) into bacterial DNA (Findlay et al., 1984; Findlay, 1993). Although some anaerobic bacteria (e.g., some groups of sulfate reducers, acetogens, and methanogens) may not be able to incorporate [^3H]TdR, many common anaerobic bacteria are known to incorporate exogenous TdR for DNA synthesis (Pollard & Moriarty, 1984). For our estimates of bacterial productivity we took three 1 cm^3 sub-samples from the homo-

genized sediment slurry of each core. Hence, 120 observations were made during the study (4 dates \times 10 cores \times 3 sub-samples). Samples from all sites were incubated at 17 °C for 3 h on a mechanical shaker with 1 nmole (20 Ci mmol⁻¹) of [³H]TdR added to 5 ml pore water. We concluded that catabolism of [³H]TdR was unlikely during a 3 h incubation because a time-course experiment showed a linear rate of isotope incorporation between 0.5 and 5 h (data not shown). Incubations were terminated by the addition of 5 ml 5% formalin. Immediately following termination, sediment samples were filtered onto a 0.45 μ m filter (Poretics), washed three times with 5% formalin, and frozen along with filter. We subsequently extracted DNA from these frozen samples (i.e., sediment samples and associated filters) with an alkaline solution (0.3 N NaOH + 1% SDS + 25 mM EDTA) for 12 h at 25 °C on a mechanical shaker. A 5 ml portion of the supernatant was chilled on ice, neutralized with 1 ml of 3 N HCl, and acidified with TCA. Carrier DNA (0.1 mg) was added to aid precipitation of DNA prior to centrifugation (15,000 \times g for 15 min at 4 °C). The supernatant was aspirated and the pellet was resuspended in 5% TCA for an additional wash. DNA was hydrolyzed from the second pellet in 5% TCA for 30 min at 95 °C. Following a final centrifugation (5000 \times g for 5 min), 1 ml aliquot of the supernatant was radioassayed to determine DPM in DNA on a scintillation counter and corrected with control samples ($n = 10$ per sampling date) which were killed with 5% formalin prior to incubation (routinely < 10% DPM of live samples). To minimize the dependence of our results on assumptions regarding carbon conversion factors and isotopic dilution (see Fallon & Boylen, 1990; Kaplan et al., 1992; Chrzanowski et al., 1993), we report bacterial productivity as DPM (in DNA) cm⁻³ h⁻¹. However, we conducted isotope dilution experiments with sediment from the extremes of the sampling gradient in order to account for potential variation in the exogenous thymidine pool across the soil-stream interface. Each of these assays used 20 samples that represented dilutions of 0, 1, 3, 5, and 10 nmoles cm⁻³ in addition to killed controls. Assays were analyzed using the reciprocal-plot method (Moriarty & Pollard, 1981; Findlay et al., 1984). These assays showed similar levels of exogenous thymidine: 4.0 nmoles and 5.5 nmoles cm⁻³ for the stream-side and upland sediments, respectively.

Bacterial biomass

Fatty acid yield was estimated as a surrogate measure of bacterial biomass (Vestal & White, 1989; Dobbs & Findlay, 1993; Haack et al., 1994). The approach assumes that lipid pools degrade rapidly outside live cells and that viable microbes continually regenerate lipid pools, thus the extractable lipid from an environmental sample represents microbial lipid at a given point in time. We estimated total cellular fatty acid methyl ester (FAME) yield using a commercially available (Microbial ID, Inc., Newark, Del.) gas chromatograph-software system. For our estimates of FAME yield we attempted to take three 1 cm³ sub-samples from the homogenized sediment slurry of each core for the July 21, July 29, and August 6 sampling dates ($n = 30$ cores), however a lack of homogenized sediment prevented us from analyzing three sub-samples from all of the cores (cores lacking three sub-samples: $n = 10$). FAME yield was not determined for the June 16 sampling date. Overall, 78 observations were made during the study. Samples were stored at -70 °C until extraction in order to minimize changes in the fatty acid pools. Briefly, lipids were removed from cells (killed and lysed in 100 °C methanol), methylated under basic conditions to increase volatility, extracted from the aqueous phase, washed in NaOH, and prepared for gas chromatography in accordance with manufacturer recommendations (see Haack et al. (1994) for an analysis of the accuracy, reproducibility, and interpretation of FAMEs profiles). FAME yield is known to vary among isolates, among whole-communities, and among procedures, therefore we report FAME yield in gas chromatograph peak area units. Peak area units are directly related to FAME yield which is closely linked to microbial biomass, hence they indicate relative differences in microbial biomass among samples. Microscopic inspection of several samples and the minor contribution of signature fatty acids from eukaryotes suggest that bacteria account for the majority (i.e., >95%) of microbial biomass in our samples. In addition, signature fatty acids for gram-positive prokaryotes, sulfate-reducing bacteria, and other anaerobic bacteria were ubiquitous among samples.

