# STREAM ORGANIC MATTER BUDGETS

Temperature fluctuation and nitrate were highly correlated with their 2nd principle component. One difference between their analysis and ours was that precipitation was highly correlated with their 1st principle component but didn't come into our analysis until the 3rd principle component. The lack of a temperature effect and the greater importance of precipitation in the study by Cushing et al. were probably results of the more limited latitudinal extent of their sites.

#### Conclusions

The 35 streams used in this study were not chosen to represent the range of physical conditions of streams throughout the world. Rather, they were chosen because of the availability of data on organic processes. However, where comparisons were possible, relationships among physical variables of the 35 streams were similar to the relationships among the same variables in more extensive studies. Stream size, water temperature, and precipitation appear to be the most important variables physically characterizing the streams. These variables set the template for organic processes occurring in streams. However, as becomes evident in analyses of organic processes, the influence of these physical processes is largely indirect through their effects on terrestrial vegetation.

#### Acknowledgements

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# A comparison of primary production in stream ecosystems

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The objective of this paper is to identify physical, chemical, and biological variables that might help explain the wide range of primary production observed in streams from a variety of biomes and locations throughout the world. We used regression approaches to search for predictive, statistical relationships that might reveal how aquatic, riparian, and watershed vari-

1997]

ables are associated with differences in primary production among 30 streams from the original data set (see Webster and Meyer 1997) for which primary production was measured.

Primary production may be defined generally as the conversion of solar energy to reduced chemical energy, or specifically as the amount of organic matter formed from inorganic carbon by photosynthetic organisms during a specified time interval (Bott 1996). The total amount of carbon fixed during the interval is the gross primary production (GPP). Common intervals used to describe GPP are a day or a year. Because plants also respire to drive their cellular metabolism, some of this fixed energy is lost as  $CO_2$ ; this process is termed autotrophic respiration (R<sub>A</sub>). The remaining fixed carbon allocated to biomass represents the net primary production (NPP). Therefore,

## $GPP = NPP + R_A$

In streams, primary producers generally are associated with benthic substrates, and include algae, cyanobacteria, bryophytes, and vascular macrophytes, although algae are usually the major producers. Large rivers may develop a self-sustaining phytoplankton assemblage, termed potamoplankton, that contributes to primary production (Hynes 1970). Benthic algae also are called periphyton, but periphyton actually is a mixture of algae, bacteria, protists, fine detritus, and other materials that attach to submersed surfaces. In practice, it is almost impossible to separate the metabolic rates of autotrophs from heterotrophs in studies of lotic primary production. Thus, these metabolic measurements also include the respiration of organisms other than plants, termed heterotrophic respiration (R<sub>H</sub>). For this reason, many investigators prefer to call the respiration term community or ecosystem respiration  $(R_{\rm F})$  to acknowledge the heterotrophic component (cf. Gregory 1983).

The focus of this paper is on annual GPP from our sample of 30 streams. We made the following predictions concerning the patterns of GPP, some of which were based on tenets of the river continuum concept (Vannote et al. 1980).

1) GPP is low in low-order (headwater) streams because of light limitation by riparian canopy, and thus GPP is negatively related to percent canopy cover;

- 2) GPP increases as stream size increases but declines in large, deep rivers;
- this stream size-GPP relationship also is reflected in correlates of stream size (e.g., discharge, gradient, channel width, watershed area);
- GPP declines with increasing latitude because of lower annual light inputs and average water temperatures;
- 5) GPP is negatively related to annual precipitation because of increased riparian vegetation (and greater shading) and more scour by floods; and
- 6) GPP is positively related to nutrient concentrations.

#### Methods

Annual GPP estimates were available for 30 streams, mostly from the northern hemisphere and predominately at latitudes between 30 and 50° (see Webster and Meyer 1997 for a complete list). To facilitate comparison across different biomes, we classified the streams into 5 broad categories based on climate and forest type: **desert** and arid land streams, **deciduous** forest streams, **boreal** coniferous forest streams, montane **coniferous** forest streams, and **other** streams (Fig. 1). The "other" group included blackwater streams, grassland streams, and tundra streams (see Webster and Meyer 1997).

