# STREAM ORGANIC MATTER BUDGETS

4

-

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 © 1997 by The North American Benthological Society J. N. Am. Benthol. Soc., 1997, 16(1):3–161 © 1997 by The North American Benthological Society

# Stream organic matter budgets<sup>1,2</sup>

# 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

Introduction (J. R. Webster and J. L. Meyer)	5
Canada Stream: a glacial meltwater stream in Taylor Valley, South Victoria Land,	•
Antarctica (D. M. McKnight and C. M. Tate)	14

<sup>1</sup> 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.

<sup>2</sup> 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.

- MCKNIGHT, D. M., AND K. E. BENCALA. 1990. The chemistry of iron, aluminum, and dissolved organic material in three acidic, metal-enriched, mountain streams, as controlled by watershed and in-stream processes. Water Resources Research 26:3087–3100.
- MEYBECK, M. 1982. Carbon, nitrogen, and phosphorus transport by world rivers. American Journal of Science 282:401–450.
- MEYER, J. L. 1990a. Production and utilization of dissolved organic carbon in riverine ecosystems. Pages 281–299 in E. M. Perdue and E. T. Gjessing (editors). Organic acids in aquatic ecosystems. John Wiley and Sons, Chichester, UK.
- MEYER, J. L. 1990b. A blackwater perspective on riverine ecosystems. BioScience 40:643–651.
- MEYER, J. L., AND R. T. EDWARDS. 1990. Ecosystem metabolism and turnover of organic carbon along a blackwater river continuum. Ecology 71:668– 677.
- MEYER, J. L., R. T. EDWARDS, AND R. RISLEY. 1987. Bacterial growth on DOC from a blackwater river. Microbial Ecology 13:13–29.
- MEYER, J. L., W. H. MCDOWELL, T. L. BOTT, J. W. EL-WOOD, C. ISHIZAKE, J. M. MELACK, B. L. PECKAR-SKY, B. J. PETERSON, AND P. A. RUBLEE. 1988. Elemental dynamics in streams. Journal of the North American Benthological Society 7:410–432.
- MIERLE, G., AND R. INGRAM. 1991. The role of humic substances in the mobilization of mercury from watersheds. Water, Air and Soil Pollution 56:349– 357.
- MOORE, T. R., AND R. J. JACKSON. 1989. Dynamics of dissolved organic carbon in forested and disturbed catchments, Westland, New Zealand. 2. Larry River. Water Resources Research 25:1331– 1339.
- MULHOLLAND, P. J., AND E. J. KUENZLER. 1979. Organic carbon export from upland and forested wetland watersheds. Limnology and Oceanography 24:960–966.
- MULHOLLAND, P. J., AND J. A. WATTS. 1982. Transport of organic carbon to the oceans by rivers of North America: a synthesis of existing data. Tellus 34: 176–186.
- MULHOŁLAND, P. J., G. V. WILSON, AND P. M. JARDINE. 1990. Hydrogeochemical response of a forested watershed to storms: effects of preferential flow along shallow and deep pathways. Water Resources Research 26:3021–3036.
- NAIMAN, R. J. 1982. Characteristics of sediment and organic carbon export from pristine boreal forest watersheds. Canadian Journal of Fisheries and Aquatic Sciences 39:1699–1718.
- NAIMAN, R. J., AND G. L. LINK. 1997. Organic matter dynamics in five subarctic streams, Quebec, Canada. Pages 33–39 in J. R. Webster and J. L. Meyer (editors). Stream organic matter budgets. Journal

of the North American Benthological Society 16: 3–161.

- 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.
- NEWBOLD, J. D., P. J. MULHOLLAND, J. W. ELWOOD, AND R. V. O'NEILL. 1982. Organic carbon spiralling in stream ecosystems. Oikos 38:266–272.
- NEWBOLD, J. D., B. W. SWEENEY, J. K. JACKSON, AND L. A. KAPLAN. 1995. Concentrations and export of solutes from six mountain streams in northwestern Costa Rica. Journal of the North American Benthological Society 14:21–37.
- OLIVER, B. G., E. M. THURMAN, AND R. L. MALCOLM. 1983. The contribution of humic substances to the acidity of colored natural waters. Geochimica et Cosmochimica Acta 47:2031–2035.
- SCHLESINGER, W. H., AND J. M. MELACK. 1981. Transport of organic carbon in the world's rivers. Tellus 33:172–187.
- TATE, C. M., AND J. L. MEYER. 1983. The influence of hydrologic conditions and successional state on dissolved organic carbon export from forested watersheds. Ecology 64:25–32.
- 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.

# Organic matter budgets for streams: a synthesis

# J. R. WEBSTER

Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia 24061 USA

# JUDY L. MEYER

Institute of Ecology, University of Georgia, Athens, Georgia 30602 USA

Estimating the efficiency of ecological processes has been a goal of ecologists since publication of Lindeman's paper on Cedar Bog Lake (Lindeman 1942, but note that for his definition of efficiency Lindeman cited an unpublished manuscript by G. E. Hutchinson). Many different definitions and kinds of ecological efficiencies have been determined in the ensuing years (e.g., Kozlovsky 1968). In an analysis of ecosys-

[Volume 16

tem budgets, the most significant efficiency is the overall efficiency with which ecosystems use available energy. Two questions are raised by this statement: 1) How do we quantify "energy available"? and 2) How do we define energy "use"? Calculations of ecosystem efficiencies for streams are further complicated by 2 additional questions: 1) How do we deal with both allochthonous and autochthonous inputs? and 2) How are our calculations affected by the transport of organic materials through and out of streams?

These questions have been addressed in a variety of ways for streams, beginning with the study of Bear Brook (Fisher and Likens 1972, 1973). In later papers, Fisher (1977) and Newbold et al. (1982) suggested other ways of calculating energy efficiency of stream ecosystems. In this synthesis we used the data presented in earlier chapters to calculate various ratios and efficiencies for stream organic matter budgets. Our objective was to use simple organic matter budgets to provide an integrated view of stream ecosystem function. To do this we used indices that express the essence of organic matter processes in streams (Fisher 1977). We began by assessing the balance of inputs and outputs for all the stream budgets, followed by a multivariate categorization of streams based on their organic matter fluxes and standing crops. We then related measures of the relative importance of allochthonous and autochthonous sources of organic matter and 4 indices of ecosystem efficiency to various physical properties of the streams.

#### Methods

This analysis is based on data for 36 organic matter budgets for 35 streams described in previous chapters. We examined inputs (GPP, litterfall and lateral movement, and groundwater), standing crops of CPOM, FPOM, and wood, and output by both respiration and export. Many of the data sets we used were incomplete. The most frequently missing budget components were groundwater DOM input, floodplain particulate input, adequate estimation of DOM and POM export during storms, and an estimate of streambed area, which is necessary to calculate export on ar areal basis for comparison with input and standing crop.

We used principal components (PC) analysis to categorize streams based on their organic

matter fluxes and standing crops. The budget components used in this analysis were GPP, litterfall, FBOM, non-wood CBOM, wood, DOM concentration, and POM concentration. Heterotrophic respiration was not included because it did not add to the explained variance of the first 2 PCs, and it precluded inclusion of several sites where  $R_{\rm H}$  had not been measured. As necessary we transformed the data to generate normal distributions (Kolmogorov–Smirnov test, p > 0.05).