POC measurement and analysis

We collected three additional sub-samples (1 cm³) from the homogenized sediment samples for analysis of POC from all cores ($n = 120$ observations). Mean dry weight was 1.01 g cm⁻³ (\pm SE = 0.07; $n = 40$

cores). Particulate organic matter was determined by measuring the difference between dried weight (drying sediment sub-sample at 70 °C for 24 h) and ashed weight (combusting at 500 °C for 4 h). Variance among sub-samples was low (mean CV = 15%; $n = 40$ cores). We assumed that organic matter was 50% carbon (Cole et al., 1988). It is important to note that POC, bacterial productivity, and FAME yield are reported and compared in terms of sediment volume (i.e. cm^3 sediment) in order to avoid spurious relationships associated with data normalized by sediment dry-weight (Bird & Duarte, 1989). C:N ratios were determined from June 16 and July 29 cores using a Carlo Erba CNS Analyzer ($n = 60$ observations).

Results

We found that bacterial productivity and biomass (i.e., FAME yield) varied over an order of magnitude throughout the soil–stream interface of Smith Creek. Most of this variability was the result of differences among cores rather than variation within cores; variation among analytical replicates ($n = 3$) for given cores remained relatively low throughout our study for both productivity (mean CV = 18%; $n = 40$ cores) and biomass (mean CV = 21%; $n = 28$ cores). Contrary to our initial hypothesis, we found that spatial variation in bacterial productivity and biomass did not follow the persistent DOC gradient across the soil–stream interface on any of the sampling dates (Tables 1 and 2). Our data from August 6 provides the most clear illustration that bacterial productivity did not vary in a consistent pattern as a function of distance

Table 1. Results from regression analyses in which bacterial productivity is the dependent variable. Mean DOC values from Figure 1 are used in analyses. n = independent cores. ** = $p \leq 0.01$

Source of data	n	Independent variables			
		DOC		POC	
		r^2	p	r^2	p
16 June	10	0.26	0.131	0.05	0.553
21 July	10	0.04	0.601	0.31	0.098
29 July	10	0.13	0.303	0.86	<0.001**
6 August	10	0.06	0.508	0.74	0.001**
All dates	40	0.02	0.396	0.09	0.064
Exclude 16 June	30	0.04	0.324	0.28	0.003**

Table 2. Results from regression analyses in which FAME yield is the dependent variable. FAME yield was not determined for samples from 16 June. Mean DOC values from Figure 1 are used in analyses. n = independent cores. * = $p \leq 0.05$; ** = $p \leq 0.01$

Source of data	n	Independent variables			
		DOC		POC	
		r^2	p	r^2	p
16 June					
21 July	10	<0.01	0.946	0.54	0.015*
29 July	10	0.26	0.129	0.61	0.008**
6 August	10	0.01	0.852	0.37	0.061
All dates	30	0.01	0.587	0.71	<0.001*