Measurements of GPP, especially those made in chambers, generally were for periphyton attached to rocks (sometimes termed epilithon). However, some sites included harvest of macrophytes, measurement of water column productivity, or inclusion of bryophytes in incubation chambers, where appropriate. The frequency of GPP estimates varied with site, ranging from 2 (e.g., ice-free period at extreme northern latitudes) to 12 (monthly at several sites) measurements. Measurements of plant standing crop (e.g., chlorophyll *a* or biomass) were not as readily available as GPP estimates, and thus we did not include standing crop in our analysis.

Several different, but widely accepted, methods were used to estimate benthic GPP of the streams. More than half of the studies (n = 17) measured O<sub>2</sub> evolution from sediments placed in closed chambers. Seven studies monitored in situ diel O<sub>2</sub> curves, and one study (Rattlesnike Springs, Washington) used the diel CO<sub>2</sub> curve. Oxygen measurements were converted to car-

[Volume 16

#### STREAM ORGANIC MATTER BUDGETS



FIG. 1. Annual gross primary production in streams used in this analysis. Acronyms are defined by Webster and Meyer (1997).

bon units based on atomic weight (C =  $O_2 \times 0.375$ ). Incubations with radiolabeled carbon (<sup>14</sup>C) were conducted in 5 studies. For <sup>14</sup>C incubations and the diel CO<sub>2</sub> curve, GPP was assumed to be 2× the NPP (<sup>14</sup>C and diel CO<sub>2</sub> approaches are believed to estimate NPP; Schindler 1978). The photosynthetic quotient used by investigators ranged from 1.0 to 1.35.

We analyzed the data using linear regression approaches. GPP was the dependent (response) variable in all regressions. Several independent (predictor) variables were chosen from the entire data set for examination. We categorized these variables into 3 groups: 1) geographic/climatic variables = latitude, mean annual water temperature, and precipitation; 2) basin/channel variables = stream order, watershed area, discharge, gradient, and channel width; 3) resource variables = nutrient concentrations and light. We had sufficient data to examine the following nutrients: SRP (soluble reactive phosphorus), TP (total phosphorus), NH<sub>4</sub>-N (ammonium-nitrogen), and NO<sub>3</sub>-N (nitrate-nitrogen). Unfortunately, there were insufficient data on irradiance for direct inclusion in the analysis; instead, we used percent riparian canopy cover (generally reported) as an inverse surrogate ior light (see below). Variables whose values ranged over several orders of magnitude (e.g., GPP, discharge, watershed area) were  $\log_{10}$ -transformed prior to analysis. In cases where only ranges of values were available (e.g., nutrient concentrations), the mean of maximum and minimum values was used in the regression. Simple linear regression (SLR) was first performed using each predictor variable and the response variable (log<sub>10</sub> GPP). In this analysis, we realize that many of the variables were correlated (e.g., area, order, and discharge) but we were searching for statistical patterns in the data set. Finally, a stepwise multiple linear regression was conducted using all significant (p < 0.05) predictors from SLRs and the response variable (log<sub>10</sub> GPP).

#### Results

GPP in the 30 streams varied by over 4 orders of magnitude, ranging from 3.5 to 5400 g C m<sup>-2</sup>  $y^{-1}$  (Fig. 1). Streams in arid regions of the US such as the Great Basin (Rattlesnake Springs, Washington; Deep Creek, Idaho) and the desert Southwest (Sycamore Creek, Arizona) (grouped as "desert") had the highest GPP. GPP was lowest for streams in deciduous forests of the eastern USA (Bear Brook, New Hampshire; Satellite Branch and Hugh White Creek, North Carolina). Average GPP for all streams was 560 g C m<sup>-2</sup> y<sup>-1</sup>.



FIG. 2. Regressions of GPP (g C  $m^{-2} y^{-1}$ ) on 3 geographic/climatic variables (A–C) and 1 basin/channel variable (D).