To assess the relative importance of allochthonous and autochthonous production, we calculated the P/R ratio  $(GPP/R_{\rm F})$  and the fraction of total inputs that were autochthonous. An ecosystem with P/R greater than 1 is generally considered autotrophic, and if P/R is less than 1 the ecosystem is heterotrophic (e.g., Odum 1971). However, this terminology is not accurate for streams (Fisher and Likens 1973, Fisher 1977, Rosenfeld and Mackay 1987). For most ecosystems the P/R ratio depends on whether the system is aggrading (P/R > 1) or degrading (P/R < 1). But for streams, with generally little long-term aggradation or degradation, the P/R ratio depends on import and export. Rosenfeld and Mackay (1987) pointed out that P/R = 1 is not a transition from streams with respiration based primarily on autochthonous production to streams based on allochthonous inputs. Depending on the efficiencies with which autochthonous production and allochthonous inputs are used in a stream, the transition value will generally be at a P/R value much less than 1.

As another measure of the relative importance of allochthonous and autochthonous production in streams, we compared allochthonous inputs with NPP, the autochthonous production available to heterotrophs, by calculating the ratio of NPP to total inputs (NPP, litterfall, lateral movement, DOM inputs).

We calculated 4 measures of efficiency (ecosystem efficiency, organic matter turnover length, stream metabolism index, and organic matter turnover time) and looked for trends in these values by comparing them to the physical characteristics of the streams (Webster and D'Angelo 1997) using linear regression. Regressions on log transformed data are reported if transformation improved the fit of the regression line.

#### Stream ecosystem efficiency

Various indices have been proposed to measure ecosystem efficiency. The basic question is

142

the extent to which the energy inputs to a stream, both allochthonous and autochthonous, are used within the stream. By "used" we mean respired, i.e., converted from organic, reduced carbon compounds to heat and CO<sub>2</sub>. The most obvious way to measure this efficiency is R<sub>F</sub> divided by total inputs, which we call simply ecosystem efficiency (Fisher and Likens 1973). However, this measure of efficiency has problems when applied to streams (Fisher 1977). If one is working with a watershed stream budget, i.e., a budget for a stream extending from headwaters to mouth (Cummins et al. 1983), this measure of efficiency depends on the length of stream (Newbold et al. 1982). For a very short stream, the inputs, especially the allochthonous inputs, are unlikely to be retained and used within that distance. On the other hand, material moving down a long stream will stay within the study area for a long time and have a high probability of being used within the study reach. If one is studying a reach budget, i.e., a budget for a reach of stream that does not include the headwaters, comparison of respiration in that reach to inputs to that reach (GPP, litterfall, lateral movement, and lateral DOM) is inappropriate because much of the material being respired may have come from upstream. If transport from upstream is included with the inputs, the estimate of efficiency will be very low because most of this material passes through the reach without being retained and used.

The stream budgets we used were a mixture of watershed and reach budgets. For most streams, we attempted to calculate a watershed budget. In doing so we assumed that all measurements (except export) were averages for the entire length of the stream. We also attempted to estimate the total streambed area. However, the data for some of the streams was applicable only to the reach: Fort River (Massachusetts), Deep Creek (Idaho), Creeping Swamp (North Carolina), and all sites >1st order in Oregon and Quebec.

# Turnover length

The dynamics of nutrients and organic matter in streams involve both mineralization and immobilization. Coupling of this cycling with downstream movement of particles and dissolved substances results in a pattern described as spiralling (Webster 1975, Wallace et al. 1977, Webster and Patten 1979). Newbold et al. (1982) pointed out that spiralling could be quantified in terms of spiralling length. Elements without significant gaseous forms have 2 components of spiralling length: uptake length, the average distance an atom or molecule travels in dissolved, inorganic form before being immobilized; and turnover length, the average distance traveled in organic form until being mineralized. For elements such as carbon with an important gaseous form and rapid exchange of the gas with the atmosphere, uptake length is not a useful concept. However, carbon (or organic matter) turnover length is a useful method of quantifying stream ecosystem efficiency (Newbold et al 1982). Theoretically, this length is the average distance a carbon atom travels from the time it enters the stream in an organic form, either by primary production or via allochthonous input, until remineralized, i.e., respired back to inorganic carbon as  $CO_2$ . Newbold et al. (1982) showed that turnover length (S) could be calculated as:

#### S = F/R,

where F is downstream flux of organic matter per unit stream width and R is respiration.

Organic matter turnover length could be calculated for most of the streams because it does not depend on having a watershed budget. However, we could not calculate turnover length for a few streams because we did not have measurements of  $R_{\rm H}$ .

# Stream metabolism index

Fisher (1977) proposed a stream metabolism index (SMI) as the ratio of observed respiration to respiration needed to prevent accumulation of organic matter (i.e., loading). For a stream reach budget, SMI is calculated as (Cummins et al. 1983):

$$SMI = (R_E \pm dS)/(GPP + LF + LM) + T + M + G - Q_AM),$$

where dS is the change in storage, LF is litterfall, LM is lateral movement, T is tributary inputs, M is upstream input, G is groundwater input, and  $Q_t$  is the ratio of downstream to upstream discharge. Some of our budgets are neither watershed budgets nor reach budgets but rather point budgets, so  $Q_t = 1$ . Because  $Q_t = 1$ , T and G must be zero. Assuming no change in storage, the equation for SMI reduces to:

$$SMI = R_E/(GPP + LF + LM)$$

for a point budget. For a watershed budget, groundwater (G) is the only upstream input and there are no tributaries (because the whole stream system is considered), so we end up with the same equation. This equation is essentially the same as ecosystem efficiency except it does not include inputs (groundwater and throughfall DOM) that also increase discharge. Thus we are assuming that groundwater and throughfall do not change streamwater concentration. If groundwater or throughfall inputs are large and have DOM concentrations very different from streamwater, this assumption will give large errors.

#### Turnover time

Sinsabaugh (1997) calculated BOM biological turnover times for streams in this data set using BOM and heterotrophic respiration. Here we calculated BOM turnover times based on both biological processing and transport (Fisher and Likens 1973). These calculations could be made using either input (BOM / total inputs) or output (BOM / total outputs), but given the very dynamic nature of export, it was more reasonable to use inputs. Also, using outputs required information on total stream bed area in order to place transport on an areal basis.

#### **Results and Discussion**

#### Balance of inputs and outputs

Over long periods of time (decades to centuries), inputs and outputs in an undisturbed stream may be balanced, but it is unlikely that they will be exactly balanced in any single year. Most of the budgets used in this study were based on data collected during a single year or at most just a few years. Exports of DOM and POM are probably the most temporally variable components of stream budgets. For example, Triska et al. (1982) found a 4-fold difference in export from WS 10 in Oregon between 2 years. Wallace et al. (1997) found that FPOM export ranged from 37 to 171 kg/y over 9 y in Satellite Branch, North Carolina. In Canada Stream (Antarctica), it appears that there is long-term

accumulation of BOM (McKnight and Tate 1997); the only input, GPP, greatly exceeds export, and observations suggest that the perennial algal mat accumulates until an extreme high flow event occurs, about every 10 y.

