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.

2368

Stream organic matter budgets—introduction

J. R. WEBSTER

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

J. L. MEYER

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

The study of energy flow in Bear Brook by Fisher and Likens (1972, 1973) provided a new way to look at stream ecosystems. Earlier studies of trophic dynamics in flowing-water ecosystems by Odum (1957), Teal (1957), Nelson and Scott (1962), and Tilly (1968) had provided a foundation, but Fisher and Likens were the first to compile a complete budget of inputs, standing crops, and outputs for a stream. The organic matter budget for Bear Brook made it possible to compare the relative importance of various sources and losses of organic matter and allowed calculation of stream ecosystem efficiency. Since that time, comprehensive organic matter budgets have been published for only a few other streams (Fisher 1977, Mulholland 1981, Triska et al. 1982), though organic matter budgets of a more limited extent have been used to study the role of fish migration in streams (Hall 1972), evaluate predictions of the river continuum concept (Minshall et al. 1983), compare streams with and without beaver (Naiman et al. 1986), and evaluate effects of watershed logging on streams (Meyer and Tate 1983, Webster et al. 1990).

Cummins et al. (1983) discussed the many problems associated with constructing a stream budget and concluded that stream ecology would not benefit from the development of budgets for numerous streams with short-term data. They noted that what was needed was determination of total stream budgets at a few selected sites with long-term data and sustained research programs. Although stream researchers continued to study organic matter dynamics over the next decade, no complete organic matter budgets were published. We observed that the information needed to construct organic matter budgets probably existed for numerous streams and that it would be useful to systematically assemble and analyze the available data to assess the current status of research on organic matter dynamics in streams and to suggest fruitful directions for future research. Consequently, we organized a workshop, which was held on 23 and 24 May 1993 prior to the NABS meeting in Calgary, Alberta. We invited individuals who we thought had data on, and interest in, organic matter dynamics in streams and encouraged them to suggest additional people who could contribute to the workshop; 57 scientists participated. At the workshop, we attempted to compile and analyze organic matter budgets for 27 streams. As a result of these discussions, we requested modified data sets for each site, and, over the next 2 y, we reanalyzed those data, sent them back to the research teams for verification and feedback, and synthesized the resulting information. This paper is the product of those efforts by many individuals. In addition to the sites represented at the workshop, we have added data from several other streams based on published information.

Three objectives guided organization of the workshop and subsequent analyses: 1) to explore relationships between physical variables of streams and their watersheds (climate, geomorphology) and organic matter dynamics using data from a broad geographic area; 2) to compare stream organic matter dynamics in a diverse array of streams to suggest determinants of observed patterns; and 3) to reveal deficiencies in currently available data on organic matter dynamics in streams.

The collection of sites that we used is not a random sample of streams throughout the world. It includes those sites represented by a participant at the workshop who took time to compile the data, plus sites where sufficient data were already published. There is a clear North American, temperate zone bias to the sites (Fig. 1), which reflects the fact that most stream organic matter studies have been done there. We feel fortunate to have at least some data from sites outside this area. Perhaps this synthesis will encourage more studies elsewhere.

The data included in this synthesis are of 2 types, physical and organic matter. The 8 physical variables are latitude, stream order (Strahler 1957), watershed area, stream width, stream