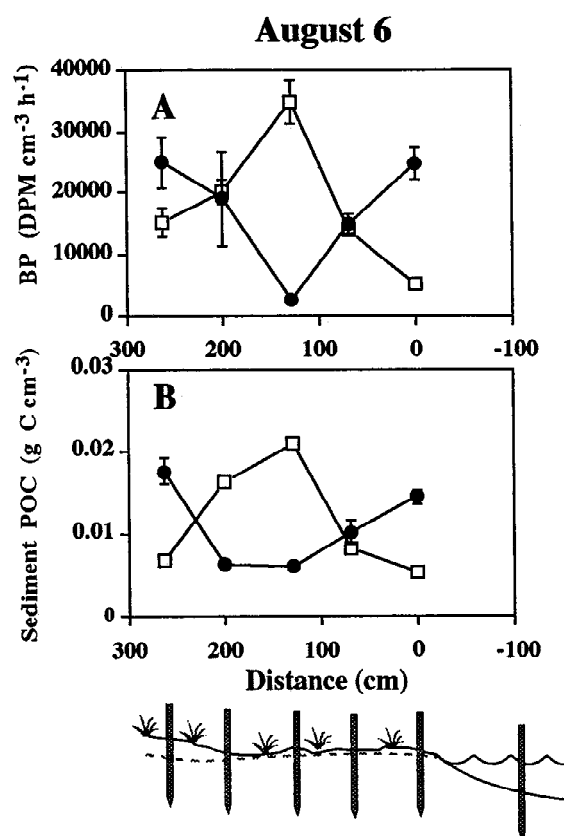


Figure 3. Variations in (A) bacterial productivity (BP) (i.e., DPM in DNA) and (B) POC across soil–stream interface on August 6 sampling date. Each point is the mean (± 1 SE, $n = 3$) from sub-samples for a given core. Squares represent transect 1 and circles represent transect 2.

across the soil–stream interface. On August 6, the two replicate transects had strikingly different patterns in bacterial productivity even though they were only ca. 0.5 m apart (Figure 3a). Overall, we did not find direct evidence in support of the idea that bacterial productivity in anoxic riparian sediments is controlled by pore-water DOC.

In contrast, we found that variations in bacterial productivity across the soil–stream interface strongly corresponded to variations in the amounts of sediment POC on July 29 ($r^2 = 0.86$; $p = 0.001$; $n = 10$ cores) and August 6 ($r^2 = 0.74$; $p = 0.001$; $n = 10$ cores), and weakly corresponded on July 21 ($r^2 = 0.31$; $p = 0.098$; $n = 10$ cores) (Table 1). For example, the contrasting patterns in bacterial productivity that occurred between replicate transects on August 6 (Figure 3a) can be explained by similar variability in sediment POC (Figure 3b). Differences in bacterial productivity within transects, among transects, and among sample dates could in general be explained by variations in the spatial distribution of POC (range: 0.005 to 0.05 g C cm⁻³). One notable exception was June 16 when POC showed a uniform decrease from upland soils to

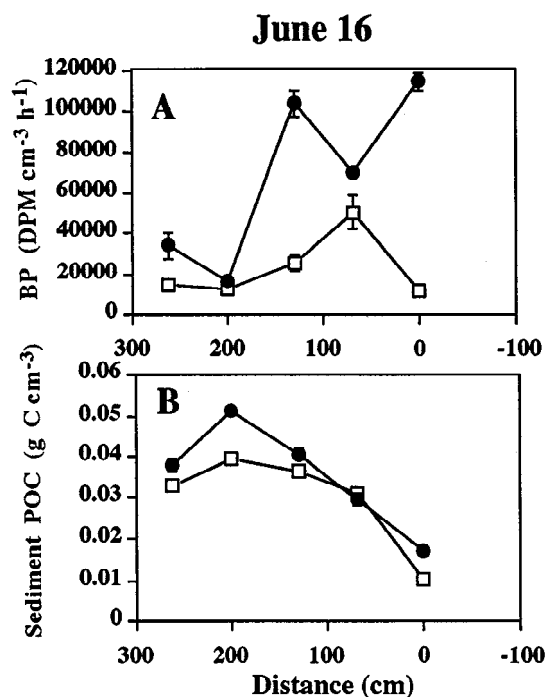


Figure 4. Variations in (A) bacterial productivity (BP) (i.e., DPM in DNA) and (B) POC across soil–stream interface on June 16 sampling date. Each point is the mean (± 1 SE, $n = 3$) from sub-samples for a given core. Squares represent transect 1 and circles represent transect 2.

