STREAM ORGANIC MATTER BUDGETS

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Stream organic matter budgets[1,2]

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Abstract. This analysis of organic matter dynamics in streams has 3 objectives: 1) to explore the relationships between physical characteristics of streams and their watersheds (climate, geomorphology) and stream organic matter dynamics using data from a broad geographic area; 2) to compare stream organic matter dynamics in a diverse array of streams in order to suggest determinants of observed patterns; and 3) to reveal deficiencies in currently available data on organic matter dynamics in streams. Streams were included in this analysis not to represent the global diversity of stream types but because organic matter data were available. In the introductory chapter we describe the kinds of data included for each stream and provide brief descriptions of previously published organic matter data for streams included in the comparative analysis but not described in individual chapters. The next 16 chapters present organic matter data for streams from North America, Europe, Australia, and Antarctica. Most of the streams represented are in the temperate zone of North America. Data presented include climate and geomorphic variables and organic matter inputs, exports, and standing crops. The chapters on individual streams are followed by 7 chapters analyzing physical features of these streams and specific components of the organic matter budgets. Stream size, water temperature, and precipitation were the most important variables setting the physical template for organic matter processes occurring in the streams. Watershed area was the best predictor of gross primary productivity (GPP), which increased with increasing watershed area. Watershed area, discharge, and soluble reactive phosphorus concentration explained 71% of the variation in GPP. Climate (latitude) and vegetation type were more important than stream order in predicting litter inputs across a broad geographic range of streams, although, within a river basin, litterfall decreased with increasing stream order. Regression of benthic organic matter (BOM) and latitude and precipitation proved useful in predicting BOM standing crop in streams at a continental scale, although BOM was also related to channel characteristics such as gradient and woody debris. Benthic respiration increased dramatically with increasing temperature (Q_{10} = 7.6), suggesting a response related not only to metabolism but also to changes in BOM quality in response to latitudinal shifts in vegetation. Terrestrial and riparian vegetation was found to play an important role in regulating suspended particulate organic matter (POM) concentration and export, with higher values observed in forested streams and in lower gradient streams with extensive floodplains. Channel slope was the best predictor of dissolved organic matter (DOM) concentration and export, probably because of its relationship with riparian wetlands and hydrologic flowpaths. In the final chapter, a synthesis of the organic matter budgets, we reached two conclusions: 1) At a global level, stream organic matter dynamics are driven primarily by climate through its effect on terrestrial vegetation. 2) Despite significant progress in understanding organic matter processes in streams, many of the differences we found among streams reflect omissions of important components of the budget, especially accurate measures of streambed area, heterotrophic respiration, standing stock of fine BOM, and groundwater inputs of DOM.

Key words: stream, organic matter, budget, primary production, litterfall, BOM, DOM, POM, respiration.

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[1] Individual chapters should be cited as follows: *Author(s).* 1997. *Chapter title.* Pages xxx–xxx *in* J. R. Webster and J. L. Meyer (editors). Stream organic matter budgets. Journal of the North American Benthological Society 16:3–161.

[2] Reprint requests for individual chapters should be sent to the appropriate senior author. Correspondence concerning the entire paper should be directed to: J. R. Webster, Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061 USA.

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Large-scale trends for stream benthic respiration

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Carbon dioxide is the ultimate product of organic matter processing; the release of one mole of CO_2 through respiration represents the dissipation of about 470 kJ of energy (Voet and Voet 1990). Within streams, benthic respiration rates are proximally controlled by the availability of electron acceptors (e.g., oxygen, nitrate), electron donors (organic matter), and inorganic nutrients. The availability of these substrates is often linked to trophic processes which, in turn, reflect local riparian and geomorphic influences and regional hydrologic and climatic patterns. The consequences of this regulatory hierarchy are that 1) spatial and temporal patterns in respiratory activity can be related to many environmental variables and 2) observed patterns are scale-dependent.

Estimating system respiration at a single location requires extensive effort. When comparisons are made among sites, large-scale signals may easily be obscured by finer-scale variation. Even if large-scale patterns are detected, experimental verification of causal mechanisms is a daunting prospect. What makes the effort worth pursuing is the possibility of establishing regression models that can predict long-term continental or global responses in ecosystem process rates from disturbance scenarios. Toward that goal, I analyzed stream benthic respiration rates in relation to stored benthic organic matter, water temperature, primary production and other system variables using data collected from 35 long-term study sites (Webster and Meyer 1997a).

Methods

The database included 22 streams with information on benthic respiration, benthic organic carbon (BOC), primary production, and mean annual water temperature (Table 1). Respiration rates were expressed as g C m^{-2} y^{-1}. Specific respiration rates (i.e., rates per g BOC) and BOC turnover times (i.e., BOC standing stock/respiration rate) were calculated using a conversion of 0.45 g C/g OM. Of the variables reported, respiration rates were presumed to be most directly linked with BOC and temperature. Secondary relationships with latitude, stream size, and primary production were also examined. The data were analyzed by linear regression assuming 1st-order exponential relationships between respiration and other independent variables.