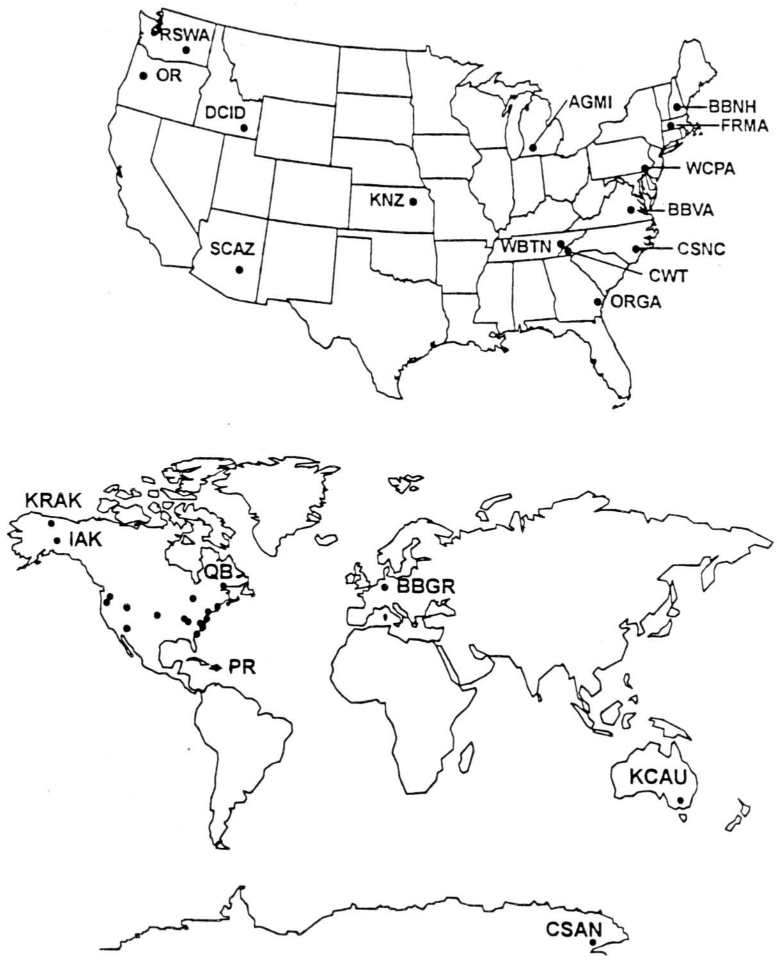

FIG. 1. Sites used in this organic matter synthesis. Acronyms are given in Table 1. OR includes all 5 Oregon sites: DCOR, MCOR, LCOR, MROR, and both years for WS 10 (W3OR, W4OR). IAK includes the 3 sites in Interior Alaska: MCAK, C2AK, and C3AK. KNZ includes both the prairie (KPKA) and gallery forest (KGKA) sites in Kansas. PR includes 3 sites in Puerto Rico: QSPR, QTPR, and RIPR. QB includes the 5 streams in Quebec: FCQB, BCQB, MTQB, MRQB, and MOQB. CWT includes both sites at Coweeta Hydrologic Laboratory: HWNC and SBNC.

gradient, mean annual water temperature, mean annual discharge, and mean annual precipitation. These variables give a very limited description of a site but do provide the basic template for analysis of organic matter dynamics. The organic matter variables are similarly limited (Fig. 2). Inputs include allochthonous inputs of direct litterfall (leaves, wood, and other material), GPP, and DOM carried in groundwater entering the stream. (Acronyms and abbreviations used throughout this paper are given in Tables 1 and 2.) The standing crop of organic matter is separated into FBOM (< 1mm), CBOM (> 1 mm, not including wood), and wood. Outputs are autotrophic and heterotrophic respiration and export of POM and DOM carried by the stream as part of dissolved, suspended, or bed load. All variables are expressed as ash-free dry mass of organic matter (AFDM).

The presentation of this synthesis is arranged as follows. Descriptions of sites where data were taken entirely from published information are included at the end of this introductory chapter. This chapter is followed by 16 chapters describing sites. In some cases the data assembled in these chapters have been previously published