stream sediments while bacterial productivity varied in an apparently independent manner (Table 1, Figure 4a & 4b). We are unable to explain the variations in bacterial productivity on the June 16 sampling date, however regional discharge was high prior to the June 16 sampling date compared to the 3 latter sampling dates (Figure 2). Excluding June 16, we found that POC was a statistically significant predictor of bacterial productivity within the riparian sediments of our study site ($r^2 = 0.28$; $p = 0.003$; $n = 30$ cores) (Table 1, Figure 5). We also found that POC was a highly significant predictor of bacterial biomass within the sediments of our study site ($r^2 = 0.71$; $p = 0.001$;

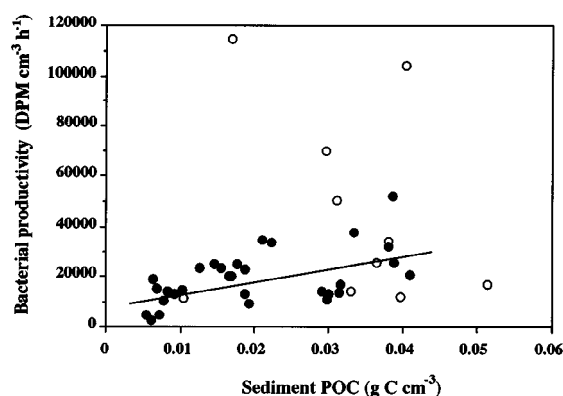


Figure 5. Bacterial productivity (DPM in DNA) as a function of sediment POC. Open circles represent the June 16 sampling date ($n = 10$) and closed circles represent the July 21, July 29, and August 6 sampling dates ($n = 30$). The June 16 sampling date is excluded from the regression analysis. Regression equation is $Y = (4.97 \times 10^5)X + 9640$, ($r^2 = 0.28$; $p = 0.003$).

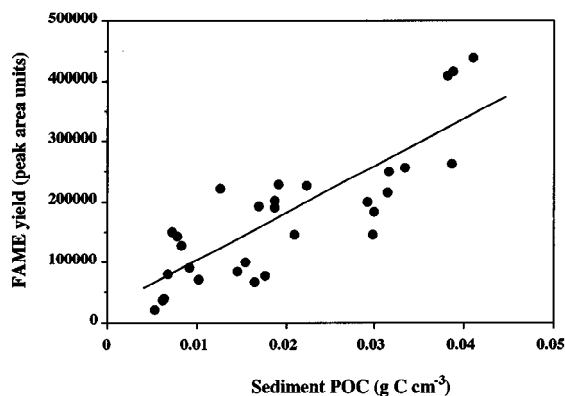


Figure 6. FAME yield (peak area units) as a function of sediment POC ($n = 30$). FAME yield represents bacterial biomass (see Methods). The June 16 sampling date is excluded from the regression analysis because FAME yield was not measured on this date. Regression equation is $Y = (8.10 \times 10^6)X + (1.14 \times 10^4)$, ($r^2 = 0.71$; $p = 0.0001$).

$n = 30$ cores) (Table 2, Figure 6). C:N ratios of organic matter varied only slightly within our study site (mean = 14.7, CV = 14.7%) indicating that variations in amounts of POC, as opposed to the quality of POC, was influencing bacterial productivity and biomass.

