STREAM ORGANIC MATTER BUDGETS

EDITED BY
J. R. WEBSTER AND JUDY L. MEYER

Made in United States of America
Reprinted from JOURNAL OF THE NORTH AMERICAN BENTHOLOGICAL SOCIETY
Vol. 16, No. 1, March 1997

J. N. Am. Benthol. Soc., 1997, 16(1):3–161

Stream organic matter budgets[1,2]

EDITED BY
J. R. WEBSTER AND JUDY L. MEYER

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.

Table of Contents

[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.

Benthic organic matter storage in streams: influence of detrital import and export, retention mechanisms, and climate

JEREMY B. JONES, JR.[1]

Environmental Sciences Division, Oak Ridge National Laboratory, P.O. Box 2008, Bldg. 1506, Oak Ridge, Tennessee 37831-6034 USA

In lotic ecosystems, BOM is a major energy source for secondary production (Minshall 1967, Benke et al. 1984), influences nutrient cycles (Mulholland et al. 1985), and affects export of DOM and POM (Bilby and Likens 1980, Bilby 1981, Smock et al. 1989). Benthic detritus also influences channel stability and retention characteristics (Keller and Swanson 1979, Mosley 1981, Webster et al. 1994) and provides habitat for stream microorganisms, macroinvertebrates (Benke et al. 1984, Huryn and Wallace 1987), and fish (Angermeirer and Karr 1984, Elliott 1986). However, in spite of the great importance of BOM to stream ecosystem function, benthic detrital storage is one of the most poorly understood components of stream organic matter budgets (Cummins et al. 1983).

Storage of BOM is governed by a broad spectrum of processes. At the scale of the river continuum, BOM tends to decrease downstream as channels become larger and riparian influences decline (Naiman and Sedell 1979, Minshall et al. 1983, Conners and Naiman 1984, Naiman et al. 1987). Individual reaches, however, are influenced not only by their position along a river continuum but also by local variations such as the character of riparian vegetation (Minshall et al. 1983, Gurtz et al. 1988) and floodplain size. Within reaches, BOM distribution is further affected by retention mechanisms, including debris dams and pools (Huryn and Wallace 1987, Smock et al. 1989, Trotter 1990, Jones and Smock 1991), channel characteristics like gradient, and interactions between main-channels and floodplains (Benke and Wallace 1990, Smock 1990).

In this synthesis I address questions of how BOM and the factors potentially governing storage vary over a range of spatial scales. BOM data were from streams with varying geomorphologies distributed in a range of biomes with vastly different vegetation characteristics. Data were analyzed by subdividing independent variables into 3 categories, 1) organic matter import and export rates, 2) channel characteristics, and 3) latitude and climate, to determine the best predictors of stream BOM. The results were used to assess how BOM storage is coupled to terrestrial litter production, in-stream primary production, and organic matter retention mechanisms.

[1] Present address: Department of Biological Sciences, University of Nevada, Las Vegas, 4505 Maryland Parkway, Las Vegas, Nevada 89154-4004 USA.

Methods

Data set

The data set consisted of 31 of the sites listed by Webster and Meyer (1997). Deep Creek in Idaho and the 3 streams in Puerto Rico lacked BOM data and were not included in this analysis. The data set also included 2 y of data from Watershed 10 in Oregon. These 2 y of data were averaged so as not to give extra weight to Watershed 10 in the analysis. Other sites commonly lacked information for one or more variables in a given analysis; consequently, many statistical tests have sample sizes <31 (sample sizes for analysis noted in Table 1). Information on detrital storage consisted of total BOM, wood, CBOM excluding wood, and FBOM; all values herein are expressed as AFDM.

Data analysis

Data were primarily analyzed using step-wise multiple linear regressions (α = 0.05-to-enter). Two criteria were used to subdivide independent variables into categories. First, covariance among variables was minimized. For example, in the analysis of channel characteristics, I included discharge as a measure of stream size, but not stream width, reasoning that discharge integrates channel width along with other channel characteristics. Second, I only included variables with potential causal effects on BOM. For each category, all 4 measures of BOM (total BOM, wood, CBOM, FBOM) were regressed against the independent variables. Independent variables included in a particular analysis are given in the results. Data were log transformed, when necessary, to achieve linearity.