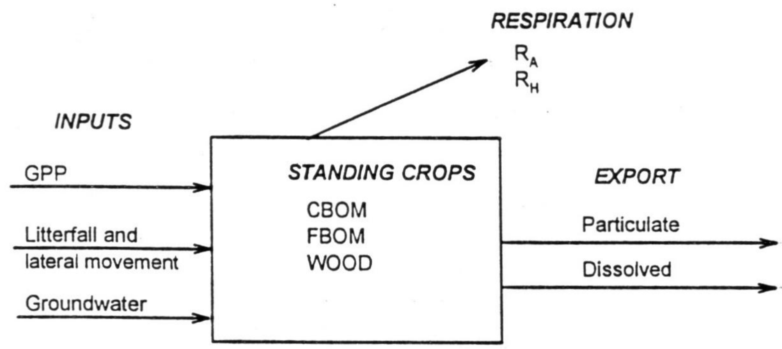

FIG. 2. The components of the stream organic matter budget used in this synthesis. Acronyms and abbreviations are given in Table 2.

in various pieces. In other chapters, most data are being published for the 1st time. The site-description chapters are followed by 7 chapters in which the authors have analyzed specific components of the organic matter budgets: physical variables (Webster and D'Angelo 1997), primary production (Lamberti and Steinman 1997), litterfall (Benfield 1997), benthic organic matter (Jones 1997), heterotrophic respiration (Sinsabaugh 1997), transported particulate organic matter (Golladay 1997), and dissolved organic matter (Mulholland 1997). Finally, we have attempted a synthesis of the total budgets (Webster and Meyer 1997). Two major conclusions have come from this synthesis. First, at the level of global comparisons, stream organic matter dynamics are driven primarily by climate, largely through its effect on terrestrial vegetation. Second, despite the significant progress that has been made in the study of organic matter processes in streams, many of the differences we found among streams reflect omissions of important components of the budgets.

The data used in this paper are available online on the Coweeta home page, http://sparc.ecology.uga.edu/. We hope that access to these data will encourage further analysis and greater awareness of the value of synthesis and inter-site comparisons. Any use of these data must cite this paper or chapters that are part of this paper.

Published studies of organic matter dynamics—site descriptions

To increase the geographic coverage and diversity of streams included in our analysis, we have incorporated data from published studies of organic matter processes in streams (Table 3). In this section, we briefly describe the streams and studies from which these data were taken.

Fort River, Massachusetts

Fisher's (1977) study of the Fort River is still one of the most complete organic matter budgets for a medium-sized stream. The Fort River is a 4th-order tributary of the Connecticut River in central Massachusetts, USA. Fisher studied a 1700-m reach that drains a 105-km² watershed. Land use in the watershed included second-growth hardwood forest on the upper slopes, agriculture in the valley, some residential development, but no industry. Primary land uses along the study reach were agriculture, grazing, and woodland. Riparian hardwood vegetation was nearly continuous on both sides of the stream. Mean discharge ranged from 280 L/s in summer to peak flows of nearly 28,000 L/s. Mean width was 14 m and mean depth was 0.48 m, and according to Fisher there was no floodplain in the study reach. Substrate ranged from cobbles and gravel in riffles to fine sand and silt in slower reaches. During summer up to 20% of the steambed was covered by aquatic macrophytes. Periphytic algae were present throughout the year and during some years were abundant in midsummer. Fisher described the water quality as generally typical of unpolluted lowland streams in New England. Soluble reactive phosphorus (SRP) averaged 25 $\mu g/L$ and was usually < 10 $\mu g/L$. NO_3-N was usually < 0.2 mg/L. Water temperature ranged from 0 to 27.5°C.

TABLE 1. Site acronyms used in this chapter and in other chapters in this paper. Sites are organized by terrestrial biome.