#### Geographic/climatic variables

GPP showed no relationship with latitude (Fig. 2A), even though the range of latitudes represented was fairly broad. GPP increased significantly with mean annual temperature ( $r^2 = 0.142$ , p = 0.044; Fig. 2B) and declined with total precipitation ( $r^2 = 0.206$ , p = 0.013; Fig. 2C). However, the 3 North American desert streams (low precipitation, high temperature) strongly influenced both regressions; if those 3 points were removed from the analysis, there was no significant relationship for any climatic variable.

#### Channel variables

Increases in annual GPP were strongly associated with increasing watershed area (Fig. 3A). Area explained over 40% of the variation in GPP ( $r^2 = 0.416$ , p < 0.001). GPP also was positively associated with discharge ( $r^2 = 0.168$ , p = 0.027) (Fig. 3B) and negatively associated with gradient ( $r^2 = 0.208$ , p = 0.015) (Fig. 3C). Discharge

and gradient are, in part, a function of watershed area (increasing discharge and declining average gradient with increasing area). There was no significant relationship between GPP and stream order (Fig. 2D) or channel width (Fig. 3D). In fact, the greatest variation in GPP was expressed in the smallest streams (but these were also the most frequently measured).

#### Resource variables

Of the nutrients examined, only soluble reactive phosphorus (SRP) was significantly related to GPP ( $r^2 = 0.382$ , p < 0.001). This relationship was steep and asymptotic, with the desert streams having the highest SRP and GPP (Fig. 4A). A 2nd-order function also was applied to the SRP–GPP regression, given the obvious nonlinear relationship between the variables, and the  $r^2$  improved to 0.479 (GPP = 1.700 + 0.023 SRP - 6.026 SRP<sup>2</sup>). Small streams draining deciduous forest had the lowest SLP and GPP. No significant relationships were observed between

98

1997]

#### STREAM ORGANIC MATTER BUDGETS



FIG. 3. Regressions of GPP (g C m<sup>-2</sup> y<sup>-1</sup>) on 4 basin/channel variables.

GPP and total phosphorus,  $NH_4$ -N, or  $NO_3$ -N (Fig. 4B–D). Indeed, the 2 forms of nitrogen each explained less than 2% of the variation in GPP.

The lack of irradiance data prompted us to use percent riparian canopy cover as an inverse surrogate for light. Values used in the regression were estimates of maximum canopy closure. GPP was significantly related to percent canopy cover ( $r^2 = 0.291$ , p = 0.003; Fig. 5). Desert streams tended to have the lowest canopy cover and highest GPP whereas deciduous forest streams had the highest canopy and lowest GPP.

#### Multiple regression analysis

The 7 significant predictors from the simple linear regressions (precipitation, watershed area, discharge, percent canopy, gradient, temperature, and SRP) were used in a stepwise multiple regression. Three significant predictors were included in the final step of the regression:

$$log_{10}GPP = 0.717 + 0.689 log_{10} Area$$
  
- 0.494 log\_{10} Discharge + 0.387log\_{10} SRP  
(F\_{3.73} = 17.2,  $p < 0.001, n = 27$ )

These 3 predictors combined explained 70% of the variation in GPP, of which watershed area explained 42%, discharge explained an additional 21%, and phosphorus explained the final 7%. A multiple regression with all 7 variables included in the model explained only a small additional amount of variation in GPP ( $r^2 = 0.73$ ).

#### Discussion

Autochthonous production is a complex function of the geomorphic, fluvial, and riparian setting of the stream. As recognized 20 y ago by Minshall (1978) and verified by the data set that we have analyzed in this paper, lotic GPP varies widely across biomes, climatic regions, and stream ecosystems. In our analysis, small to me-

99



FIG. 4. Regression of GPP (g C  $m^{-2} y^{-1}$ ) on 4 resource variables—nutrient concentrations.

dium-sized streams with a limited canopy (e.g., desert streams) tended to have high benthic GPP, presumably because light did not limit photosynthesis. In contrast, small streams in heavily forested areas had low GPP (e.g., mountain streams in Oregon and North Carolina).