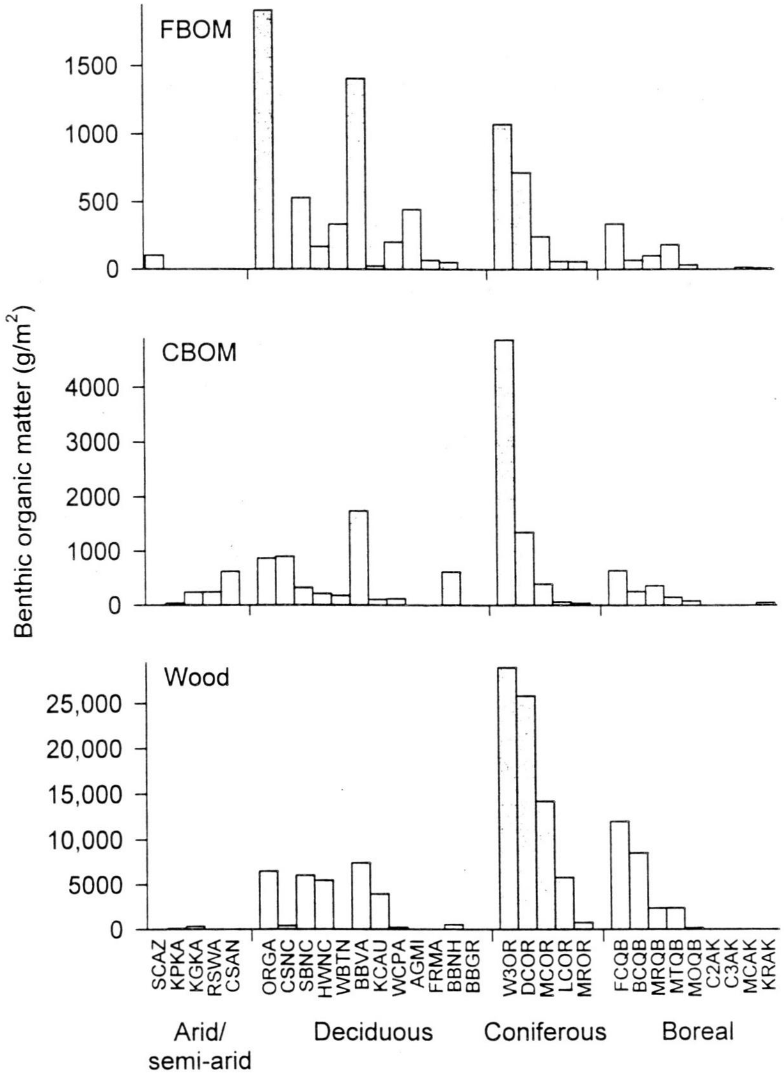

FIG. 1. FBOM, CBOM, and wood storage in study streams. Refer to Webster and Meyer (1997) for listing of stream abbreviations.

Besides the regressional analysis, a map of BOM in streams of the contiguous United States was constructed to assess how BOM is distributed at this broad spatial scale. The map was made by plotting total BOM in streams by latitude and longitude then fitting contour lines to the data using a distance-weighted least squares smoothing (SYGRAPH, SYSTAT, Inc, Evanston, Illinois). The map was restricted to the contiguous United States due to lack of BOM data from other regions. Two additional maps were constructed illustrating annual precipitation and predicted BOM (storage predicted from multiple regression results) in the United States for comparison with the map of observed BOM in streams.

Results

Storage of BOM in streams was highly variable, ranging 5 orders of magnitude from only 20 g BOM/m^2 in Monument Creek, Alaska, to 35,000 g BOM/m^2 in the Oregon headwater stream of Watershed 10 (Fig. 1). Wood accounted for the most of benthic detritus averaging 62% of total BOM. The contribution of wood to the total pool of BOM in streams was highly variable, however; streams higher than 65° latitude stored little wood, whereas 98% of BOM in Lookout Creek, Oregon, was wood (Fig. 1). The next largest component, CBOM, accounted for an average of 24% of benthic detritus. As with wood storage, the proportion of total BOM attributable to CBOM was highly variable ranging from only 1% in Lookout Creek to over 86% in the Kuparuk River (Alaska) and Canada Stream (Antarctica). The smallest fraction of BOM was FBOM (14% overall; Fig. 1). FBOM varied from only 1% in Lookout Creek to 60% of BOM in Walker Branch, Tennessee.

Import and export rates of organic matter

Total BOM and wood storage were directly related to input rate of leaf litter into streams ($p < 0.05$, Table 1; Fig. 2). Whereas there was much unexplained variance between BOM and litterfall, streams receiving <200 g m^{-2} y^{-1} of litter stored < 2400 g wood/m^2. In contrast, wood storage in streams accruing >600 g m^{-2} y^{-1} of litter was highly variable, ranging from 400 to 29,000 g/m^2.

FBOM was inversely correlated with NEP ($p < 0.001$; Fig. 2, Table 1). Thus, the Ogeechee River in Georgia and Buzzards Branch in Virginia had the greatest storage of FBOM although they had the lowest in-stream rate of organic matter production. Conversely, autotrophic streams like Rattlesnake Springs in Washington and Sycamore Creek in Arizona stored little FBOM compared with other streams (Fig. 2).

Channel characteristics

Total BOM and wood were directly related to channel gradient (Fig. 3, Table 1) with greatest storage in streams with steeper channels. CBOM storage was also correlated with channel gradient ($r = 0.66$, $p < 0.001$). However, after wood storage entered the step-wise regression model, the partial correlation coefficient between CBOM and channel gradient declined to a nonsignificant value of 0.21 ($p \geq 0.05$; Table 1) and thus gradient was excluded from the model. The relationship between wood and channel gradient is exemplified by the Oregon streams. In the high gradient (>40%) 1st-order streams Watershed 10 and Devil's Club Creek, wood storage was >25,000 g wood/m^2. In contrast, in the lower gradient (<3%) 5th-order Lookout Creek and 7th-order McKenzie River, wood storage was <5800 g wood/m^2. Notable exceptions to the association between wood and gradient were 2 blackwater streams (Buzzards Branch and the Ogeechee River) and the Quebec headwater streams (First Choice Creek and Beaver Creek), which had very low channel gradients but stored considerable amounts of wood (Fig. 3).

CBOM retained and stored in streams was directly related to wood standing stocks ($p < 0.001$; Fig. 3, Table 1). Streams with the highest wood storage, such as Watershed 10, Devil's Club Creek and Mack Creek, and 2 of the blackwater streams (Buzzards Branch and Ogeechee River) also stored the greatest amounts of CBOM. Likewise, FBOM was correlated with wood ($r = 0.46$, $p = 0.037$). However, following entry of CBOM into the step-wise regression model (Table 1), the relationship between FBOM and wood was nonsignificant ($r = 0.01$) and hence wood was excluded from the final model.