Tundra	
CSAN	Canada Stream, Antarctica
KRAK	Kuparuk River, Alaska
Boreal coniferous forest	
MCAK	Monument Creek, Alaska
C2AK	Caribou Creek tributary C–2, Alaska
C3AK	Caribou Creek tributary C–3, Alaska
FCQB	First Choice Creek, Quebec
BCQB	Beaver Creek, Quebec
MRQB	Muskrat River, Quebec
MTQB	Matamek River, Quebec
MOQB	Moisie River, Quebec
Montane coniferous forest	
W3OR	WS10, Oregon, 1973 data
W4OR	WS10, Oregon, 1974 data
DCOR	Devil's Club Creek, Oregon
MCOR	Mack Creek, Oregon
LCOR	Lookout Creek, Oregon
MROR	McKenzie River, Oregon
Deciduous forest	
BBGR	Breitenbach, Germany
BBNH	Bear Brook, New Hampshire
WCPA	White Clay Creek, Pennsylvania
KCAU	Keppel Creek, Australia
WBTN	Walker Branch, Tennessee
SBNC	Satellite Branch (WS55), North Carolina
HWNC	Hugh White Creek, North Carolina
AGMI	Augusta Creek, Michigan
FRMA	Fort River, Massachusetts
Deciduous forest, blackwater streams	
BBVA	Buzzards Branch, Virginia
CSNC	Creeping Swamp, North Carolina
ORGA	Ogeechee River, Georgia
Tropical forest	
QSPR	Quebrada Sonadora, Puerto Rico
QTPR	Quebrada Toronja, Puerto Rico
RIPR	Rio Icacos, Puerto Rico
Aridlands, grassland and desert	
RSWA	Rattlesnake Springs, Washington
KGKA	Kings Creek, Kansas, gallery forest site
KPKA	Kings Creek, Kansas, prairie site
SCAZ	Sycamore Creek, Arizona
DCID	Deep Creek, Idaho

Deep Creek, Idaho

Data on Deep Creek were published by Minshall (1978) in his paper on autotrophic production in streams. Other information on Deep Creek was included in the paper on organic matter budgets in streams published by Cummins et al. (1983). Deep Creek is a 2nd-order, hard-water stream in the Great Basin desert in southern Idaho, USA. The dominant riparian vegetation was sagebrush. Width ranged from 1 to 6 m, and mean depth ranged from 10 to 60 cm. Mean discharge was 90 L/s, ranging from 60 to 700 L/s. In our analysis, we used Minshall's (1978) data for Station 3, which had the highest autotrophic production of his 3 sites. Most of the production was by periphyton, but production by macrophytes was also substantial. His data were converted to g from kcal by dividing by 5 kcal/g. Also, his value for GPP was modified to include dark respiration.

Creeping Swamp, North Carolina

Mulholland's (1981) study of Creeping Swamp was the 1st stream organic matter budget for a wetland ecosystem. This 3rd-order swamp–stream lies on the Coastal Plain of North Carolina, USA. Its watershed was extensively wooded (65%), with most of the remaining area in row agriculture; the wide floodplain was almost entirely forested with deciduous hardwoods. Stream water was moderately acid (pH 4.3–5.7), colored, and high in DOM. Dissolved inorganic nitrogen was moderately high (0.23 mgN/L) and SRP was low (4 µg/L) (Kuenzler et al. 1977). The 8-km segment studied by Mulholland was delimited upstream and downstream by gages monitored by the US Geological Survey. Mulholland used the floodplain edge as the lateral boundaries of the stream because this area is routinely inundated for relatively long periods each year (> 50% inundation for 4–6 mo each year). Thus stream width varied from 100 to 600 m and averaged 400 m.

Oregon streams

We have included data from 5 streams in Oregon, USA. These include the unnamed stream draining Watershed 10 of the H. J. Andrews Experimental Forest, which we refer to as WS 10. This stream was studied intensively in 1972–1974 before the watershed was logged (Triska et al. 1982, 1984). Our site description is taken from these 2 papers. The other 4 streams, Devil's Club Creek, Mack Creek, Lookout Creek,

TABLE 2. Organic matter acronyms and abbreviations used in this chapter and in other chapters in this paper.