FIG. 5. Regression of GPP (g C  $m^{-2} y^{-1}$ ) on 1 resource variable—% overhanging riparian canopy.

Larger, deep rivers (e.g., Ogeechee River, Georgia; Moisie River, Quebec) had moderate levels of benthic GPP, possibly because of reduced shading by vegetation offset by some light attenuation by the dissolved and suspended load of water. These patterns generally are consistent with predictions of the river continuum concept (Vannote et al. 1980) as tested and modified by others (Cushing et al. 1983, Minshall et al. 1983). Part of this consistency in results may stem from the fact that some of the same streams used to test the river continuum concept were also included in our analysis. However, the results in the present paper are based on a broader sampling of streams than the river continuum, suggesting that these patterns are robust.

We originally predicted that GPP would be low in small streams because of light limitation by riparian canopy. This prediction was supported by an analysis of discharge (Fig. 3B) but not by the analysis of stream order (Fig. 2D). GPP varied over 5 orders of magnitude in both 1st- and 2nd-order streams. Thus, local riparian conditions appeared to override the predicted relationship of GPP to stream order (Vannote et al. 1980), a pattern supported by the negative relationship between % canopy and GPP (Fig. 5). Although canopy data are not as directly linked to primary production as irradiance, they appear to be a relatively good surrogate. In studies that have examined GPP versus irradiance in streams of different orders, a strong and direct relationship exists (Bott et al. 1985, Naiman et al. 1987).

Our 2nd prediction was that GPP would increase with stream size, but would decline again in large rivers. The first part of this prediction was supported to some extent, but there was only a modest decline in GPP in large rivers. Discharge was a significant, but weak, linear predictor of GPP. If the desert streams are disregarded, GPP appeared to reach an asymptote at a discharge of about 1 m<sup>3</sup>/s (Fig. 3B). Thus, larger rivers appear to be as productive as medium-sized streams. The absence of a significant relationship between GPP and stream order may be due to: 1) a sampling bias toward low-order streams in the regression; 2) the broad range of local conditions reflected in loworder streams whereas larger rivers may integrate regional conditions; and 3) the subjectivity inherent in assigning stream order (Gordon et al. 1992). For example, because of differences in hydrologic regime and drainage network form, the discharges of similar order streams can vary widely in different geographic areas (Richards 1982).

Watershed area was the best single predictor of GPP, perhaps because watershed size is a coarse-grain measure that summarizes many features relevant to lotic primary production. For example, nutrient inputs from terrestrial sources should increase with watershed size; but because discharge also increases, nutrient concentrations may either increase or decrease. Streams of arid regions (with large watershed: stream size ratios) have high levels of insolation and warm water that can stimulate GPP and  $R_A$ . For 2 geographic sites, GPP was available for a range of stream sizes (5 sites in the Matamek/ Moisie river systems of Quebec; 5 sites in the Mackenzie River system of Oregon). For the Matamek/Moisie rivers, GPP increased with stream size and was the highest in the 9th-order Moisie River. In Oregon, GPP increased with stream size except between the 5th-order Look-

out Creek and the 7th-order Mackenzie River, where GPP was about equal. The 6th-order Ogeechee River, a Georgia blackwater stream, had much higher GPP than smaller streams in forested mountains of North Carolina. A limitation of this data set, however, is the lack of measurements from very large rivers, where GPP may in fact decline.

Our 3rd prediction was that the stream size– GPP relationship would also be reflected in correlates of stream size (e.g., discharge, gradient, channel width). This prediction was generally supported, although relationships were weaker than for watershed area. GPP increased with discharge and declined with gradient. However, there was no relationship between GPP and channel width; width may be an insensitive metric because it is dependent on channel form and site-specific conditions (Gordon et al. 1992).