Discussion

Our results show strong heterogeneity in bacterial productivity and biomass across a soil–stream interface, even though pore-waters displayed a consistent pattern in DOC across the soil–stream interface. Our results did not support our primary hypothesis that bacterial productivity would vary as a function of pore-water DOC concentrations along the riparian flow path. Instead, our results suggest that POC is important in explaining the heterogeneity of bacterial productivity and biomass within anoxic riparian sediments at our study site (Figures 5 and 6). This finding contrasts with studies that have emphasized DOC as the dominant control of bacterial activity in oxic, stream-hyporheic sediments through which stream-surface water percolates (Findlay et al., 1993; Vervier et al., 1993; Jones et al., 1995). Our result is especially surprising considering the marked decrease in DOC (5.5 to 1.0 mg l⁻¹) along a relatively short (ca. 3 m) flow path. Although the range in POC (range: 0.005–0.05 g C cm⁻³; $n = 40$ cores) is greater than the range in DOC, sediment POC does not follow a stable cline across the soil–stream interface. Nevertheless, POC could explain only ca. 28% of the total measured variation in bacterial productivity (Figure 6), indicating that additional variables (e.g., inorganic nutrients, electron acceptors, grazing) are also important in regulating bacterial productivity in sediments at our study site or the proportions of TdR incorporating bacteria vary among samples. Yet even a statistically weak relationship between bacterial productivity and POC may have considerable ecological significance if POC is the principle energy source for bacteria. Further, POC explained 71% of the total measured variation in bacterial biomass. The strength of these relationships is amplified when one considers the modest range in POC we report relative to ranges reported in review papers that make similar comparisons among aquatic ecosystems using log–log plots (e.g., Cole et al., 1988; Sander & Kalff, 1993). In addition, our findings are in agreement with several recent studies in shallow-hyporheic sediments in which relationships between sediment organic matter and bacterial biomass (Fischer et al., 1996), respiration

(Pusch, 1996), and productivity (Marxsen, 1996) have been documented.

While others have measured bacterial productivity in shallow-sandy sediments in which stream-surface water percolates (Hendricks, 1996; Marxsen, 1996), we are unaware of measurements across a riparian soil–stream interface. This lack of information is surprising given the potential importance of this area in influencing the biogeochemistry of streams. Based on our measured isotopic dilution of 4.75 nmole cm⁻³, a conversion factor of 2×10^{18} bacterial cells per mole [³H]TdR incorporated (Moriarty, 1986), an average bacterial cell size of 0.2 μm^3 (Haack et al., 1988), and C content per cell of 2.0×10^{-7} $\mu\text{g C } \mu\text{m}^{-3}$ (Simon & Azam, 1989), we estimate the mean bacterial productivity across the soil–stream interface to be 0.27 $\mu\text{g C cm}^{-3}\text{h}^{-1}$. This estimate exceeds the range reported by Hendricks (1996) for the Maple River in Michigan and is similar to the mean estimate reported by Marxsen (1996) for the Breitenbach in Germany, 0.23 $\mu\text{g C cm}^{-3}\text{h}^{-1}$. In addition, this productivity estimate does not differ dramatically from those reported for sediments in a wide array of aquatic ecosystems (see Cole et al., 1988). Furthermore, our observed relationship between bacterial productivity and POC fits closely with a predictive model based on data from several different freshwater and marine aquatic ecosystems in which POC ranges several orders of magnitude (derived from Cole et al., 1988) (Figure 7).

Although variations in bacterial productivity were apparently unrelated to the stable cline in DOC, the mean production rate that we report (0.27 $\mu\text{g C cm}^{-3}\text{h}^{-1}$) is ample to account for the decline in

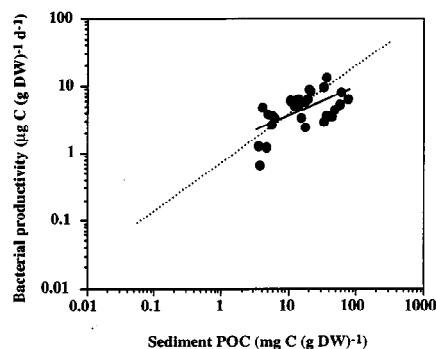


Figure 7. Comparison of bacterial productivity and POC relationship found in our study (solid line) with that for sediments across freshwater and marine ecosystems (dashed line) by Cole et al. (1988).