GPP	Gross primary production
NPP	Net primary production (GPP − R_A)
NEP	Net ecosystem production (GPP − R_E, also called net daily metabolism or net community production)
R_A	Autotrophic (plant) respiration
R_H	Heterotrophic respiration
R_E	Total ecosystem (or community) respiration $R_E = R_A + R_H$)
AFDM	Ash free dry mass
POM	Particulate organic matter
CPOM	Coarse particulate organic matter (usually > 1 mm)
FPOM	Fine particulate organic matter (usually particules < 1 mm)
DOM	Dissolved organic matter (usually < 0.45 μm)
DOC	Dissolved organic carbon
BOM	Benthic organic matter
CBOM	Coarse benthic organic matter
FBOM	Fine benthic organic matter

and the McKenzie River, were studied as part of the River Continuum Project (e.g., Minshall et al. 1983).

WS 10 is a small, 1st-order stream in the western Cascade Mountains of Oregon, USA. Prior to logging, it drained a 10.24-ha watershed of 450-y-old Douglas-fir with an understory of western hemlock. The slope of the stream is very steep (45 cm/m) with side slopes ranging up to 90 cm/m. Discharge averaged 5.5 L/s but was highly seasonal, ranging from 0.23 L/s in summer to 140 L/s during winter storms. Width of the stream ranged from 0.25 cm at the headwaters to 1–1.5 m at the downstream end (defined by a weir). The streambed was a series of small pools connected by free-fall zones or riffles running over bedrock. Most of the pools were formed upstream of accumulations of woody debris. NO_3-N averaged 6 μg/L, NH_4-N was almost undetectable, and mean SRP was 42 μg/L (Triska et al. 1984). Parameters for the organic matter budget were measured in 1972–1973 and again in 1973–1974, so we have included both budgets for this stream in our analysis. Although most parameters were similar between years, twice as much precipitation fell during the 2nd year. As a result, export of both DOM and POM was significantly higher, 3× for DOM and nearly 7× for POM. Despite the large export the 2nd year, there was still net retention of organic matter during both years (Triska et al. 1982).

The 4 sites in Oregon used in the River Continuum Project were all in the McKenzie River drainage, beginning within the H.J. Andrews Experimental Forest. Like WS 10, all sites are characterized by a maritime climate with high rainfall or snowfall occurring in autumn through spring and very low flows in summer. The dominant forest vegetation throughout the area is Douglas-fir and western hemlock, with red alder at lower elevations. Our site descriptions and data used in this synthesis were taken from reports published by Moeller et al. (1979), Naiman and Sedell (1979a, 1979b, 1980), Cummins et al. (1983), Minshall et al. (1983), and Bott et al. (1985). Devil's Club Creek is a 1st-order stream heavily shaded by forest canopy, with very little autotrophic production and very large amounts of woody debris. This stream drains into Mack Creek, a 3rd-order stream characterized by a stairstep of pools, free-fall zones, and turbulent water around large boulders. Substrate in the study area was mostly loose cobble. Woody debris was abundant but less than in Devil's Club Creek. The forest canopy was mostly closed with patches of light reaching the stream at midday. Mack Creek is a major tributary of Lookout Creek, a 5th-order stream. Lookout Creek was dominated by shallow riffles interspersed with small pools and a substrate of large cobbles, gravel, and bedrock. There was relatively little woody debris, the canopy was open, and primary production was a major organic input. Lookout Creek discharg-

TABLE 3. Site characteristics and organic matter parameters for miscellaneous sites. A standard conversion of 1 gC per 2 g AFDM was used in many calculations. In most cases R_A was assumed to be 50% of GPP, and R_H was calculated as R_E minus R_A. Dash indicates no data available. Acronyms and abbreviations are given in Tables 1 and 2.