Geographic patterns

The storage of BOM in streams exhibited a distinct geographic pattern and was related to precipitation (Fig. 4, Table 1). The similarity in patterns of BOM storage and precipitation in the contiguous United States is quite striking (Fig. 5A and 5B). Streams in the southeastern United States, a region receiving substantial precipitation (75 to 215 cm/y; Karl et al. 1994), had BOM storage ranging from 600 to 10,500 g BOM/m^2. In the Pacific Northwest, where mean annual precipitation varies from 70 to 320 cm, storage was even greater, ranging from 800 to 34,900 g BOM/m^2. In contrast, in the dryer western and midwestern United States, where precipitation is typically < 70 cm/y, BOM was < 600 g BOM/m^2 (Fig. 5A).

Discussion

Stream ecologists have long recognized that the quantity and quality of stream BOM reflect adjacent riparian vegetation. This observation is epitomized by the River Continuum Concept (RCC), which describes a longitudinal reduction in BOM due to broadening of channels and consequent reduced contribution of riparian inputs (Vannote et al. 1980). While the RCC predicts a general longitudinal pattern of organic matter storage for a range of streams and rivers, there

TABLE 1. Results from step-wise multiple regression analysis of BOM (total BOM, wood, CBOM, and FBOM) versus organic matter import and export rates (litterfall, NEP, and DOM and POM export), channel characteristics (for total BOM and wood, model independent variables were channel gradient, discharge and stream-order; for CBOM, wood was also included in model; for FBOM, wood and CBOM were included in model), and latitude and climate (precipitation and temperature). A total of 12 regression analyses were conducted. Within each category (e.g., organic matter import and export rates), all 4 measures of BOM were regressed against the independent variables. Only independent variables that entered the models are listed.

Dependent variables[a]		Independent variables[b]			Test results			
Variable	Intercept	Variable	Correlation coefficient	Constant	Multiple r^2	Sample size	F-ratio	p-value
Organic matter import and export rates								
Total BOM	74.86	Litterfall	0.43	13.80	0.20	29	6.79	0.015
Wood	154.4	Litterfall	0.48	13.61	0.27	27	9.12	0.006
CBOM	—	—	—	—	—	29	—	≥0.05
FBOM	188.9	NEP	−0.76	−0.519	0.58	24	29.76	<0.001
Channel characteristics								
Total BOM	1677	Gradient	0.77	54,283	0.59	28	36.94	<0.001
Wood	1377	Gradient	0.74	46093	0.54	26	28.63	<0.001
CBOM	51.12	Wood	0.77	0.097	0.58	27	34.65	<0.001
FBOM	175.0	CBOM	0.59	0.279	0.34	25	11.78	0.002
Latitude and climate								
ln Total BOM	4.965	Precipitation	0.65	0.019	0.43	29	19.95	<0.001
ln Wood	29.13	Latitude	−0.62	−0.500	0.66	28	18.16	<0.001
		Precipitation	0.75	0.037				
		Temperature	0.25	−0.728				
ln CBOM	3.619	Precipitation	0.41	0.011	0.17	30	5.63	0.025
ln FBOM	7.195	Latitude	−0.67	−0.085	0.52	25	14.00	<0.001
		Precipitation	0.62	0.010				

[a] Total BOM, wood, CBOM, FBOM = g/m^2
[b] Litterfall, NEP = $g\ m^{-2}\ y^{-1}$; gradient = m/m; latitude = degrees; precipitation = cm/y; temperature = °C

are frequent exceptions due to local influences. As pointed out by Minshall et al. (1983), variations in riparian conditions, organic matter influx from tributaries, location-specific lithology and geomorphology, and extent of floodplains, in addition to position along a river continuum, all influence BOM.

Stream BOM and terrestrial linkages

At the broad scale of the contiguous United States, the distribution of stream BOM is very similar to the pattern of terrestrial litter production. In the United States, litter production is greatest in the Southeast and Northwest with rates ranging from 290 to 670 g dry mass $m^{-2}\ y^{-1}$ (Bray and Gorham 1964). In contrast, in the arid and semiarid interior United States, litter production is much lower and typically <200 g dry mass $m^{-2}y^{-1}$. Meentemeyer et al. (1982) reported that global litterfall is correlated with actual evapotranspiration and latitude (r^2 = 0.79). Actual evapotranspiration is a particularly informative measure for terrestrial ecosystem production because it integrates both energy and moisture availability to plants (Meentemeyer 1978). Similarly, in the present study BOM was related to precipitation (Table 1), which describes the water available for terrestrial photosynthesis and subsequent detritus available to streams.

The interpretation of BOM storage at the scale of the contiguous United States is constrained due to lack of data for many regions (Fig. 5A). Using the regressional relationship between BOM and precipitation (Table 1), I extrapolated beyond the spatial array of streams represented using mean annual precipitation data from Karl et al. (1990; 1211 precipitation stations with 48

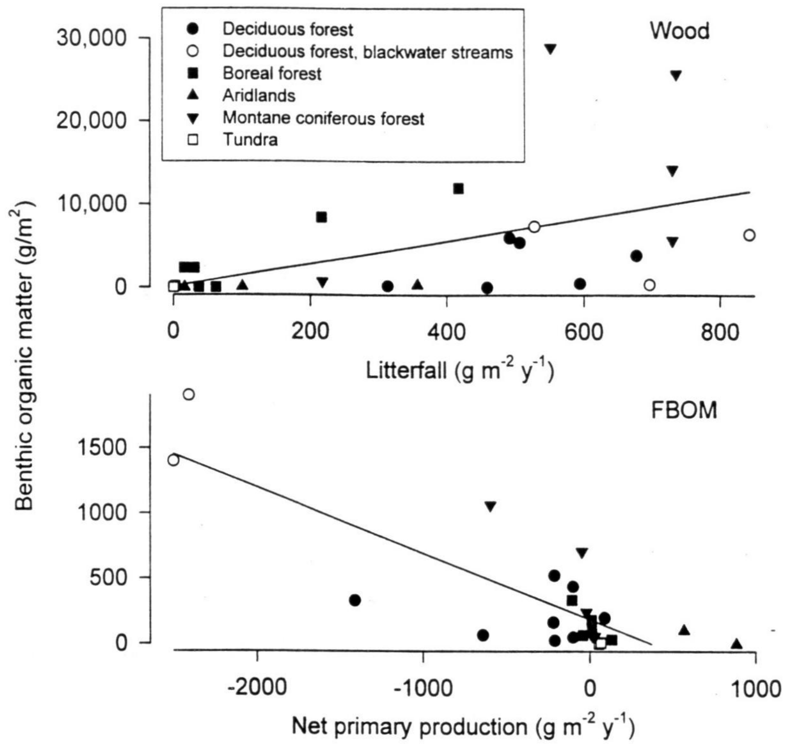

FIG. 2. Wood storage versus annual litterfall and FBOM storage versus annual net primary production.