DOC across our study site, even using conservative assumptions. For example, if we assume that pore-water DOC concentration declines from 5 mg/L to 1 mg/L along a flow path through a cubic meter of sediment in which water velocity is 10 cm h⁻¹ (> 10-fold the reported estimate) and porosity is 25%, then we can calculate a predicted 'maximum' rate of DOC loss of 1000 mg C every 10 h (i.e., 0.1 μg C cm⁻³h⁻¹). Even if we assume a high bacterial growth efficiency (carbon allocated to biomass/total carbon utilized) of 50%, then our estimate of bacterial carbon demand would be ca. 0.56 μg C cm⁻³h⁻¹ and exceed the predicted 'maximum' rate of DOC loss by > 5-fold. Hence, loss of DOC along the riparian flow path at this study site may still be mediated by microbial metabolism even though bacterial productivity and biomass are heterogeneous. In other words, our results do not refute the hypothesis that DOC declines are mediated by microbial metabolism.

The question of whether DOC, POC, or other factors dominate as the control on bacterial production in stream and riparian sediments is complex. The flux of DOC through sediments can be influenced by biological (e.g., metabolism), chemical (e.g., adsorption), and physical (e.g., dilution) factors (see Kaplan & Newbold, 1993). For example, DOC can adsorb to sediment surfaces, thus forming sediment-bound POC (McDowell, 1985; McKnight et al., 1992; Fiebig & Marxsen, 1992; Fiebig, 1997). Research on hyporheic flow paths that flow parallel to streams (as opposed to flow paths from upland soils through riparian sediments) has shown concomitant decreases in DOC and bacterial activity (Findlay et al., 1993; Jones et al., 1995), but the potential role of POC in this relationship can still not be discounted (Vervier et al., 1993; Findlay & Sobczak, 1996). In many streams episodic burial of POC during high discharge may replenish POC in near-stream riparian sediments (Metzler & Smock, 1990), yet in the absence of such disturbance events sediment-bound POC may result from DOC adsorption and microbial assimilation (Findlay & Sobczak, 1996). In addition, patterns in pore-water chemistry sampled from wells that integrate a relatively large volume of sediment may be difficult to relate to microbial activity in a much smaller amount of sediment from localized cores. Hence, DOC and POC supply to sediment-bound bacteria along sub-surface flow paths may not be independent. It is likely that the relative importance of DOC and POC as microbial controls in soil-stream interfaces varies in space and time. The results from this study suggest the potential significance

of POC as a control on bacterial productivity and biomass in near-stream sediments, yet there is clearly a need for additional studies on bacterial activity in soil-stream interfaces from contrasting catchments.

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References

- Bird, D. F. & C. M. Duarte, 1989. Bacteria-organic matter relationship in sediments: a case of spurious correlation. *Can. J. Fish. Aquat. Sci.* 46: 904-908.
- Chrzanowski, T. H., K. Simek, R. H. Sada & S. Williams, 1993. Estimates of bacterial growth rate constants from thymidine incorporation and variable conversion factors. *Microb. Ecol.* 25: 121-130.
- Cole, J. J., S. Findlay & M. L. Pace, 1988. Bacterial production in fresh and salt water ecosystems: a cross-system overview. *Mar. Ecol. Prog. Ser.* 43: 1-10.
- Dobbs, F. C. & R. H. Findlay, 1993. Analysis of microbial lipids to determine biomass and detect the response of sedimentary microorganisms to disturbance. In P. F. Kemp, B. F. Sherr, E. B. Sherr & J. J. Cole (eds), *Handbook of Methods in Aquatic Microbial Ecology*. Lewis Publishers: 347-358.
- Dosskey, M. G. & P. M. Bertsch, 1994. Forest sources and pathways of organic matter transport to a blackwater stream: a hydrologic approach. *Biogeochemistry* 24: 1-19.
- Fallon, R. D. & C. W. Boylen, 1990. Bacterial production in freshwater sediments: cell specific versus system measurements. *Microb. Ecol.* 19: 53-62.
- Fiebig, D., 1997. Microbiological turnover of amino acids immobilized from groundwater discharged through hyporheic sediments. *Limnol. Oceanogr.* 42: 763-768.
- Fiebig, D. & J. Marxsen, 1992. Immobilization and mineralization of dissolved free amino acids by stream-bed biofilms. *Freshwat. Biol.* 28: 129-140.
- Findlay, S., 1993. Thymidine incorporation into DNA as an estimate of sediment bacterial production. In P. F. Kemp, B. F. Sherr, E. B. Sherr & J. J. Cole (eds), *Handbook of Methods in Aquatic Microbial Ecology*. Lewis Publishers: 505-508.
- Findlay, S. E. G., J. L. Meyer & R. T. Edwards, 1984. Measuring bacterial production via rate of incorporation of [³H]thymidine into DNA. *J. Microbiol. Meth.* 2: 57-72.
- Findlay, S. & W. V. Sobczak, 1996. Variability in removal of dissolved organic carbon in hyporheic sediments. *J. n. am. Benthol. Soc.* 15: 35-41.