	FRMA[a]	DCID[b]	CSNC[c]	W3OR[d]	W4OR[d]
Physical characteristics					
Latitude (°N)	42	43	35	45	45
Order	4	2	3	1	1
Watershed area (ha)	10,700	44,700	8000	10.2	10.2
Streambed area (m^2)	—	—	—	300	300
Gradient (m/m)	0.02	0.002	0.00054	0.45	0.45
Mean annual water temperature (°C)	14	18.3	—	8	8
Mean annual discharge (L/s)	2718	—	1126	5.5[i]	5.5[i]
Mean annual precipitation (cm)	110	41	120	240	240
Mean stream width (m)	14	6	400	0.7	0.7
Inputs ($g\ m^{-2}\ y^{-1}$)					
Gross primary production	609	3540	56.4	77	77
Leaffall	384	2.4	696	537	567
Lateral movement	—	—	0	667	1111
DOM input; thrufall and groundwater	134	—	49	350	877
Standing crops (g/m^2)					
CBOM (not including wood)	—	—	900	4607	5117
FBOM	68	—	—	1067	1067
Wood	—	—	400	28,993	28,973
Outputs					
Autotrophic respiration ($g\ m^{-2}\ y^{-1}$)	304.5	2170.4	28.2	50	50
Heterotrophic respiration ($g\ m^{-2}\ y^{-1}$)	945.5	231.7	654	627	617
Particulate transport (kg/y)	167,150	—	73,000	37	245
Dissolved transport (kg/y)	538,000	—	1,300,000	96	310

[a] Fisher (1977)
[b] Minshall (1978). A conversion of 5 kcal = 1 g AFDM was used. GPP was calculated as NPP plus 24-h plant respiration
[c] Mulholland (1981)
[d] From Triska et al. (1982) except as noted
[e] Directly or calculated from Minshall et al. (1983) except as noted
[f] From Cummins et al. (1981) except as noted
[g] McDowell and Asbury (1994) and W. H. McDowell, University of New Hampshire, personal communication
[h] From Bott et al. (1985). Metabolism calculated using PQ = 1.2 and RQ = 0.85
[i] Triska et al. (1984)
[j] Calculated from Cummins et al. (1983)
[k] Calculated from Naiman and Sedell (1979a). CBOM includes wood 0.1–10 cm
[l] Moeller et al. (1979)

es into Blue River, a tributary of the McKenzie River. The McKenzie River is a 7th-order stream draining the western Cascade Mountains. Morphologically, it was 85% riffle-runs with a few alcoves or pools. The substrate was cemented cobble and large boulders. Primary production by periphyton, moss, and aquatic macrophytes was important. The 3 lower order streams had similar temperature regimes with winter lows of about 1°C and summer maxima of about 15–18°C. The annual temperature range in the McKenzie River was somewhat narrower, 3–12°C. Nutrient levels in the 3 smaller streams were fairly similar with relatively high phosphorus (SRP up to 15 μg/L), but NO_3-N was often at or near limits of detection. In the McKenzie River, NO_3-N averaged 0 to 4.2 μg/L and SRP ranged from 28 to 50 μg/L.

TABLE 3. Extended.

DCOR[e]	MCOR[e]	LCOR[e]	MROR[e]	AGMI[f]	QTPR[g]	RIPR[g]	QSPR[g]
45	45	45	45	42	18	18	18
1	3	5	7	1	1	3	3
20	600	6050	130,000	38[e]	16.2	326	262
300	—	—	—	1050[h]	—	—	—
0.4	0.13	0.03	0.006	0.008[e]	0.2	0.014	0.24
6.3	5.7	8.5	7.1	8.9[h]	22	—	—
1.7	92	3660	55,000	13[j]	9	380	208
230	230	230	230	152[j]	315	430	438
0.6	3	12	40	1.5	2.5	—	—
36.5[h]	77.6[h]	141.4[h]	148.3[h]	64[h]	—	—	—
736[j]	730[j]	730[j]	218[j]	448[j]	400	400	400
—	—	—	—	—	—	—	—
—	—	—	—	394.8[j]	—	—	—
1012[k]	388[k]	61[k]	34[k]	126	—	—	—
538[k]	244[k]	61[k]	59[k]	440	—	—	—
23,750[k]	14,250[k]	5750[k]	750[k]	—	—	—	—
18.2[h]	38.8[h]	70.7[h]	74.1[h]	32[h]	—	—	—
65.6[h]	58.9[h]	55[h]	44.6[h]	133[h]	—	—	—
51	1340	58,865	1,176,000	2253[e]	211	24,970	3947
86[l]	2031[l]	80,800[l]	1,908,000[l]	3444[l]	1068	61,266	38,951