We predicted that higher latitude and associated declines in the length of the growing season, in total solar input, and in mean annual water temperature would reduce GPP. We found no relationship between GPP and latitude, but a weak positive relationship between GPP and average water temperature. Higher water temperature may stimulate autotrophic respiration (and thus GPP). Perhaps more importantly, temperature is positively related to insolation, which may explain why open-canopy desert streams had the highest temperature and GPP.

Our 5th prediction was that GPP would be negatively associated with annual precipitation as a result of at least 2 possible mechanisms. First, higher precipitation should result in more riparian vegetation and thus greater shading of the stream. Second, concentrated precipitation could result in scouring of benthic algae by floods. This prediction was supported in that streams with the highest precipitation in their watersheds tended to have the lowest GPP. However, higher discharge was positively related with GPP, and discharge was a significant predictor in the multiple regression. The positive influence of discharge on GPP may be related to increased loading of nutrients into the stream with storm runoff (cf. McDiffett et al. 1989, Stevenson 1990), although high discharge does not imply a variable hydrograph. Each stream probably has a unique, complex relationship between hydrology, riparian vegetation, and benthic primary production.

Finally, we predicted that GPP would be pos-

itively associated with nutrient concentrations in the water. This prediction assumes that primary production is limited more by nutrients than by other resources such as light (c.f. Hill and Knight 1988, Steinman 1992, Rosemond 1993). SRP was the only nutrient positively related to GPP in our analysis. This result is consistent with the belief that phosphorus generally is more limiting than nitrogen in freshwater ecosystems (Schindler 1978, Hecky and Kilham 1988); however, there are streams where algal growth clearly is limited by nitrogen (Grimm and Fisher 1986, Lohman et al. 1991). In addition, the significance of dissolved inorganic nutrient concentration in streamwater is questionable, as it is the nutrient concentration of tissue that influences metabolism (cf. Dodds 1993). Furthermore, high nutrient concentrations may be a result of low demand by autotrophs, thereby resulting in an inverse relationship between GPP and nutrients. Thus, the relationship between lotic GPP and the absolute concentration of any nutrient should be interpreted with caution.

We compared our results for streams with some past analyses done for lakes. Brylinsky and Mann (1973) analyzed lake productivity data from the International Biological Program and concluded that variables related to solar input (most notably latitude) were the best predictors of primary production for 55 lakes ranging from the tropics to the Arctic. However, they suggested that for a narrower range of latitudes, nutrient loading could assume greater importance. Later, when more nutrient data were available, Schindler (1978) concluded that phosphorus input was the best predictor of primary production in the north temperate region (only a single tropical lake, and no southern hemisphere lakes were analyzed) while acknowledging the significance of solar input over a broader latitudinal range. Our analyses of streams suggest that lotic GPP is a complex function of geomorphology, hydrology, and resources for aquatic and riparian plants. Large-scale features (e.g., latitude) had little influence in our analysis, but unlike Brylinsky and Mann's (1973) study, tropical streams were absent from our data set. Watershed size, which influences and integrates many other features of river systems including local irradiance and discharge, emerged as the best predictor of GPP. Consistent with the lake analyses, nutrient concentra-

tion (as SRP) and insolation (as canopy) also were significant predictors of lotic GPP.

Perhaps more than any other measurement made in stream ecology, the method used has a critical influence on apparent rates of primary production (Bott et al. 1978, Marzolf et al. 1994). For example, Marzolf et al. (1994) compared metabolism measured from upstream-downstream changes in DO with that measured from DO changes in chambers and found that 24-h community respiration rates were 3 to  $4 \times$  lower in chambers than in the whole-stream technique. They attributed this difference to the failure of chambers to include the metabolism of macrophytes, macrofauna, and organic sediments. Although we assume that geomorphology, climate, and biota have stronger effects on metabolic rates than do differences in methods, this assumption has not been tested rigorously and should be considered when interpreting patterns of lotic GPP.

#### Conclusions

In our analysis of lotic primary production, we found high variation in GPP among different streams, especially among streams of the same apparent order. Concepts of stream function frequently are based on stream order; our analysis suggests that assumptions about GPP based on order should be made with caution, at least when generalizing over large scales or across different hydrologic regimes. Within a specific river network, inferences based on stream order appear to be fairly robust (e.g., Minshall et al. 1983, Sheath et al. 1986, Naiman et al. 1987).