Some of the stream budgets had large differences between input and output (Fig. 1). In the Ogeechee River, Georgia, outputs greatly exceeded inputs (Fig. 1A); however, expressed as a percent of standing crop or of inputs (retention efficiency, Mulholland 1981), the difference was small (Fig. 1B). The absolute numbers were large for this large river, but the fractional changes were small. The large discrepancy for Augusta Creek, Michigan, may have resulted from our putting together a budget from a variety of sources (Webster and Meyer 1997). We used particulate and dissolved transport data from Moeller et al. (1979) and Minshall et al. (1983). If we had instead used the transport data reported by Cummins et al. (1983), the estimate of transport export would have been about  $\frac{1}{10}$  as high and outputs would have much more closely balanced inputs. However, the transport data given by Cummins et al. were based on concentrations measured considerably farther downstream. For First Choice Creek, Quebec, the discrepancy is due to the inclusion of a large input of groundwater DOM, which is not included for other Quebec sites (Naiman and Link 1997). For Buzzards Branch, Virginia, outputs exceeded input because several important inputs were not included in the budget: groundwater DOM, floodplain leaf inputs, and floodplain primary production (Smock 1997). Similarly, Mulholland (1997a) suggested that outputs exceeded inputs in Walker Branch, Tennessee, because inputs of FPOM from ephemeral tributaries were not measured. Newbold et al. (1997) speculated that the main reason outputs exceeded inputs for White Clay Creek, Pennsylvania, was because storm outputs were included in the budget but inputs of POM and DOM from ephemeral rills, overland flow, and soil drainage during storms were not included. Outputs also were much greater than inputs in Sycamore Creek, Arizona, because of the large output of DOM. Jones et al. (1996, 1997) suggested that algal primary production is the major source of DOM to Sycamore Creek. In the budget data for Sycamore Creek, DOM export was an average of data from 5 y when discharge averaged 1.35 L/s, whereas GPP was measured during a sin-

144



FIG. 1. Input–output balance for 17 of the streams used in this study. SC is standing crop of benthic organic matter. Stream acronyms are defined by Webster and Meyer (1997).

gle year with an average flow of 0.25 L/s. Because of the very episodic nature of export in desert streams, it would be surprising to see a balanced budget for any one year.

With the exception of First Choice Creek, the negative discrepancies (output > input) were generally larger than positive ones (input > output). We had assumed that the situation would be reversed because of underestimation of storm transport. However, these data suggest that a more frequent problem of stream budgets is incomplete measurements of inputs, particularly groundwater DOM inputs and inputs that occur during storms (floodplain inputs, inputs from ephemeral channels, overland flows, etc.).

Categorization of streams based on organic matter budget components

Our initial analysis of the budget data was to categorize the streams based on a principal components (PC) analysis of the major budget components. PC 1 was positively correlated with litterfall and benthic organic matter and negatively correlated with GPP (Table 1). PC 1 explained 41% of the variance and clearly separated the streams along a continuum from those covered by a dense forest canopy to desert streams with little shading and high GPP (Fig. 2). PC 2 was strongly correlated with both POM and DOM concentrations. Streams at the upper

	PC 1	PC 2
Correlations between PC's and original variables		
Ln (GPP + 1)	-0.410	-0.021
Litterfall	0.429	-0.118
Ln (CBOM)	0.464	-0.196
Square root (FBOM)	0.434	0.125
$Ln \pmod{+1}$	0.468	-0.012
Ln (DOM)	-0.026	0.707
Ln (POM)	0.157	0.658
Proportion of variance explained by PC	0.417	0.226
Cumulative proportion of variance explained	0.417	0.643

TABLE 1. Results of a principal components (PC) analysis of organic characteristics of the streams.

end of PC 2 were those with high DOM, including most of the Quebec streams, especially Beaver Creek, and the southeastern coastal plain streams: Creeping Swamp, Buzzards Branch, and the Ogeechee River (Fig. 2). Also, several streams with relatively high POM, Hugh White Creek (North Carolina) and White Clay Creek, were high on this PC.

In general the streams in Fig. 2 can be separated into 3 groups: 1) lowland streams with





high DOM, 2) small streams in mesic areas with heavy shading and low transport concentrations, and 3) unshaded streams in both cold and hot deserts. Also, the several non-mountain streams in deciduous forest areas of eastern United States (White Clay Creek, Augusta Creek, Fort River, and Walker Branch) cluster near the center of the figure. At this scale of comparison, climate and gradient appear to be major regulators of organic matter dynamics in streams. Two streams appear somewhat anomalous. Hugh White Creek, a small mountain stream, fell in with the lowland, blackwater streams apparently because high transport of DOM and POM during storms results in high average annual concentrations. Also, First Choice Creek should not be with the high gradient mountain streams; however, both Mulholland (1997b) and Golladay (1997) noted guestions about the discharge data for this stream. There is no clear stream-size separation or gradient evident in Fig. 2, although streams in Oregon and Quebec are generally arranged along PC 1 with smaller streams on the right and larger streams (with lower litter inputs and higher GPP) towards the left.

## P/R ratio

For the streams we examined, P/R averaged 0.69, ranging from 0.0 (virtually no GPP) for Buzzards Branch to 1.66 for the Moisie River (Quebec) and Kings Creek (Kansas) prairie site. In fact, nearly half of the streams had P/R > 1(Fig. 3). As is usually predicted, P/R increased with increasing stream order (Fig. 3A,  $r^2 = 0.35$ , p = 0.001, n = 27), but there was considerable scatter around this trend. The sites within single river systems in Oregon and Quebec fell almost exactly along the regression line. However, the 2 sites on Kings Creek where the stream starts in grassland and then enters a gallery forest, illustrated the opposite trend. The relationship between P/R and discharge (Fig. 3B) was similar to P/R versus order though not quite as good (Fig. 3B,  $r^2 = 0.23$ , p = 0.013, n = 26, discharge log transformed). There was no significant relationship between P/R and width ( $r^2 =$ 0.05, p = 0.24 n = 27, width log transformed).

Two types of streams deviated significantly from the general trend in Fig. 3. First, arid-land streams fell well above the line, i.e., they had P/R ratios greater than predicted by their size. However, in a multiple regression using precipitation and discharge as independent variables, precipitation did not add significantly to the explained variance in P/R. The high P/R of these streams is due to the low terrestrial primary production and consequent minimal stream shading and leaf fall into the stream. Second, the 3 low-gradient, blackwater streams of southeastern United States (Buzzards Branch, Creeping Swamp, and the Ogeechee River) had P/R ratios well below the regression line. In these streams the inputs of leaves from the productive floodplain forest are the major source of instream respiration and production. Also, shading from the forest and the lack of stable benthic substrates limit autochthonous production.