Augusta Creek, Michigan

Augusta Creek has been studied by many researchers at Kellogg Biological Station (e.g., Manny and Wetzel 1973, Petersen and Cummins 1974, Wetzel and Manny 1977), and 3 sites along Augusta Creek were used in the River Continuum Project. In this synthesis, we used data from the 1st-order Smith site (Moeller et al. 1979, Cummins et al. 1981, 1983, Minshall et al. 1983, Bott et al. 1985). A tributary of the Kalamazoo River in southern Michigan, USA, Augusta Creek meanders through a watershed of recent glacial till with hardwood forest, row agriculture, pastures, and extensive wetlands. At the Smith site, the stream was covered by a canopy of deciduous shrubs and mixed hardwoods, though diatom blooms occurred in the spring. It was a moderately stained, hardwater stream (160–210 mg/L alkalinity, Manny and Wetzel 1973) with high levels of nitrogen (1.15 mg/L NO_3-N) but lower total phosphorus (27 μg/L) (Bott et al. 1985). The substrate at the Smith site was gravel extensively covered by accumulations of organic matter. Manny and Wetzel (1973) described Augusta Creek as undisturbed except for the introduction of brown trout.

Puerto Rican streams

Although studies of tropical streams have increased in the past few years, these streams have been greatly under-represented in most syntheses of stream research. No tropical stream has been sufficiently studied to allow construction of a comprehensive organic matter budget; however, considerable work has been done on streams in Puerto Rico. Using data from the study by McDowell and Asbury (1994), we included physical characteristics and DOM and POM data for 3 streams, the Quebrada Toronja, Rio Icacos, and Quebrada Sonadora. These streams flow through the Luquillo Experimental Forest at the eastern end of Puerto Rico. The watersheds supported small farms and selective tree harvest before the area became National Forest about 70 y ago. Vegetation types include tabonuco forest (Quebrada Toronja), colorado forest (Rio Icacos), and mixed colorado and palm forest (Quebrada Sonadora). The forests are periodically subject to severe hurricane damage. The Quebrada Sonadora and Quebrada Toronja have very steep slopes (20 and 24 cm/m), but the Rio Icacos is considerably less steep (1.4 cm/m). Streambed substrates of the 3 streams are very different. The Rio Icacos is almost entirely sand with occasional boulders, the Quebrada Sonadora streambed consists primarily of bedrock, cobbles, and boulders, and the Quebrada Toronja substrate is predominately mudstone bedrock and cobbles with smaller deposits of unconsolidated clay and sand. Stream temperatures range from 19 to 21°C and have little seasonal or diel fluctuation. Over the course of the 3-y study by McDowell and Asbury, streamflow ranged from 81 to 7500 (L/s) for the Rio Icacos, 11 to 14,000 for Quebrada Sonadora, and 8 to 155 for Quebrada Toronja. Nutrient concentrations were similar in all 3 streams: total dissolved phosphorus averaged 2 μg/L, NH_4-N was about 15 μg/L, and NO_3-N was 64 μg/L.

Acknowledgements

We thank the University of Calgary and NABS for their support of the workshop, which was the stimulation for this paper. Support for the preparation of this chapter came from the Coweeta site of the Long-Term Ecological Research (LTER) Program of the National Science Foundation (BSR9011661), and support for the publication of the entire paper was provided by the LTER Network Office (DEB9300679). We thank Gary Lamberti for reviewing the information for the Oregon streams and Pat Mulholland for reviewing the information about Creeping Swamp.