TABLE 1. Mean annual water temperature, benthic organic carbon (BOC) standing stock, and heterotrophic respiration rate for 22 intensively studied streams. Specific respiration rates and BOC turnover times were calculated assuming a conversion of 0.45 g C/g OM. Site acronyms defined by Webster and Meyer (1997b). NA = not available.

Site	Mean annual water temp (°C)	BOC (g/m^2)	GPP (g C m^{-2} y^{-1})	Respiration (g C m^{-2} y^{-1})	Specific respiration (y^{-1})	BOC turnover (y)
HWNC	12	2621	3	100	0.038	26.3
RSWA	14	109	2430	816	7.496	0.1
W30R	8	15,600	35	282	0.018	55.3
W40R	8	15,821	35	278	0.018	57.0
ORGA	18.5	4154	229	1199	0.289	3.5
AGMI	8.9	255	29	60	0.235	4.3
FRMA	14	36	274	426	11.848	0.1
DCOR	6.3	12,533	16	30	0.002	425.0
MCOR	5.7	6697	35	27	0.004	252.7
LCOR	8.5	2642	64	25	0.009	106.8
MROR	7.1	379	67	20	0.053	18.9
MRQB	5.9	632	74	20	0.031	31.8
BCQB	5.7	1971	26	20	0.010	99.1
FCQB	4.7	2910	16	46	0.016	62.9
BBNH	6	537	2	46	0.085	11.8
KCAU	10.3	1821	475	332	0.182	5.5
BBVA	15	4728	NA	1125	0.238	4.2
KGKA	13.1	255	73	32	0.125	8.0
KPKA	13	58	101	11	0.181	5.5
SCAZ	19	49	850	167	3.407	0.3
WBTN	13	250	86	677	2.712	0.4
SBNC	12.4	3081	2	97	0.031	31.9

Results

BOC storage was inversely related to mean annual stream temperature with an estimated decretion rate of −0.191/deg (Fig. 1A). Benthic respiration was directly proportional to temperature with an estimated rate constant of +0.219/deg, corresponding to a Q_{10} value of 8.9 (Fig. 1B). Because of these inverse trends, specific respiration rates changed dramatically with water temperature (Fig. 1C). The estimated rate constant was +0.410/deg (Q_{10} = 60.3) with BOC turnover times spanning 5 orders of magnitude from 0.13 to 425 y (Fig. 1D).

Not surprisingly, $\log_e$ respiration was inversely related to latitude ($r^2 = 0.22$, $F = 5.62$, $\alpha = 0.03$, a = 9.82, b = −0.125), but it showed no relationship to stream order, which might also be presumed to affect water temperature. Data on gross primary production and respiration were available for 26 streams, but the two process rates were not significantly correlated. Eleven of