#### Allochthonous versus autochthonous input

The streams used in this study ranged from being entirely dependent on autochthonous production (Canada Stream) to entirely allochthonous (Buzzards Branch). There was no general relationship between NPP as a fraction of total inputs (NPP + litterfall + lateral movement + DOM inputs) and stream order (Fig. 4A,  $r^2 =$ 0.09, p = 0.11, n = 29) or discharge (Fig. 4B,  $r^2$ = 0.14, p = 0.046, n = 28, discharge log transformed). However, the desert streams were again clear outliers to this relationship. With these 4 streams removed, the relationship became significant (dashed lines in Fig. 4, order:  $r^2 = 0.49$ , p < 0.001, n = 25; discharge:  $r^2 = 0.42$ , p < 0.001, n = 25, discharge log transformed). Because many of the studies used in this analysis did not have measurements of lateral allochthonous inputs (lateral movement) and most did not have measurements or estimates of DOM inputs, Fig. 4 overestimates the importance of NPP. This comparison also does not include the relative quality and use of allochthonous versus autochthonous inputs. For example, allochthonous DOM and peat are the dominant inputs to the Kuparuk River, but because of their refractory nature are probably little used by the stream community (Harvey et al. 1997). The most meaningful comparison would be of the fractions of R<sub>H</sub> based on autochthonous versus allochthonous inputs (Rosenfeld and Mackay 1987). However, this partitioning of R<sub>H</sub> cannot be done with available data. This sort of analysis has been done with production of some stream insects (e.g., Benke and Wallace 1980,

J. R. WEBSTER AND J. L. MEYER (EDITORS)

[Volume 16



FIG. 3. P/R ratios for the streams used in this study. The lines are fitted regression lines. Stream acronyms are defined by Webster and Meyer (1997).

1997) and an entire macroinvertebrate assemblage in a headwater stream (Hall 1996). However, analysis of whole stream  $R_H$  (c.f., Wetzel 1995) would require a carbon tagging experiment (radioactive or stable isotope) where either all NPP or all allochthonous inputs were tagged. For some streams it may be possible to use naturally occurring stable isotopes to analyze organic matter dynamics (e.g., Rounick et al. 1982, Rosenfeld and Roff 1992).

#### Stream ecosystem efficiency

Ecosystem efficiencies (Fig. 5) ranged from less than 1% (First Choice Creek) to 473% (Buzzards Branch). The very low value for First Choice Creek was because of the very high input of groundwater DOM and the short reach that was studied (Naiman and Link 1997). At the other extreme, the very high ecosystem efficiency of Buzzards Branch resulted from not including inputs of leaves from the floodplain and groundwater DOM (Smock 1997). The ecosystem efficiency for Walker Branch was also greater than 100%, which Mulholland (1997a) concluded was because FPOM inputs from ephemeral streams were not included in the budget. It is clear that the extremes calculated for ecosystem efficiencies reflect primarily what was and what was not measured and included in the budget. The median ecosystem efficiency was 36%, and the median for just watershed budgets was 31%.

Ecosystem efficiencies for the reach budgets

#### STREAM ORGANIC MATTER BUDGETS



FIG. 4. Ratios of NPP to total inputs (NPP + litterfall + lateral movement + groundwater) for the streams used in this study. The solid lines are fitted regression lines for all the data and their slopes were not significantly different from zero. The dashed lines are regression lines for all data except the arid land streams (Deep Creek, Rattlesnake Springs, Sycamore Creek, and Canada Stream). Slopes of the dashed lines were significantly different from zero.

were mostly very high (median = 63%) because we did not include transport into the reach as an input. We could have assumed that transport into the reach equaled transport out and recalculated the budgets, but we would have had to assign each reach a length in order to apportion the transport into an area. The results would then depend on an arbitrary choice of reach length.

An alternative way to measure ecosystem efficiency is to compare inputs with transport loss. If we assume that the standing crop of organic matter in a stream is unchanged from year to year, then the difference between inputs and transport loss should be equal to  $R_E$  and

efficiency calculated in this way should equal ecosystem efficiency. However, this calculation can be done only for watershed budgets because we need to know the total source area (streambed area) for the export. For the 16 streams for which data were available, this efficiency varied from -700 to over 90% (Fig. 6). The median ecosystem efficiency calculated in this way was 35%, very similar to the median calculated by the previous method. The values less than zero were generally the result of unmeasured inputs (Walker Branch, White Clay Creek, Buzzards Branch). High estimates of this efficiency can result from under-estimating transport. For example, Gray (1997) noted that transport esti-

# J. R. WEBSTER AND J. L. MEYER (EDITORS)

[Volume 16



# Watershed budgets

Reach budgets

FIG. 5. Ecosystem efficiencies for the streams used in this study. Efficiency was calculated as  $R_E$  divided by total inputs. The streams are separated into two groups, those with watershed budgets and those with reach budgets. Within each group, streams are listed from lowest discharge on the left to highest discharge on the right. Stream acronyms are defined by Webster and Meyer (1997).



FIG. 6. Ecosystem efficiencies for the streams used in this study. Efficiency was calculated as inputs minus export divided by total inputs. This figure includes only those streams with watershed budgets. Streams are listed from lowest discharge on the left to highest discharge on the right. Stream acronyms are defined by Webster and Meyer (1997).

1997]

#### STREAM ORGANIC MATTER BUDGETS



FIG. 7. Turnover lengths for the streams used in this study. The line is a fitted regression line. Stream acronyms are defined by Webster and Meyer (1997).

mates for both sites on Kings Creek were conservative because stormflow transport was not adequately considered in his calculations. The year of study also greatly affects this estimate of efficiency because of large year-to-year differences in transport. For example, the efficiency for WS 10 was more than twice as large in 1973 as in 1974, the year of higher rainfall and transport (Triska et al. 1982). Also, Cushing (1997) noted that spates only occur in Rattlesnake Springs, Washington, about once every 4 y. A budget calculated in a year of spate would be very different from one calculated in a dry year. For Augusta Creek the transport export greatly exceeded inputs resulting in the large negative efficiency. The large discrepancy (large negative efficiency) for Augusta Creek may result from putting together a budget from a variety of sources (Webster and Meyer 1997) as we discussed earlier.

# Turnover length

Turnover length ranged from 300 m (Rattlesnake Springs) to 43,700 km (Moisie River). Turnover length was highly correlated with discharge (Fig. 7,  $r^2 = 0.60$ , p < 0.001, n = 26, both variables log transformed). It is intuitive that in larger, deeper streams more organic material is transported past a point than is used there and that small streams have shorter turnover lengths, that is, they are more efficient in using organic matter than larger streams (Newbold et al. 1982). The relative efficiencies of streams may be judged by their deviation from the regression line in Fig. 7. For example, Beaver Creek had a relatively long turnover length for a 2nd-order stream; that is, it was relatively inefficient. Rattlesnake Springs and Creeping Swamp had relatively short turnover lengths-they were relatively efficient. The low efficiency of Beaver Creek does not have an obvious explanation. Compared with the other streams in Quebec (Naiman and Link 1997) and relative to its size, Beaver Creek had a low standing crop of nonwoody BOM and consequently low R<sub>H</sub>. Creeping Swamp was relatively efficient because the water in this low-gradient stream flows slowly over an actively respiring stream bed. However, note also that the budget for Creeping Swamp was based on a stream width of 400 m, the width of the floodplain that is inundated for much of the year (Mulholland 1981). When we used a typical non-flood width of 6 m (L. A. Smock, Virginia Commonwealth University, personal communication), the plot of Creeping Swamp fell slightly above the regression line. Rattlesnake Springs was relatively efficient perhaps because its primary energy base, algal production, is labile and used rapidly. WS 10 had a much shorter turnover length in 1973 than in 1974, the year of higher discharge. Walker Branch, despite the fact that transport was mea-

# J. R. WEBSTER AND J. L. MEYER (EDITORS)

[Volume 16



FIG. 8. Stream metabolism indices for the streams used in this study. Streams are listed from lowest discharge on the left to highest discharge on the right. Stream acronyms are defined by Webster and Meyer (1997).

sured in a relatively high flow year, appeared to be very efficient.