to 122 years of data per station). The benefits of this extrapolation are 2-fold. First, BOM can be predicted a priori in streams using precipitation data for a region. Second, if, after measuring detrital storage, observed BOM differs from predicted levels, the factors controlling BOM variance within a given region can then be explored.

The predicted pattern of detrital storage in streams of the contiguous United States (BOM predicted using the regression, Table 1; Fig. 5C) is very similar to observed levels (Fig. 5A), although predicted values underestimate actual values. In the eastern United States, the region best represented in the workshop data set (9 of the 19 streams in the contiguous USA are in the East), BOM increased from <2000 g BOM/m^2 in the north to 10,000 g BOM/m^2 in the south (Fig. 5A). The predicted values of BOM in the eastern USA showed the same general pattern although predicted levels underestimated observed (1500 g BOM/m^2 predicted for the Southeast compared with 10,000 g BOM/m^2 observed; Fig. 5C). In the mid-section of the country there were few data (only 2 streams in this region) and thus little resolution of BOM storage. The regressional equation, however, provides a tool to resolve potential variability in storage for this region. Based upon the BOM and precipitation relationship, storage in the country's mid-section is predicted to decline from a high of 1300 g BOM/m^2 in the southeast to <300 g BOM/m^2 farther north (Fig. 5C). In the far western United States observed levels range from <2000 to >20,000 g BOM/m^2 (Fig. 5A). The contour lines fit to the observed data indicated that much of the western United States has streams that store large quantities of organic matter. Isopleths, however, are strongly affected by the organic-matter-rich streams in Oregon (Fig. 5A), a region of high precipitation (Fig. 5B). Much of the western USA is arid and semiarid (Fig. 5B), which limits terrestrial organic matter production. Thus, in contrast to high BOM storage indicated from the observed data, predicted BOM is <1000 g BOM/m^2 for the entire area (Fig. 5C).

The predictions derived using the regressional equation describing the relationship between BOM and precipitation can be further assessed using published data. Table 2 lists BOM report-

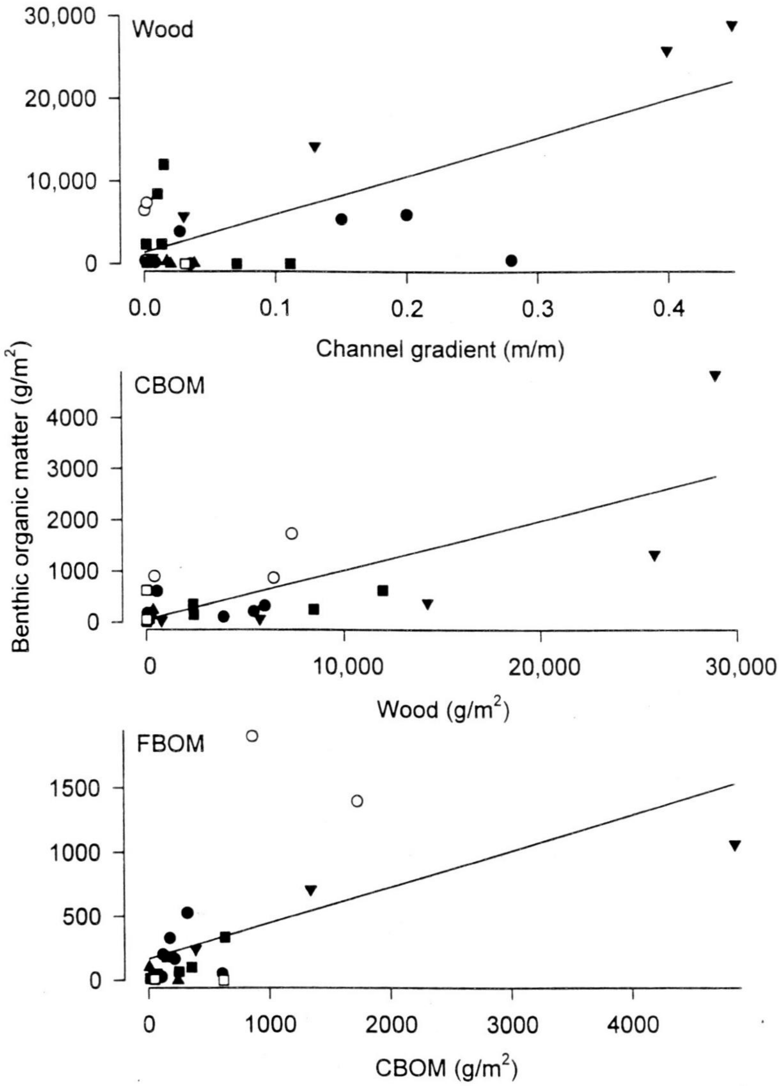

FIG. 3. Wood storage versus channel gradient, CBOM versus wood storage, and FBOM versus CBOM. Symbols as in Figure 2.