Streams draining large watersheds tended to have higher GPP than those draining smaller areas. Many features, such as light, nutrient input, temperature, hydrology, and others, may be driving this general relationship. Our multiple regression analysis suggests that to make a rough prediction of annual GPP for a stream, at a minimum, measurements of watershed area, mean annual discharge, and average SRP should be taken. Further refinement of this analysis will be possible when additional information is available for many streams, including: 1) direct measurements of irradiance; 2) frequency and intensity of flood disturbance; and 3) consumption of autotrophs (either directly with assays or indirectly from herbivore density or biomass), which may have considerable influence

[Volume 16

on autotrophic standing crop and production (Lamberti and Moore 1984, Steinman 1996).

Although our analysis has revealed some general relationships that we hope are useful in other lotic studies, every stream will tend to have a unique set of factors that controls the rate of primary production. Evaluation of site-specific observational data combined with rigorous experimentation to test specific hypotheses at appropriate scales will be the most powerful means of revealing mechanisms that govern primary production in a particular stream.

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# Comparison of litterfall input to streams

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Allochthonous organic matter is an important source of energy for many streams and the major energy source for woodland streams or streams with well developed riparian corridors of vegetation (e.g., Cummins et al. 1983). Litterfall may be defined as allochthonous material entering streams from riparian vegetation. It may include leaves and leaf fragments, floral parts, bark, wood (branches and twigs), cones and nuts, fruits, and other plant parts (Bray and Gorham 1964). Litter may reach streams by direct fall or lateral movement (blowing or slicing down the stream banks). The relative arcounts of material reaching streams by these 2 routes

vary considerably. Lateral movement may vary with wind patterns, aspect, bank slope, and other site-specific factors (Wallace et al. 1992). For example, lateral movement accounted for about 24% of total litter input to 4 southern Appalachian streams (Webster et al. 1995), about 66% in a Douglas fir-hemlock forest stream in the western US (Sedell et al. 1982), but only about 10% in a eucalyptus forest stream in Australia (Campbell et al. 1992). The composition of litterfall varies with vegetation type and location. As a general average, non-leaf litterfall for forests around the world is about 30% (Bray and Gorham 1964) but may be up to 70% in some forests in southeastern Australia (Blackburn and Petr 1979, Briggs and Maher 1983).

In temperate deciduous forests, the bulk of litterfall occurs in autumn but material may continue entering streams by lateral movement over the remainder of the year. Needle-fall from coniferous evergreen trees varies considerably with species and location and may range from distinctly seasonal to irregular throughout the year (Bray and Gorham 1964). Litterfall from tropical wet forest trees and shrubs is usually non-synchronous and leaves enter streams relatively evenly over the entire year (Stout 1980).

In streams with broadly developed valleys or in lowland systems, litter may be entrained from the floodplain as streams rise during periods of increasing discharge (Cuffney 1988). Conversely, litter may be deposited on the floodplain as streams retreat during falling hydrographs (Post and de la Cruz 1977, Shure and Gottschalk 1985). Floodplain entrainment/deposition cycles of litter during changing hydrographs may also occur in smaller, montane streams (Wallace et al. 1992) and tundra streams (Peterson et al. 1986). Thus floodplain areas may be sources or sinks for litterfall depending on hydrodynamics, topography, sediment loads, and other factors (Cuffney 1988). In some floodplain systems, litterfall may be largely processed on the floodplain and the resulting particles entrained by streams during high flows (Smock 1990).

The objectives of this chapter are to summarize data on direct fall and lateral movement of litter to streams that were included in the earlier site-description chapters, and to analyze whether patterns of direct litterfall to these streams might be explained on the basis of local or spe-

# STREAM ORGANIC MATTER BUDGETS

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Edited by J. R. Webster and Judy L. Meyer

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# 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.