#### Stream metabolism index

SMIs ranged from 0.1 (Devil's Club Creek) to 4.7 (Buzzards Branch) with a median of 0.5 (Fig. 8). For both Buzzards Branch and Walker Branch, SMI values greater than 1 reflect unmeasured inputs as described earlier. The only other value greater than 1.0 was Fort River (SMI = 1.26). Our value differs from that calculated by Fisher (1977, SMI = 0.64) because he based his calculations on a reach whereas we calculated SMI based on a point for comparison with other streams. Newbold et al. (1982) also calculated SMIs for several streams but they used a different formula based on turnover length. Our calculation for Bear Brook, New Hampshire, also differs from that calculated by Cummins et al. (1983) because we used somewhat different data (Findlay et al. 1997). Mulholland's (1981) SMI for Creeping Swamp (SMI = 0.94) is very similar to ours (SMI = 0.91).

Most of the SMIs were less than 1, many much less. The streams with very small SMIs included 3 of the streams in Oregon (Devil's Club Creek, Mack Creek, and Lookout Creek), First Choice Creek, Bear Brook, and the Kings Creek gallery forest site. There are no obvious

commonalties among these sites. The observation that nearly all SMIs were less than 1 is consistent with the fact that some of the organic matter entering streams ends up in oceans. This observation also implies that total organic matter (TOM = POM + DOM) concentrations of streams should increase downstream. However, this conclusion is not consistently supported in other analyses. Golladay (1997) found that POM concentrations were generally lower for the larger streams within the group of streams draining forested watersheds, though Mulholland (1997b) found that DOM concentrations were higher in larger streams. For all streams, regression of TOM concentration versus stream order was not significant (Fig. 9A,  $r^2 = 0.09$ , p = 0.11, n = 30), but TOM concentration did increase significantly with discharge (Fig. 9B,  $r^2 =$ 0.22, p = 0.008, n = 30, discharge log transformed). Looking just at streams within a single river system, there were no significant stream size trends for streams in either Oregon (data from Moeller et al. 1979 and Minshall et al. 1983) or Quebec (Naiman and Link 1997), whereas DOM increased with stream size in the Ogeechee River (Sabater et al. 1993). In another study, Wallace et al. (1982) saw no increase in POM over 4 orders in Dryman Fork North Carolina, but DOM did increase dow.istream; combined DOM and POM also increased down-



FIG. 9. Total organic matter concentrations (DOM + POM) in the streams used in this study. The lines are fitted regression lines.

stream. However, Golladay and Taylor (1995) found that POM decreased downstream in Itchawaynochaway Creek, Georgia.

On a smaller scale, studies of Hugh White Creek have shown downstream increases in both POM and DOM (Meyer and Tate 1983, Webster and Golladay 1984). The SMI for this stream was 0.38, based on an ecosystem respiration of 224.5 g m<sup>-2</sup> y<sup>-1</sup> and total inputs (GPP, litterfall, and lateral movement) of 583.3 g m<sup>-2</sup>  $y^{-1}$  (Webster et al. 1997). For the 8085 m<sup>2</sup> of streambed area, inputs add 2.9 T/y of TOM to the stream. Using these values and headwater spring concentrations for POM of 0.8 mg/L (Webster and Golladay 1984) and DOM of 0.6 mg/L (Meyer and Tate 1983, assuming DOM is 50% carbon), the average annual downstream concentration should be 3.2 mg/L. This value can be compared with the 10.2 mg/L that was based on POM data from Webster et al. (1990) and DOM data from Meyer and Tate (1983). These values suggest that we either overestimated transport or that transport was unusually high in the years it was measured. In either case, the data show a downstream increase in TOM concentration. The general paucity of other data supporting a downstream increase in TOM concentration in most cases is probably due to inadequate estimation of annual transport.

Newbold et al. (1982) suggested that turnover length and SMI may be complementary measures of stream organic matter dynamics. SMI measures organic matter use relative to lateral inputs, while turnover length measures organic J. R. WEBSTER AND J. L. MEYER (EDITORS)



FIG. 10. Turnover times for the streams used in this study. The lines are fitted regression lines.

matter use relative to upstream inputs. However, for the data we analyzed in this study, there was no significant correlation between these 2 parameters (r = 0.03, p = 0.89, n = 26).

#### Turnover time

Turnover times based on inputs ranged from about 2 wk (Rattlesnake Springs) to 33 y (Devil's Club Creek, Oregon). Where turnover time could be calculated based on either inputs or outputs (17 sites), the 2 estimates were very well correlated (r = 0.87, p < 0.001, n = 17), and differences reflected the balance between inputs and outputs discussed previously. Turnover times were longest in streams with large amounts of wood, particularly the Oregon streams (Fig. 10A,  $r^2 = 0.53$ , p < 0.001, n = 28).

These streams with large standing crop of wood were generally in areas of high rainfall and dense forest vegetation so turnover time was also significantly related to precipitation (Fig. 10B,  $r^2 = 0.27$ , p = 0.003, n = 30). However, even though areas of low rainfall have little stream shading and high GPP, turnover time was not significantly related to GPP ( $r^2 = 0.07$ , p = 0.15, n = 30). Streams with long turnover times were generally small; but the relationships shown in Fig. 11 were not statistically significant and the variability explained by stream size was very low (Fig. 11A, turnover time vs. order:  $r^2 = 0.08$ , p = 0.12, n = 30; Fig. 11B, turnover time vs. In discharge:  $r^2 = 0.10$ , p = 0.25, n = 30).

If wood standing crop was not included in the calculations of turnover time, then turnover time was significantly related only to stream gradient

1997]

# STREAM ORGANIC MATTER BUDGETS



FIG. 11. Turnover times for the streams used in this study. The lines are fitted regression lines; however, their slopes were not significantly different from zero.

 $(r^2 = 0.17, p = 0.025, n = 29)$ . However, the significance of this relationship was almost entirely due to high CBOM in high-gradient Oregon streams. For these streams, however, the CBOM category included small wood.

# *Problems of evaluating stream organic matter budgets*

Cummins et al. (1983) reviewed the problems of evaluating organic matter budgets for streams. Given the number of studies that have been done since then, we need to reconsider these problems. Our revisitation of some of the topics discussed by Cummins et al. includes both general and specific problems encountered in this synthesis. We have also considered some of the problems unique to a comparison of data from various sites.

*Missing data.*—Many of the 36 budgets were missing data for one or more of the physical or organic matter parameters we used in our synthesis. While the large number of sites was useful, few of our calculations were done with the full set of sites because 4 important parameters were often missing. 1) Stream bed area: we could not calculate watershed budgets without this information. 2) Heterotrophic respiration: perhaps advances in technology (Marzolf et al. 1994) will allow this essential information to be measured in more streams in future studies. 3) FBOM standing crop: even when measured, the adequacy of the methods was uncertain. 4) Groundwater DOM input: where we did have estimates of groundwater DOM input, they were usually annual stream discharge times average groundwater concentration. This estimate may be adequate in some areas, but seasonal and spatial variation in groundwater and seep concentrations often need to be considered (Meyer and Tate 1983).