ed in 18 studies in North America that were not contributed to the data set (data were not included in the regressional analysis). For western streams (studies 1–4, Table 2), reported BOM storage ranged from 10 to 890 g BOM/m^2 and typically was <500 g BOM/m^2. BOM predicted from precipitation is <500 g BOM/m^2 for most of the West. Similarly, in the northern United States (streams 5–8, Table 2), BOM storage ranged from 100 to 970 g BOM/m^2, in close agreement with predicted storage of 600 to 1100 g BOM/m^2. In the southern and eastern United States (streams 9–18, Table 2), however, there was a poorer fit between predicted and reported storage. Organic matter storage is variable in this region, ranging 500-fold from only 10 g BOM/m^2 in the Middle Oconee River in Georgia (Nelson and Scott 1962) to 5270 g BOM/m^2 in Grady Branch, North Carolina (Golladay et al. 1989), and suggesting that factors beyond climate and latitude are important. In particular, the relationship between BOM and precipitation does not incorporate more localized influences such as catchment and stream size, and geo-

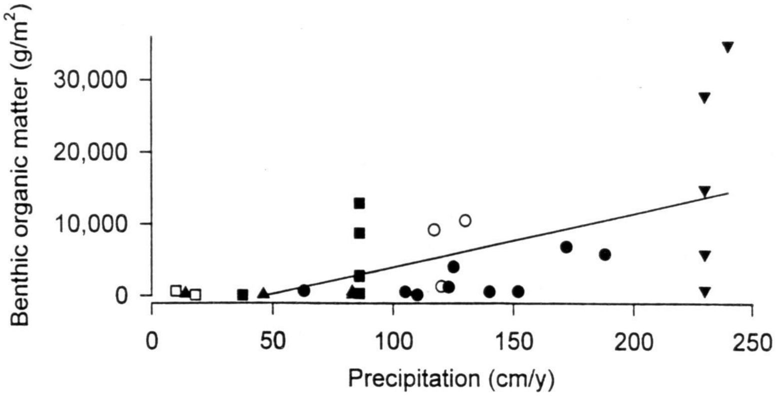

FIG. 4. Benthic organic matter versus precipitation. Symbols as in Figure 2.

morphology. Thus, while the accuracy of BOM storage predicted from the regression equation is variable, particularly in the southeastern United States, the relationship does describe a general pattern at a subcontinental scale and, as such, has applicability for understanding BOM storage across broad regions.

Deriving a relationship between BOM storage and precipitation has utility beyond estimating BOM storage for unstudied regions or streams. Given current concern about global climate change, future stream organic matter storage under different climate scenarios can be predicted. If precipitation increases with a change in climate then stream BOM may also increase as a result of increasing litter production. Obviously the relationship between BOM and precipitation is based on a limited data set (29 sites). The equation, however, generates testable predictions of BOM both in response to temporal change and for regions in which we currently lack information.

Channel geomorphology

The distribution and storage of BOM in streams are not only dependent on terrestrial organic matter production and import but are also regulated by the arrangement and abundance of POM retention mechanisms. In the regression of BOM storage versus channel characteristics, channel gradient was highly correlated with total BOM, wood, and CBOM (Table 1). General characteristics of streams such as substrate size, drainage basin morphology, and stream hydrology are related to channel gradient; high gradient streams tend to be small, drain steeply sloped basins, have large rocks and boulders (or flow over bedrock), and have high current velocities, features potentially affecting BOM. Leaf retention and organic matter storage in streams generally increase with sediment particle size and bed roughness (Webster et al. 1987). For example, in 2 streams in western North Carolina, BOM standing crops and retention rate of leaves were greater in riffles than in bedrock outcrops (Huryn and Wallace 1987), potentially due to lack of obstructions on bedrock that would retain and store organic matter (Webster et al. 1994). Similarly, the retention rate of leaves in sand-bottomed streams dramatically declines as flow rate increases in contrast to high-gradient cobble-dominated streams, which tend to remain retentive with increased flow (Jones and Smock 1991). Streams with sand and bedrock substrates function similarly in that they lack obstruction that retain and store POM.

Channel gradient, besides influencing stream substrate, also affects water depth. For a given discharge, water column depth is inversely related to gradient. Leaf transport distances and retention rate in 3 streams in the southern Appalachian Mountains were significantly correlated with depth presumably because of differences in POM particles striking obstructions such as logs or rocks (Webster et al. 1994). The probability of impinging on an obstruction increases as stream depth declines. In the present study, the direct relationship between storage and stream gradient observed probably results, in part, from variations in channel substrate and water column depth.