Literature Cited

BENFIELD, E. F. 1997. Comparisons of litterfall input to streams. Pages 104–108 *in* J. R. Webster and J. L. Meyer (editors). Stream organic matter budgets. Journal of the North American Benthological Society 16:3–161.

BOTT, T. L., J. T. BROCK, C. S. DUNN, R. J. NAIMAN, R. W. OVINK, AND R. C. PETERSEN. 1985. Benthic community metabolism in four temperate stream systems: an inter-biome comparison and evaluation of the river continuum concept. Hydrobiologia 123:3–45.

CUMMINS, K. W., M. J. KLUG, G. M. WARD, G. L. SPINGLER, 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 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. Plenum Press, New York.

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., 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.

HALL, C. A. S. 1972. Migration and metabolism in a temperate stream ecosystem. Ecology 53:585–604.

JONES, J. B. 1997. Benthic organic matter storage in streams: influence of detrital import and export, retention mechanisms, and climate. Pages 109–119 *in* J. R. Webster and J. L. Meyer (editors). Stream organic matter budgets. Journal of the North American Benthological Society 16:3–161.

KUENZLER, E. J., P. J. MULHOLLAND, L. A. RULEY, AND R. P. SNIFFEN. 1977. Water quality in North Carolina Coastal Plain streams and effects of channelization. Report No. 127. University of North Carolina Water Resources Rearch Institute, Raleigh.

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.

MANNY, B. A., AND R. G. WETZEL. 1973. Diurnal changes in dissolved organic and inorganic carbon and nitrogen in a hardwater stream. Freshwater Biology 3:31–43.

MCDOWELL, W. H., AND C. E. ASBURY. 1994. Export of carbon, nitrogen, and major ions from three tropical montane watersheds. Limnology and Oceanography 39:111–125.

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. 1978. Autotrophy in stream ecosystems. BioScience 28:767–771.

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. 1997. 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 J. R. SEDELL. 1979a. Benthic organic matter as a function of stream order in Oregon. Archiv für Hydrobiologie 87:404–422.

NAIMAN, R. J., AND J. R. SEDELL. 1979b. Characterization of particulate organic matter transported by some Cascade Mountain streams. Journal of the Fisheries Research Board of Canada 36:17–31.

NAIMAN, R. J., AND J. R. SEDELL. 1980. Relationship between metabolic parameters and stream order in Oregon. Canadian Journal of Fisheries and Aquatic Sciences 37:834–847.

NAIMAN, R. J., J. M. MELILLO, AND J. E. HOBBIE. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). Ecology 67:1254–1269.

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.

ODUM, H. T. 1957. Trophic structure and productivity of Silver Springs, Florida. Ecological Monographs 27:55–112.

PETERSEN, R. C., AND K. W. CUMMINS. 1974. Leaf processing in a woodland stream. Freshwater Biology 4:345–368.

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.

STRAHLER, A. N. 1957. Quantitative analysis of watershed geomorphology. Transactions of the American Geophysical Union 38:913–920.

TEAL, J. M. 1957. Community metabolism in a temperate cold spring. Ecological Monographs 27: 283–302.

TILLY, L. J. 1968. The structure and dynamics of Cone Spring. Ecological Monographs 38:169–197.

TRISKA, F. J., J. R. SEDELL, K. CROMACK, S. V. GREGORY, AND F. M. MCCORISON. 1984. Nitrogen budget for a small coniferous forest stream. Ecological Monographs 54:119–140.

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.

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., 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. Organic matter budgets for streams: a synthesis. Pages 141–161 *in* J. R. Webster and J. L. Meyer (editors). Stream organic matter budgets. Journal of the North American Benthological Society 16:3–161.

WETZEL, R. G., AND B. A. MANNY. 1977. Seasonal changes in particulate and dissolved organic carbon and nitrogen in a hardwater stream. Archiv für Hydrobiologie 80:20–39.