Missing parameters .- Inputs from the flood plain and ephemeral channels were not explicitly included in our budgets but turned out to be very important to balancing the budgets. For most of the budgets, allochthonous inputs were based on bankfull channel width. However, where streams have extensive flood plains or ephemeral channel networks, broader areas of input must be considered. For the Ogeechee River, floodplain litterfall was included by estimating litterfall to the entire river and flood plain and then dividing by river width (Meyer et al. 1997). Also, inputs to the Creeping Swamp flood plain were included by considering the stream to be as wide as the flood plain (Mulholland 1981). In most cases, floodplain inputs were not included. Even in small streams, the part of the channel that is only occasionally filled with water is an important and often ignored part of the stream ecosystem (Wallace et al. 1997).

Need for long-term data.—When considering a large spatial scale, changes occurring on a long temporal scale become important (Gregory et al. 1991). Though we attempted to work only with sites that we could call undisturbed, past disturbances such as fires, hurricanes, extreme storms, logging, tree diseases (e.g., chestnut blight), and even past climate change may continue to influence characteristics of the streams. Even though the data used in this study often came from sites of long-term ecological research, most of the parameters had been measured only for a single year. Only in one case did we have complete data from 2 y (WS 10), and this example illustrated the type of year-toyear variability that is common. Wallace et al. (1997) based their budget on averages of data collected over as long as 9 y. They suggested that headwater streams at Coweeta may undergo multi-year cycles of BOM accumulation and loss. Similarly, McKnight and Tate (1997) estimated that algal mat accumulation and scour in Canada Stream may occur on a cycle of about 10 y. Given the long-term climatic and hydrologic data at most sites, it should be possible to

estimate the long-term variability in some organic matter parameters. For example, Webster et al. (1990) used empirical relationships between storm flow and POM concentrations to estimate annual POM export each year for 47 y.

Adequate measurement of storm transport.—For many years it has been recognized that a large fraction of annual POM export can occur in a very short period of time (e.g., Bormann et al. 1969). Thus we assumed at the outset that our budgets would generally reflect an underestimation of POM export. Although underestimation of export may have occurred, our analyses suggest that underestimation of inputs was a greater problem. Use of rating curves, other empirical relationships between flow and POM concentration (Webster et al. 1990), and flow proportional sampling (Cuffney and Wallace 1988) have made it possible to obtain reasonably accurate estimates of annual export.

Difficulties of measuring POM standing crop.-Sampling CBOM, FBOM, and wood in streams is often difficult because of patchy distribution and deep storage. Typical measurements of CBOM with a Surber sampler positioned in mid-stream certainly underestimate CBOM (e.g., Webster 1983). However, other samplers used in a stratified sampling scheme have greatly improved CBOM estimates. FBOM is even more difficult to sample as reflected by paucity of FBOM measurements in streams. The extremely patchy distribution of wood makes its estimation very time-consuming, and adequate estimates of wood standing crop exist for only a few streams. The line-intercept method has been shown to be very useful for estimating large wood (e.g., Wallace and Benke 1984) but has been used at only a few sites.

Units and methods.—For the most part in this study, we were not troubled by conversion of units. As necessary, all data were converted to g OM. Usually we used standard conversion factors: OM is 45–50% carbon, 5 kcal/g dry weight, photosynthetic quotient of 1.0 to 1.35, respiratory quotient of 0.85 to 1.0. The conversion factors used were the most appropriate for the stream being studied. The one area where methods are critical is in measurement of primary production and ecosystem respiration. Three methods were used: whole-stream  $O_2$  or  $CO_2$  change,  $O_2$  change in chambers, and <sup>14</sup>C uptake in chambers (Lamberti and Steinman 1997). V/hole-stream methods have usually been used

# STREAM ORGANIC MATTER BUDGETS

Linkage	How this linkage is modified by terrestrial vegetation
1. Source of water	Transpiration, interception
2. Channel form	Regulates erosion rates
3. Source of nutrients	Modifies weathering rates, nutrient uptake
4. Source of dissolved organic matter	A product of plant decomposition
5. Shading (light and temperature)	Height, extent, and density (leaf area) of vege- tation
6. Source of allochthonous material	Quantity, quality, and timing of litterfall
7. Source of wood	Size and type of wood
8. Source of sediment	Retention in the terrestrial system and within the stream (debris dams)
9. Habitat and food for biota	Provides habitat for instream predators such as birds, raccoons, and alligators, and pro- vides food for some stream dwelling ani- mals such as beaver and hippopotamuses

TABLE 2. Linkages between streams and terrestrial ecosystems that are modified by terrestrial vegetation. Modified and extended from Hynes (1975) and Gregory et al. (1991).

in larger streams and thus usually have resulted in higher values of primary production than chamber measurements (Webster et al. 1995). However, in a direct comparison of methods, Bott et al. (1978) found that whole-stream methods gave lower primary production values than chamber methods. Perhaps recent modification of the whole-stream method (Marzolf et al. 1994) will provide better understanding of the differences among methods and more reliable estimates for both primary production and ecosystem respiration.

Comparison of watershed and reach budgets.— Cummins et al. (1983) noted that calculations made on watershed and reach (or point) budgets are not comparable. We have made comparisons of some parameters for all streams (SMI, turnover length), but we caution that in making these comparisons we have assumed that measurements made in downstream reaches are applicable to the entire stream network. There are no stream budgets for streams larger than 1st order that adequately estimate all budget parameters taking into consideration the variability over the entire stream network.

#### Conclusions

Ecological processes in streams may be observed at spatial scales ranging from a global perspective to happenings on a single substrate particle (Minshall 1988); but explaining the patterns observed depends on the scale and the nature of the process being observed (Fisher 1992). Invertebrate and fish distributions along a river might best be explained by hydraulic patterns (Statzner and Borchardt 1992), but processes such as primary production and invertebrate trophic dynamics are better explained by stream size, i.e., the river continuum (Vannote et al. 1980) as demonstrated by Naiman et al. (1987). Organic matter budgets offer an integrated view of stream ecosystem function and generate indices that express the essence of organic process in streams (Fisher 1977). When we analyzed organic matter budgets, we found that stream size remained an important predictor of organic processes but was frequently obscured by factors related to the geoclimatic region. The effects of the geoclimatic region were generally expressed through effects on watershed vegetation.

Ross (1963) observed that the distribution of many stream insect species was clearly related to terrestrial biomes. He pointed out that the climatic conditions necessary for a particular terrestrial biome plus the factors imposed by the terrestrial ecosystem produced a unique set of conditions within streams. Hynes (1975) detailed the many ways in which the "valley rules the stream," and Gregory et al. (1991) elaborated the influences of riparian vegetation on streams. Certainly riparian vegetation has a dominating influence on streams, but even vegetation in the watershed far removed from the stream regulates the water and nutrients reaching a stream. In Table 2 we have listed the major linkages between terrestrial ecosystems and streams and suggested how these linkages are modified by terrestrial vegetation.

Fisher and Grimm (1991) pointed out that cross ecosystem comparisons may reveal broad principles of ecosystem science but understanding of mechanisms shaping ecosystem structure and function still require detailed studies. Thus, we would not expect stream comparisons at a global level to provide information about the mechanisms of stream function, but rather they should provide generalities that might guide more specific studies. Global comparisons of streams require consideration of 3 major factors that vary in both time and space: climate, longitudinal succession (stream size), and disturbance (Minshall 1988). We have tried to minimize effects of disturbance by only using data from undisturbed streams; however, past disturbances undoubtedly have altered the characteristics of many of these streams (Benfield 1995) and some of the streams drain watersheds that have been highly modified by human activity, e.g., White Clay Creek and the Ogeechee River. In general our results show that stream size is a major factor in comparisons within a single stream system or within a geoclimatic region. According to Minshall et al. (1983), the stream size effect must be visualized as a sliding scale, which is shifted upstream or downstream depending on climate, geology, and riparian vegetation. On a broader level, climate, primarily through its influence on terrestrial vegetation, largely determines the stream characteristics we have analyzed.