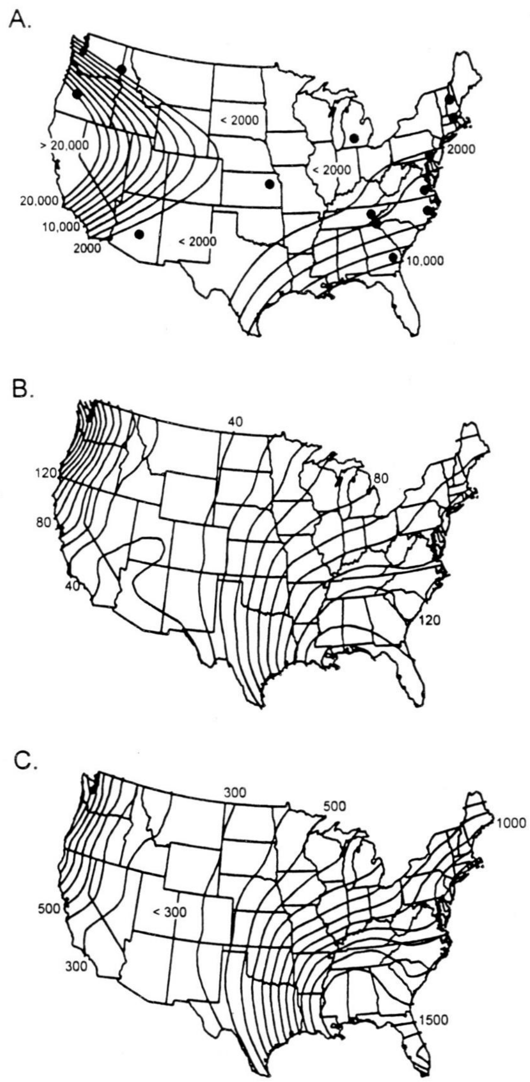

FIG. 5. BOM storage (g AFDM/m^2) in streams (panels A and C) and precipitation (cm/y; panel B) in the contiguous United States. Panel A isopleths interpolated from BOM data (location of sites indicated by filled circles). Precipitation data from Karl et al. (1990; 1211 precipitation stations and 48 to 122 years of data per station). Panel C BOM isopleths are predicted from the regression between BOM versus precipitation (1n BOM = 0.019 Precipitation + 4.965; Table 1). Contour intervals between isopleths are 2000 g AFDM/m^2 (panel A), 10 cm precipitation/y (panel B), and 100 g AFDM/m^2 (panel C).

Woody debris

The storage of CBOM and FBOM were directly related to wood standing stocks. Many studies have illustrated the important role of woody debris in removing transported POM from the water column and subsequent storage. Debris dams in Buzzards Branch accounted for 50–77% of retention of leaves removed from the water column (Jones and Smock 1991). Further, leaves traveled 9-fold farther in reaches cleared of debris dams compared with undisturbed control reaches (Smock et al. 1989). Similarly, in a 3rd-order stream in Indiana, leaves traveled 1.5 times farther in reaches lacking debris dams than in reaches containing at least one accumulation of wood (Ehrman and Lamberti 1992). In a comparison of drainage basins with different logging histories, leaves traveled farther in a stream draining a catchment clear-cut 13 y earlier than in a reference stream, presumably due to reduced storage of large wood (Webster et al. 1994). The authors conjectured that leaf retention in the disturbed stream may remain low for several centuries.

Woody debris not only affects POM retention, but also increases BOM storage and reduces organic matter export. In a 1st-order stream in the Hubbard Brook Experimental Forest, 75% of BOM was stored in debris dams although dams covered only 8% of streambed area (Bilby and Likens 1980). As the areal extent of debris dams declined to 5% and 1% in 2nd-order and 3rd-order streams, BOM storage behind dams dropped to 58% and 20%, respectively. Following clearing of all debris dams from the 2nd-order reach, POM export increased 5-fold (Bilby 1981) and BOM storage declined 63% (Bilby and Likens 1980). Likewise, debris dams in Buzzards Branch in eastern Virginia stored 85% of BOM though they covered only 6% of streambed area (Smock et al. 1989). Interestingly, in another stream in eastern Virginia (Colliers Creek), debris dams covered 5% of the streambed but stored only 21% of BOM (Smock et al. 1989). Colliers Creek has a lower gradient than Buzzards Branch (0.03 versus 0.08%) and therefore probably lacks stream power to move POM into dams.

Future research needs

Our understanding of organic matter storage is limited in several facets. First, temporal as-

TABLE 2. Total storage of benthic organic matter in streams of the contiguous United States and southern Canada.

Location	Order	BOM (gAFDM/m²)	Notes	Reference
1. Blaney Creek, Mayfly Creek, Spring Creek, British Columbia, Canada	2	200–480		Richardson 1992
2. Salmon River, Idaho	2–8	40–370	Wood not measured	Minshall et al. 1983, 1992
3. Little Beaver Creek, Colorado	3	10–200		Short and Ward 1981
4. Tesuque Creek tributaries, New Mexico	2	90–890	Wood not measured	Trotter 1990
5. McCaughly Creek, Michigan	1	430		Petersen et al. 1989
6. Augusta Creek, Michigan	1–3	140–590	Wood not measured	King and Cummins 1989
7. Kalamazoo River, Michigan	2–5	750–970	Wood not measured	Cummins et al. 1981
8. Buck Run, Pennsylvania	5	100	Wood not measured	Minshall et al. 1983
9. East Fork Trinity River tributaries, Texas	2–4	10–60		Hill et al. 1992
10. Buttahatachie River, Mississippi	4	60	Wood not measured	Naimo et al. 1988
11. Colliers Creek, Virginia	1	4300		Smock 1990
12. Grady Branch, North Carolina	1	5270		Golladay et al. 1989
13. Stillhouse Branch, North Carolina	1	1300	Small wood only	Lugthart and Wallace 1992
14. Ball Creek, North Carolina	2	560	Wood > 1 cm	Huryn and Wallace 1987
15. Ash Branch, Georgia	3	910–1020	Wood only	Benke and Wallace 1990
16. Cowpen Creek, Georgia	3	820–990	Wood only	Benke and Wallace 1990
17. Black Creek, Georgia	4	4980	Wood only	Wallace and Benke 1984
18. Middle Ocanee River, Georgia	5	10	Wood not measured	Nelson and Scott 1962

pects of BOM are poorly understood because most studies are limited to only 1 y, even though BOM storage is often variable across years (Cummins et al. 1983). As organic matter production varies temporally due to factors such as disturbance by flooding (Grimm 1987, Smock et al. 1994, Jones et al. 1995) and forest clearcutting (Golladay et al. 1989), stream detrital storage also changes. Multi-year studies of BOM storage are needed. Second, most studies of organic matter storage are limited to the benthic layer. The hyporheic zone is potentially a major site for organic matter storage. For streams in which both benthic and hyporheic storage have been measured, the latter accounts for 25–90% of total stored organic matter (Cummins et al. 1983, Metzler and Smock 1990, Jones et al. 1997). Deep subsurface storage must be considered in future studies to determine its importance in a range of streams. Finally, the full suite of organic matter retention and storage mechanisms must be explored. Debris dams have received the lion's share of attention as detrital storage sites although other retention mechanisms such as pools and floodplains are also important, especially in streams lacking wood. BOM storage must be considered with respect to a number of processes operating on a range of scales.