- Findlay, S., D. Strayer, C. Gombala & K. Gould, 1993. Metabolism of streamwater dissolved organic carbon in the shallow hyporheic zone. *Limnol. Oceanogr.* 38: 1493–1499.
- Fischer, H., M. Pusch & J. Schwoerbel, 1996. Spatial distribution and respiration of bacteria in stream-bed sediments. *Arch. Hydrobiol.* 137: 281–300.
- Groffman, P. M., A. J. Gold & R. C. Simmons, 1992. Nitrate dynamics in riparian forests: microbial studies. *J. env. Qual.* 21: 666–671.
- Haack, S. K., T. M. Burton & K. Ulrich, 1988. Effects of whole-tree harvest on epilithic bacterial populations in headwater streams. *Microb. Ecol.* 16: 165–181.
- Haack, S. K., H. Garchow, D. A. Odelson, L. J. Forney & M. J. Klug, 1994. Accuracy, reproducibility, and interpretation of fatty acid methyl ester profiles of model bacterial communities. *Appl. env. Microbiol.* 60: 2483–2493.
- Hanson, G. C., P. M. Groffman & A. J. Gold, 1994. Symptoms of nitrogen saturation in a riparian wetland. *Ecol. Applic.* 4: 750–756.
- Hedin, L. O., 1990. Factors controlling sediment community respiration in woodland stream ecosystems. *Oikos* 57: 94–105.
- Hedin, L. O. & M. B. Brown, 1994. Watershed-level coupling of nitrogen and sulfur in a heterogeneous landscape. *Verh. int. Ver. Limnol.* 25: 1477–1482.
- Hedin, L. O., J. C. von Fischer, N. E. Ostrom, B. P. Kennedy, M. G. Brown & G. P. Robertson, 1998. Thermodynamic constraints on nitrogen transformations and other biogeochemical processes at soil–stream interfaces. *Ecology* 79: 684–703.
- Hendricks, S. P., 1996. Bacterial biomass, activity, and production within the hyporheic zone of a north-temperate stream. *Arch. Hydrobiol.* 136: 467–487.
- Jones, J. B., Jr., S. G. Fisher & N. B. Grimm, 1995. Vertical hydrologic exchange and ecosystem metabolism in a Sonoran Desert stream. *Ecology* 76: 942–952.
- Kaplan, L. A. & J. D. Newbold, 1993. Biogeochemistry of dissolved organic carbon entering streams. In T. E. Ford (ed.), *Aquatic Microbiology: an Ecological Approach*. Blackwell Scientific Publications: 139–166.
- Kaplan, L. A., T. L. Bott & J. K. Bielicki, 1992. Assessment of [³H]thymidine incorporation into DNA as a method to determine bacterial productivity in stream bed sediments. *Appl. env. Microbiol.* 58: 3614–3621.
- Likens, G. E., 1984. Beyond the shoreline: a watershed-ecosystem approach. *Verh. int. Ver. Limnol.* 22: 1–22.
- Marxsen, J., 1996. Measurement of bacterial production in stream-bed sediments via leucine incorporation. *FEMS Microb. Ecol.* 21: 313–325.
- McClain, M. E., J. E. Richey & T. P. Pimentel, 1994. Groundwater nitrogen dynamics at the terrestrial-lotic interface of a small catchment in the Central Amazon Basin. *Biogeochemistry* 27: 113–127.