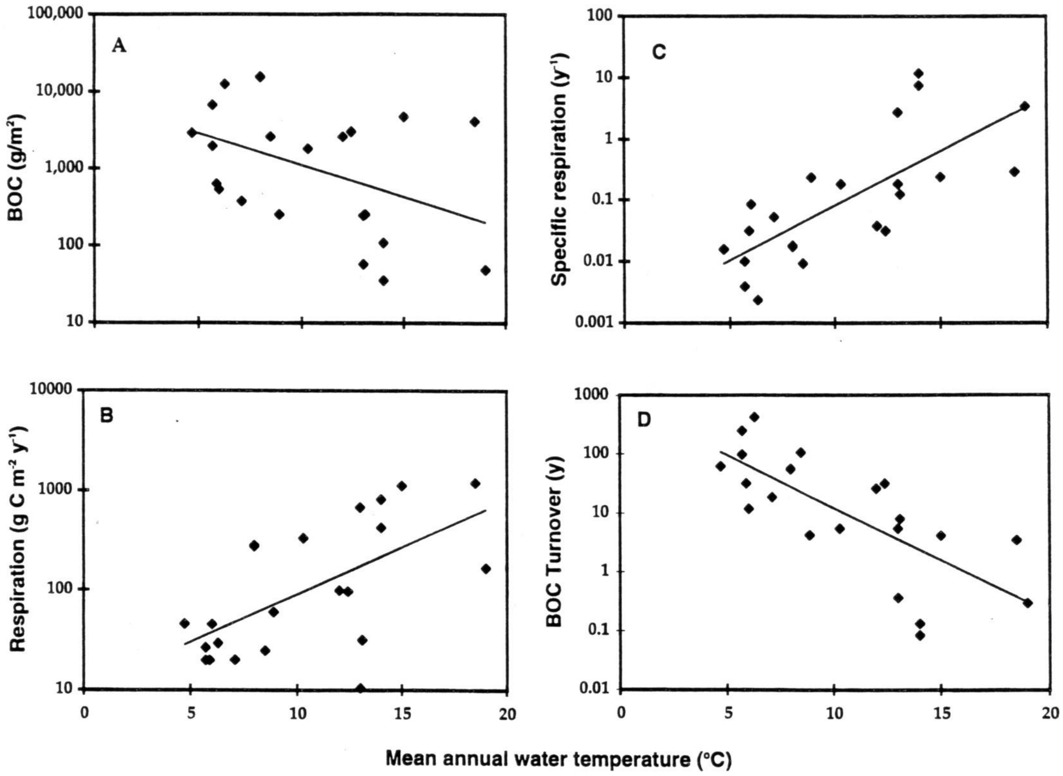

FIG. 1. Log$_e$ BOC standing stock (A), log$_e$ heterotrophic respiration (B), log$_e$ specific respiration (C), and BOC turnover time (D) as functions of mean annual water temperature for 22 streams. All regressions are statistically significant. For BOC: $r^2 = 0.18$, $F = 4.47$, $\alpha = 0.05$, a = 8.93, b = −0.1912; for heterotrophic respiration: $r^2 = 0.38$, $F = 12.4$, $\alpha = 0.002$, a = 2.32, b = 0.2185; for specific respiration: $r^2 = 0.54$, $F = 23.4$, $\alpha = 0.0001$, a = −6.61, b = 0.410; for BOC turnover time: regression statistics same as specific respiration.

the 26 streams had GPP/R ratios greater than one which suggests that respiration has been underestimated in some systems.

Discussion

Because respiration is an integrative biotic variable, it is often measured in the course of ecological studies. It is therefore somewhat surprising how little is known about respiration patterns in streams across geographic and latitudinal gradients. Webster et al. (1995) reviewed data on benthic respiration rates from 61 streams in the eastern deciduous biome of the USA. The mean value for these eastern streams, 739 g C m^{-2} y^{-1} (range = 41–2943, SD = 859, $n = 61$), is 3× greater than the mean value of 265 g C m^{-2} y^{-1} (range = 10–1200, SD = 364, $n = 22$) that I calculated from the long-term data set, which spans a much larger geographic range. Like GPP/R ratio, this discrepancy suggests that respiration has been underestimated in at least some of the streams. Within the eastern deciduous biome, there was no statistically significant relationship between benthic respiration and latitude (Webster et al. 1995).

The unresponsiveness of stream respiration to water temperature in the eastern US, stands in sharp contrast with the emergent pattern from the long-term data set. If both patterns are valid, the expansion from the biome or ecoregion scale to the continental scale must involve subsuming one suite of regulatory factors beneath another higher-order set. Although the mechanisms of regulation at the continental scale are unclear, available evidence suggests they are associated with changes in the quantity and quality of BOC among ecoegions (Jones 1997).

The apparent rate constant for the temperature effect on specific respiration is too large by more than an order of magnitude to be a simple metabolic response. Therefore, other covariates must be amplifying the trend. Potential covariates include a decline in BOC quality with increasing latitude caused by shifts in the dominant vegetation, and lower nutrient availability with increasing latitude due to sequestration and immobilization by stored OM. Jones (1997) reported that the abundance of FBOM is correlated with the abundance of CBOM, which in turn is correlated with the abundance of wood, which is correlated with latitude and precipitation. These trends suggest a latitudinal gradient in mean BOM particle size which might amplify the apparent temperature response of respiration, because, as a first approximation, microbial activity per unit OM is a function of the ratio of surface area to volume of the particles.

It is also possible that sampling biases are contributing to the respiration trend. I suggest that in high gradient mountain streams, it is relatively "easy" to estimate BOC because the sediments are shallow and a high fraction of the BOC consists of woody boles and associated debris dams. However, this same heterogeneity also makes it difficult to accurately estimate system respiration. Conversely, in more homogeneous, low-gradient systems, estimating BOC is complicated by shoals and deep hyporheic channels, perhaps leading to underestimates, while estimates of areal respiration may be somewhat easier to acquire.

Even without knowing the mechanisms of amplification, the large-scale pattern is interesting. If interpreted literally, it portends dramatic changes for stream ecosystems in the exigency of global warming: a 50% increase in benthic respiration for each 1°C rise in mean annual water temperature. Because streams within an ecoregion show only weak relationships with temperature, it appears that saltational changes in stream structure and function are associated with shifts in major climatic and vegetation zones. Thus, even if significant climate change occurs over the next several decades, several centuries might be required for a stream to reestablish a new equilibrium condition with its watershed.

Although current data suggest that alterations in stream respiration with temperature will be modest unless a watershed is pushed into a new biome, the database for such conclusions is sparse and there is good reason to question the adequacy of respiration data from only 22 sites. The apparent contrast between intra-biome and inter-biome patterns highlights the need for large-scale studies that focus on the mechanisms controlling the abundance and metabolism of organic matter.

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Suspended particulate organic matter concentration and export in streams

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From an ecosystem perspective, POM concentration and export are significant characteristics of streams. The transport of material links upstream and downstream communities trophically into an integrated ecosystem. Most POM transported in streams is fine material (<1 mm) (Sedell et al. 1978, Cudney and Wallace 1980,