Acknowledgements

Thanks to Drs. J. R. Webster and J. L. Meyer for organizing the Stream Organic Matter Workshop and to all of the participants who contributed their data, insights and ideas. Thanks also to Drs. R. R. Snook and P. J. Mulholland for constructive comments on an earlier version of this chapter, Dr. W. M. Post for information on terrestrial litter production, and R. Daniels from the Carbon Dioxide Information Analysis Center at Oak Ridge National Laboratory for assistance with the precipitation data. Support for this manuscript was provided by a Global Change Distinguished Postdoctoral Fellowship from the United States Department of Energy. Work was performed at Oak Ridge National Laboratory, Lockheed Martin Energy Systems, Inc. under contract DE-AC05-84OR21400 with the US Department of Energy.

Literature Cited

ANGERMEIRER, P. L., AND J. R. KARR. 1984. Relationships between woody debris and fish habitat in a small warm-water stream. Transactions of the American Fisheries Society 113:716–726.

BENKE, A. C., T. C. VAN ARSDALL, D. M. GILLESPIE, AND F. K. PARRISH. 1984. Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. Ecology 54:25–63.

BENKE, A. C., AND J. B. WALLACE. 1990. Wood dynamics in the coastal plain blackwater stream. Canadian Journal of Fisheries of Aquatic Sciences 47:92–99.

BILBY, R. E. 1981. Role of organic debris dams in regulating the export of dissolved and particulate organic matter from a forested watershed. Ecology 62:1234–1243.

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

BRAY, J. R., AND E. GORHAM. 1964. Litter production in forests of the world. Advances in Ecological Research 2:101–158.

CONNERS, M. E., AND R. J. NAIMAN. 1984. Particulate allochthonous inputs: relationships with stream size in an undisturbed watershed. Canadian Journal of Fisheries and Aquatic Sciences 41:1473–1484.

CUMMINS, K. W., M. J. KLUG, G. M. WARD, G. L. SPENGLER, R. W. SPEAKER, R. W. OVINK, D. C. MAHAN, AND R. C. PETERSEN. 1981. Trends in particulate organic matter fluxes, community processes and macroinvertebrate functional feeding groups along a Great Lakes drainage basin river continuum. Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie 21:841–849.

CUMMINS, K. W., J. R. SEDELL, F. J. SWANSON, G. W. MINSHALL, S. G. FISHER, C. E. CUSHING, R. C. PETERSEN, AND R. L. VANNOTE. 1983. Organic matter budgets for stream ecosystems: problems in their evaluation. Pages 299–353 *in* J. R. Barnes and G. W. Minshall (editors). Stream ecology: application and testing of general ecological theory. Plenum Press, New York.

ELLIOT, S. T. 1986. Reduction of dolly varden population and macrobenthos after removal of logging debris. Transactions of the American Fisheries Society 115:392–400.

EHRMAN, T. P., AND G. A. LAMBERTI. 1992. Hydraulic and particulate matter retention in a 3rd-order Indiana stream. Journal of the North American Benthological Society 11:341–349.

GOLLADAY, S. W., J. R. WEBSTER, AND E. F. BENFIELD. 1989. Changes in stream benthic organic matter following watershed disturbance. Holarctic Ecology 12:96–105.

GRIMM, N. B. 1987. Nitrogen dynamics during succession in a desert steam. Ecology 68:1157–1170.

GURTZ, M. E., G. R. MARZOLF, K. T. KILLINGBECK, D. L. SMITH, AND J. V. MCARTHUR. 1988. Hydrologic and riparian influences on the import and storage of coarse particulate organic matter in a prairie stream. Canadian Journal of Fisheries and Aquatics Sciences 45:655–665.

HILL, B. H., T. J. GARDNER, AND O. F. EKISOLA. 1992. Benthic organic matter dynamics in Texas prairie streams. Hydrobiologia 242:1–5.

HURYN, A. D., AND J. B. WALLACE. 1987. Local geomorphology as a determinant of macrofaunal production in a mountain stream. Ecology 68: 1932–1942.

JONES, J. B., S. G. FISHER, AND N. B. GRIMM. 1995. Vertical hydrologic exchange and ecosystem metabolism in a Sonoran Desert stream. Ecology 76: 942–952.

JONES, J. B., J. D. SCHADE, S. G. FISHER, AND N. B. GRIMM. 1997. Organic matter dynamics in Sycamore Creek, a desert stream in Arizona, USA. Pages 78–82 *in* J. R. Webster and J. L. Meyer (editors). Stream organic matter budgets. Journal of the North American Benthological Society 16:3–161.

JONES, J. B., AND L. A. SMOCK. 1991. Transport and retention of particulate organic matter in two low-gradient headwater streams. Journal of the North American Benthological Society 10:115–126.

KARL, T. R., D. R. EASTERLING, AND P. Y. GROISMAN. 1994. United States historical climatology network—national and regional estimates of monthly and annual precipitation. Pages 830–905 *in* T. A. Boden, D. P. Kaiser, R. J. Sepanski, and F. W. Stoss (editors). Trends '93: A compendium of data on global change. ORNL/CDIAC-65. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, Tennessee.

KARL, T. R., C. N. WILLIAMS, AND R. T. QUINLAN. 1990. United States Historical Climatology (HCN) Serial Temperature and Precipitation Data. NDP-019/R1. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, Tennessee.