- McDowell, W. H., 1985. Kinetics and mechanisms of dissolved organic carbon retention in a headwater stream. *Biogeochemistry* 1: 329–352.
- McDowell, W. H. & G. E. Likens, 1988. Origin, composition, and flux of dissolved organic carbon in the Hubbard Brook Valley. *Ecol. Monogr.* 58: 177–195.
- McKnight, D. M., K. E. Bencala, G. W. Zellweger, G. R. Aiken, G. L. Feder & K. A. Thorn, 1992. Sorption of dissolved organic carbon by hydrous aluminum and iron oxides occurring at the confluence of deer creek with the Snake River, Summit County, Colorado. *Envir. Sci. Technol.* 26: 1388–1396.
- Metzler, G. M. & L. A. Smock, 1990. Storage and dynamics of sub-surface detritus in a sand-bottomed stream. *Can. J. Fish. aquat. Sci.* 47: 588–594.
- Moriarty, D., 1986. Measurement of bacterial growth rates in aquatic systems from rates of nucleic acid synthesis. In K. C. Marshall (ed.), *Advances in Microbial Ecology*, Vol. 9. Plenum Press: 245.
- Moriarty, D. & P. Pollard, 1981. DNA synthesis as a measure of bacterial productivity in seagrass sediments. *Mar. Ecol. Prog. Ser.* 5: 151–156.
- Pollard, P. C. & D. Moriarty, 1984. Validity of the tritiated thymidine method for estimating bacterial growth rates: measurement of isotope dilution during DNA synthesis. *Appl. env. Microbiol.* 48: 1076–1083.
- Pusch, M., 1996. The metabolism of organic matter in the hyporheic zone of a mountain stream, and its spatial distribution. *Hydrobiologia* 323: 107–118.
- Pusch, M. & J. Schwoerbel, 1994. Community respiration in hyporheic sediments of a mountain stream (Steina, Black Forest). *Arch. Hydrobiol.* 130: 35–52.
- Sander, B. C. & J. Kalf, 1993. Factors controlling bacterial production in marine and freshwater sediments. *Microb. Ecol.* 26: 79–99.
- Simon, M. & F. Azam, 1989. Protein content and protein synthesis rates of planktonic marine bacteria. *Mar. Ecol. Prog. Ser.* 51: 201–213.
- Thurman, E. M., 1985. *Organic geochemistry of natural waters*. Martinus Nijhoff/Dr W. Junk Publishers, The Hague.
- Vervier, P., M. Dobson & G. Pinay, 1993. Role of interaction zones between surface and ground waters in DOC transport and processing: considerations for river restoration. *Freshwat. Biol.* 29: 275–284.
- Vestal, J. R. & D. C. White, 1989. Lipid analysis in microbial ecology. *BioScience* 39: 535–541.
- Wetzel, R. G. & B. A. Manny, 1977. Seasonal changes in particulate and dissolved organic carbon and nitrogen in a headwater stream. *Arch. Hydrobiol.* 80: 20–39.
- Wetzel, R. G., 1990. Land–water interfaces: metabolic and limnological regulators. *Verh. int. Ver. Limnol.* 24: 6–24.
- White, P. A., J. Kalf, J. B. Rasmussen & J. M. Gasol, 1991. The effect of temperature and algal biomass on bacterial production and specific growth rate in freshwater and marine habitats. *Microb. Ecol.* 21: 99–118.