# Acknowledgements

Support for the preparation of this chapter was provided by a grant to the Coweeta site of the Long-Term Ecological Research Program of the National Science Foundation (BSR9011661).

#### Literature Cited

- BENFIELD, E. F. 1995. Historical land-use and streams. Bulletin of the North American Benthological Society 12:241–248.
- BENKE, A. C., AND J. B. WALLACE. 1980. Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. Eco<sup>1</sup>ogy 61:108– 118.
- BENKE, A. C., AND J. B. WALLACE. 1997. Trophic basis

of production among riverine caddisflies: implications for food web analysis. Ecology (in press).

- BORMANN, F. H., G. E. LIKENS, AND J. S. EATON. 1969. Biotic regulation of particulate and solution losses from a forest ecosystem. BioScience 19:600–611.
- BOTT, T. L., J. T. BROCK, C. E. CUSHING, S. V. GREGORY, D. KING, AND R. C. PETERSEN. 1978. A comparison of methods for measuring primary productivity and community respiration in streams. Hydrobiologia 60:3–12.
- CUFFNEY, T. F., AND J. B. WALLACE. 1988. Particulate organic matter export from three headwater streams: discrete versus continuous measurements. Canadian Journal of Fisheries and Aquatic Sciences 45:2010–2016.
- CUMMINS, K. W., J. R. SEDELL, F. J. SWANSON, G. W. MINSHALL, S. G. FISHER, C. E. CUSHING, R. C. PE-TERSEN, 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.
- CUSHING, C. E. 1997. Organic matter dynamics in Rattlesnake Springs, Washington, USA. Pages 39– 43 in J. R. Webster and J. L. Meyer (editors). Stream organic matter budgets. Journal of the North American Benthological Society 16:3–161.
- FINDLAY, S., G. E. LIKENS, L. HEDIN, S. G. FISHER, AND W. H. MCDOWELL. 1997. Organic matter dynamics in Bear Brook, Hubbard Brook Experimental Forest, New Hampshire, USA. Pages 43–46 in J. R. Webster and J. L. Meyer (editors). Stream organic matter budgets. Journal of the North American Benthological Society 16:3–161.
- FISHER, S. G. 1977. Organic matter processing by a stream-segment ecosystem: Fort River, Massachusetts, U.S.A. Internationale Revue der gesamten Hydrobiologie 62:701–727.
- FISHER, S. G. 1992. Pattern, process and scale in freshwater systems: some unifying thoughts. Pages 575–591 in P. S. Giller, A. G. Hildrew, and D. G. Raffaelli (editors). Aquatic ecology. Scale, pattern and process. Blackwell, London.
- FISHER, S. G., AND N. B. GRIMM. 1991. Streams and disturbance: Are cross-ecosystem comparisons useful? Pages 196–221 in J. Cole, G. Lovett, and S. Findlay (editors). Comparative analyses of ecosystems. Patterns, mechanisms, and theories. Springer-Verlag, New York.
- FISHER, S. G., AND G. E. LIKENS. 1972. Stream ecosystem: organic energy budget. BioScience 22:33-35.
- FISHER, S. G., AND G. E. LIKENS. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecological Monographs 43:421–439.
- GOLLADAY, S. W. 1997. Suspended particulate organic matter concentration and export in streams.

Pages 122–131 *in* J. R. Webster and J. L. Meyer (editors). Stream organic matter budgets. Journal of the North American Benthological Society 16: 3–161.

- GOLLADAY, S. W., AND B. W. TAYLOR. 1995. Characteristics of coastal plain streams: measurements of suspended particulate organic and inorganic matter in Ichawaynochaway Creek. Pages 380–383 *in* K. J. Hatcher (editor). Proceedings of the 1995 Georgia Water Resources Conference. University of Georgia, Athens.
- GRAY, L. J. 1997. Organic matter dynamics in Kings Creek, Konza Prairie, Kansas, USA. Pages 50–54 *in* J. R. Webster and J. L. Meyer (editors). Stream organic matter budgets. Journal of the North American Benthological Society 16:3–161.
- GREGORY, S. V., F. J. SWANSON, W. A. MCKEE, AND K. W. CUMMINS. 1991. An ecosystem perspective of riparian zones. BioScience 41:540–551.
- HALL, R. O. 1996. Bacterivory and organic matter flow in stream food webs. PhD Thesis. University of Georgia, Athens.
- HARVEY, C. J., B. J. PETERSON, W. B. BOWDEN, L. A. DEEGAN, J. C. FINLAY, A. E. HERSHEY, AND M. C. MILLER. 1997. Organic matter dynamics in the Kuparuk River, a tundra river in Alaska, USA. Pages 23–28 in J. R. Webster and J. L. Meyer (editors). Stream organic matter budgets. Journal of the North American Benthological Society 16:3– 161.
- HYNES, H. B. N. 1975. The stream and its valley. Verhandlung der Internationalen Vereinigung für theoretische und angewandte Limnologie 19:1– 15.
- JONES, J. B., S. G. FISHER, AND N. B. GRIMM. 1996. A long-term perspective of dissolved organic carbon transport in Sycamore Creek, Arizona, USA. Hydrobiologia 317:183–188.
- 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.
- KOZLOVSKY, D. C. 1968. A critical evaluation of the trophic level concept. 1. Ecological efficiencies. Ecology 49:48–50.
- LAMBERTI, G. A., AND A. D. STEINMAN. 1997. A comparison of primary production in stream ecosystems. Pages 95–104 in J. R. Webster and J. L. Meyer (editors). Stream organic matter budgets. Journal of the North American Benthological Society 16:3–161.
- LINDEMAN, R. L. 1942. The trophic-dynamic aspect of ecology. Ecology 23:399–418.
- MARZOLF, E. R., P. J. MULHOLLAND, AND A. D. STEIN-MAN. 1994. Improvements to the diurnal up-

stream-downstream dissolved oxygen change technique for determining whole-stream metabolism in small streams. Canadian Journal of Fisheries and Aquatic Sciences 51:1591–1599.