KELLER, E. A., AND F. J. SWANSON. 1979. Effects of large organic material on channel form and fluvial processes. Earth Surface Processes and Landforms 4:361–380.

KING, D. K., AND K. W. CUMMINS. 1989. Factors affecting autotrophic–heterotrophic relationships of a woodland stream. Journal of Freshwater Ecology 5:219–230.

LUGTHART, G. J., AND J. B. WALLACE. 1992. Effects of disturbance on benthic functional structure and production in mountain streams. Journal of the North American Benthological Society 11:138–164.

MEENTEMEYER, V. 1978. Macroclimate and lignin control of litter decomposition rates. Ecology 59:465–472.

MEENTEMEYER, V., E. O. BOX, AND R. THOMPSON. 1982. World patterns and amounts of terrestrial plant litter production. BioScience 32:125–128.

METZLER, G. M., AND L. A. SMOCK. 1990. Storage and dynamics of subsurface detritus in a sand-bottomed stream. Canadian Journal of Fisheries and Aquatic Sciences 47:588–594.

MINSHALL, G. W. 1967. Role of allochthonous detritus in the trophic structure of a woodland springbrook community. Ecology 48:138–149.

MINSHALL, G. W., R. C. PETERSEN, T. L. BOTT, C. E. CUSHING, K. W. CUMMINS, R. L. VANNOTE, AND J. R. SEDELL. 1992. Stream ecosystem dynamics of the Salmon River, Idaho: an 8th-order system. Journal of the North American Benthological Society 11:111–137.

MINSHALL, G. W., R. C. PETERSEN, K. W. CUMMINS, T. L. BOTT, J. R. SEDELL, C. E. CUSHING, AND R. L. VANNOTE. 1983. Interbiome comparison of stream ecosystem dynamics. Ecological Monographs 53:1–25.

MOSLEY, M. P. 1981. The influence of organic debris on channel morphology and bedload transport in a New Zealand forest stream. Earth Surface Processes and Landforms 6:571–579.

MULHOLLAND, P. J., J. D. NEWBOLD, J. W. ELWOOD, L. A. FERREN, AND J. R. WEBSTER. 1985. Phosphorus spiraling in a woodland stream: seasonal variations. Ecology 66:1012–1023.

NAIMAN, R. J., J. M. MELILLO, M. A. LOCK, T. E. FORD, AND S. R. REICE. 1987. Longitudinal patterns of ecosystem processes and community structure in a subarctic river continuum. Ecology 68:1139–1156.

NAIMAN, R. J., AND J. R. SEDELL. 1979. Benthic organic matter as a function of stream order in Oregon. Archiv für Hydrobiologie 87:404–422.

NAIMO, T. J., J. B. LAYZER, AND A. C. MILLER. 1988. Benthic community metabolism in two northern Mississippi streams. Journal of Freshwater Ecology 4:503–515.

NELSON, D. J., AND D. C. SCOTT. 1962. Role of detritus in the productivity of a rock outcrop community in a Piedmont stream. Limnology and Oceanography 7:396–413.

PETERSEN, R. C., K. W. CUMMINS, AND G. M. WARD. 1989. Microbial and animal processing of detritus in a woodland stream. Ecological Monographs 59:21–39.

RICHARDSON, J. S. 1992. Coarse particulate detritus dynamics in small, montane streams of southwestern British Columbia. Canadian Journal of Fisheries and Aquatic Sciences 49:337–346.

SHORT, R. A., AND J. V. WARD. 1981. Benthic detritus dynamics in a mountain stream. Holarctic Ecology 4:32–35.

SMOCK, L. A. 1990. Spatial and temporal variation in organic matter storage in low-gradient, headwater streams. Archiv für Hydrobiologie 118:169–184.

SMOCK, L. A., G. M. METZLER, AND J. E. GLADDEN. 1989. Role of debris dams in the structure and functioning of low-gradient headwater streams. Ecology 70:764–775.

SMOCK, L. A., L. C. SMITH, J. B. JONES, AND S. M. HOPPER. 1994. Effects of drought and a hurricane on a coastal headwater stream. Archiv für Hydrobiologie 131:25–38.

TROTTER, E. H. 1990. Woody debris, forest-stream succession, and catchment geomorphology. Journal of the North American Benthological Society 9:141–156.

VANNOTE, R. L., G. W. MINSHALL, K. W. CUMMINS, J. R. SEDELL, AND C. E. CUSHING. 1980. The river continuum concept. Canadian Journal of Fisheries and Aquatic Sciences 37:130–137.

WALLACE, J. B., AND A. C. BENKE. 1984. Quantification of wood habitat in subtropical coastal plain streams. Canadian Journal of Fisheries and Aquatic Sciences 41:1643–1652.

WEBSTER, J. R., E. F. BENFIELD, S. W. GOLLADAY, B. H. HILL, L. E. HORNICK, R. F. KAZMIERCZAK, AND W. B. PERRY. 1987. Experimental studies of physical factors affecting seston transport in streams. Limnology and Oceanography 32:848–863.

WEBSTER, J. R., A. P. COVICH, J. L. TANK, AND T. V. CROCKETT. 1994. Retention of coarse organic particles in streams in the southern Appalachian Mountains. Journal of the North American Benthological Society 13:140–150.

WEBSTER, J. R. AND J. L. MEYER. 1997. Stream organic matter budgets—introduction. Pages 5–13 *in* J. R. Webster and J. L. Meyer (editors). Stream organic matter budgets. Journal of the North American Benthological Society 16:3–161.

Large-scale trends for stream benthic respiration

ROBERT L. SINSABAUGH

Biology Department,
University of Toledo,
Toledo, Ohio 43606 USA

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