- MCKNIGHT, D. M., AND C. M. TATE. 1997. Canada Stream: a glacial meltwater stream in Taylor Valley, South Victoria Land, Antarctica. Pages 14–17 *in J. R. Webster and J. L. Meyer (editors). Stream* organic matter budgets. Journal of the North American Benthological Society 16:3–161.
- MEYER, J. L., A. C. BENKE, R. T. EDWARDS, AND J. B. WALLACE. 1997. Organic matter dynamics in the Ogeechee River, a blackwater river in Georgia, USA. Pages 82–87 *in* J. R. Webster and J. L. Meyer (editors). Stream organic matter budgets. Journal of the North American Benthological Society 16: 3–161.
- MEYER, J. L., AND C. M. TATE. 1983. The effects of watershed disturbance on dissolved organic carbon dynamics of a stream. Ecology 64:33-44.
- MINSHALL, G. W. 1988. Stream ecosystem theory: a global perspective. Journal of the North American Benthological Society 7:263–288.
- 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.
- MOELLER, J. R., G. W. MINSHALL, K. W. CUMMINS, C. E. CUSHING, R. C. PETERSEN, G. L. LARSON, J. R. SEDELL, AND R. L. VANNOTE. 1979. Transport of dissolved organic carbon in streams of differing physiographic characteristics. Organic Geochemistry 1:139–150.
- MULHOLLAND, P. J. 1981. Organic carbon flow in a swamp-stream ecosystem. Ecological Monographs 51:307-322.
- MULHOLLAND, P. J. 1997a. Organic matter dynamics in the West Fork of Walker Branch, Tennessee, USA. Pages 61–67 in J. R. Webster and J. L. Meyer (editors). Stream organic matter budgets. Journal of the North American Benthological Society 16: 3–161.
- MULHOLLAND, P. J. 1997b. Dissolved organic matter concentration and flux in streams. Pages 131–141 *in J. R. Webster and J. L. Meyer (editors). Stream* organic matter budgets. Journal of the North American Benthological Society 16:3–161.
- NAIMAN, R. J., AND G. L. LINK. 1997. Organic matter dynamics in 5 subarctic streams, Quebec, Canada. Pages 33–39 in J. R. Webster and J. L. Meyer (editors). Stream organic matter budgets. Journal of the North American Benthological Society 16: 3–161.
- 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.

- NEWBOLD, J. D., T. L. BOTT, L. A. KAPLAN, B. W. SWEE-NEY, AND R. L. VANNOTE. 1997. Organic matter dynamics in White Clay Creek, Pennsylvania, USA. Pages 46–50 in J. R. Webster and J. L. Meyer (editors). Stream organic matter budgets. Journal of the North American Benthological Society 16: 3–161.
- NEWBOLD, J. D., P. J. MULHOLLAND, J. W. ELWOOD, AND R. V. O'NEILL. 1982. Organic carbon spiralling in stream ecosystems. Oikos 38:266–272.
- ODUM, E. P. 1971. Fundamentals of ecology. Saunders, Philadelphia.
- ROSENFELD, J. S., AND R. J. MACKAY. 1987. Assessing the food base of stream ecosystems: alternatives to the P/R ratio. Oikos 50:141–147.
- ROSENFELD, J. S., AND J. C. ROFF. 1992. Examination of the carbon base in southern Ontario streams using stable isotopes. Journal of the North American Benthological Society 11:1–10.
- Ross, H. H. 1963. Stream communities and terrestrial biomes. Archiv für Hydrobiologie 59:235–242.
- ROUNICK, J. S., M. J. WINTERBOURN, AND G. L. LYON. 1982. Differential utilization of allochthonous and autochthonous inputs by aquatic invertebrates in some New Zealand streams: a stable carbon isotope study. Oikos 39:191–198.
- SABATER, F. J. L. MEYER, AND R. T. EDWARDS. 1993. Longitudinal patterns of dissolved organic carbon concentration and suspended bacterial density along a blackwater river. Biogeochemistry 21: 73–93.
- SINSABAUGH, R. L. 1997. Large-scale trends for stream benthic respiration. Pages 119–122 in J. R. Webster and J. L. Meyer (editors). Stream organic matter budgets. Journal of the North American Benthological Society 16:3–161.
- SMOCK, L. A. 1997. Organic matter dynamics in Buzzards Branch, a blackwater stream in Virginia, USA. Pages 54–58 in J. R. Webster and J. L. Meyer (editors). Stream organic matter budgets. Journal of the North American Benthological Society 16: 3–161.
- STATZNER, B., AND D. BORCHARDT. 1992. Longitudinal patterns and processes along streams: modelling ecological responses to physical gradients. Pages 113–140 in P. S. Giller, A. G. Hildrew, and D. G. Raffaelli (editors). Aquatic ecology. Scale, pattern and process. Blackwell, London.
- TRISKA, F. J., J. R. SEDELL, AND S. V. GREGORY. 1982. Coniferous forest streams. Pages 292–332 *in* R. L. Edmonds (editor). Analysis of coniferous forest ecosystems in the western United States. Hutchinson Ross, Stroudsburg, Pennsylvania.
- 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.
- WALLACE, J. B., T. F. CUFFNEY, S. L. EGGERT, AND M. R. WHILES. 1997. Stream organic matter inputs, storage, and export for Satellite Branch at Coweeta Hydrologic Laboratory, North Carolina, USA. Pages 67–74 in J. R. Webster and J. L. Meyer (editors). Stream organic matter budgets. Journal of the North American Benthological Society 16: 3–161.
- WALLACE, J. B., D. H. ROSS, AND J. L. MEYER. 1982. Seston and dissolved organic carbon dynamics in a southern Appalachian stream. Ecology 63:824– 838.
- WALLACE, J. B., J. R. WEBSTER, AND W. R. WOODALL. 1977. The role of filter-feeders in flowing waters. Archiv für Hydrobiologie 79:506–532.
- WEBSTER, J. R. 1975. Analysis of potassium and calcium dynamics in stream ecosystem on three southern Appalachian watersheds of contrasting vegetation. PhD Thesis. University of Georgia, Athens.
- WEBSTER, J. R. 1983. The role of benthic macroinvertebrates in detritus dynamics of streams: a computer simulation. Ecological Monographs 53:383– 404.
- WEBSTER, J. R., AND D. J. D'ANGELO. 1997. A regional analysis of the physical characteristics of streams. Pages 87–95 in J. R. Webster and J. L. Meyer (editors). Stream organic matter budgets. Journal of the North American Benthological Society 16:3– 161.
- WEBSTER, J. R., AND S. W. GOLLADAY. 1984. Seston transport in streams at Coweeta Hydrologic Laboratory, North Carolina, U.S.A. Verhandlung der Internationalen Vereinigung für theoretische und angewandte Limnologie 22:1911–1919.
- WEBSTER, J. R., S. W. GOLLADAY, E. F. BENFIELD, D. J. D'ANGELO, AND G. T. PETERS. 1990. Effects of forest disturbance on particulate organic matter budgets of small streams. Journal of the North American Benthological Society 9:120–140.
- 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.
- WEBSTER, J. R., J. L. MEYER, J. B. WALLACE, AND E. F. BENFIELD. 1997. Organic matter dynamics in Hugh White Creek, Coweeta Hydrologic Laboratory, North Carolina, USA. Pages 74-78 in J. R. Webster and J. L. Meyer (editors). Stream organic matter budgets. Journal of the North American Benthological Society 16:3–161.

89.

- WEBSTER, J. R., AND B. C. PATTEN. 1979. Effects of watershed perturbation on stream potassium and calcium dynamics. Ecological Monographs 49:51-72.
- Webster, J. R., J. B. Wallace, and E. F. Benfield. 1995. Organic processes in streams of the eastern United States. Pages 117-187 in C. E. Cushing, G.

W. Minshall, and K. W. Cummins (editors). River and stream ecosystems. Elsevier, Amsterdam. WETZEL, R. G. 1995. Death, detritus, and energy flow in aquatic ecosystems. Freshwater Biology 33:83-

Received: 29 May 1996 Accepted: 31 October 1996