J. N. Am. Benthol. Soc., 2007, 26(3):375–389
© 2007 by The North American Benthological Society

Spiraling down the river continuum: stream ecology and the U-shaped curve

Jackson R. Webster[1]

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

Abstract. The spiraling concept provides an explicit approach to modeling the longitudinal linkages within a river continuum. I developed a spiraling-based model for particulate organic C dynamics in the Little Tennessee River to synthesize existing data and to illustrate our current understanding of ecosystem processes in river ecosystems. The Little Tennessee River is a medium-sized river flowing ~100 km through the southern Appalachian Mountains of northern Georgia and western North Carolina (USA). Across this distance, allochthonous inputs decrease and autochthonous production increases, resulting in a U-shaped curve of energy input. The model was set up as an advecting seston compartment interacting with 3 benthic compartments: coarse benthic organic matter, fine benthic organic matter, and autotrophs. Model-estimated ecosystem respiration was consistently lower than measured values, suggesting a need to evaluate our measurements of whole-stream metabolism. Also, model-predicted seston concentrations were generally lower than measured values, reflecting a need to consider additional sources of organic C in the model. For the whole river system, leaves accounted for 19% of inputs, primarily near the headwaters, and the remaining input was from instream primary production in the lower reaches of the river. Almost ½ of the input was respired, 28% by autotrophic respiration and 21% by heterotrophic respiration, and the remaining 51% was transported downstream. Ecosystem efficiency was ~50% along the length of the river, and turnover length increased from several hundred meters at the headwaters to >100 km downstream. Based on various measures, the transition from heterotrophy to autotrophy ranged from 25 to >100 km downstream from the headwaters. As this model illustrates, a consequence of downstream transport is that much of the particulate C in streams is metabolized a considerable distance downstream from where it enters the stream. This longitudinal linkage is essential to our understanding of stream ecosystems.

Key words: stream, model, metabolism, spiraling, river continuum, Little Tennessee River.

Scientists feel comfortable with relationships in which one variable, the dependent variable, changes in direct proportion to changes in another variable. Relationships where changes of the independent variable cause a positive response at one end of the spectrum and a negative response at the other end are much less satisfying, but these U-shaped or hump-backed curves are often interesting. A common example is the effect of temperature on simple biological processes—a temperature increase at low temperatures accelerates biological processes, but the same increase at high temperatures slows down processes as proteins are denatured. In general, these U-shaped curves are observed where the relationship between the 2 variables is not a direct causal link but rather an indirect relationship in which the independent variable is acting through 2 (or more) direct causal links. Such a relationship occurs in the river continuum (Vannote et al. 1980) when we look at various processes vs stream order or any other measure of stream size. If we plot energy input along a continuum from forested headwaters to a medium-sized river (1st to ~7th order), we see a decrease in energy input over the first several orders and then an increase in the downstream reaches (e.g., Naiman et al. 1987). This pattern is the result of 2 causal pathways. As the stream becomes larger, it widens and allochthonous input decreases. But as it widens, riparian shading decreases and autochthonous inputs increase. The result is a U-shaped curve of energy input.

Exceptions to this pattern (e.g., Winterbourn 1981) include streams that begin in grasslands or deserts or where desert streams lose flow downstream. However, it is incorrect to think of these exceptions as demonstrating that the River Continuum Concept (RCC) does not apply to these streams. The RCC is more than a description of a pattern found in many streams, such as those in eastern North America. Although the

[1] E-mail address: jwebster@vt.edu

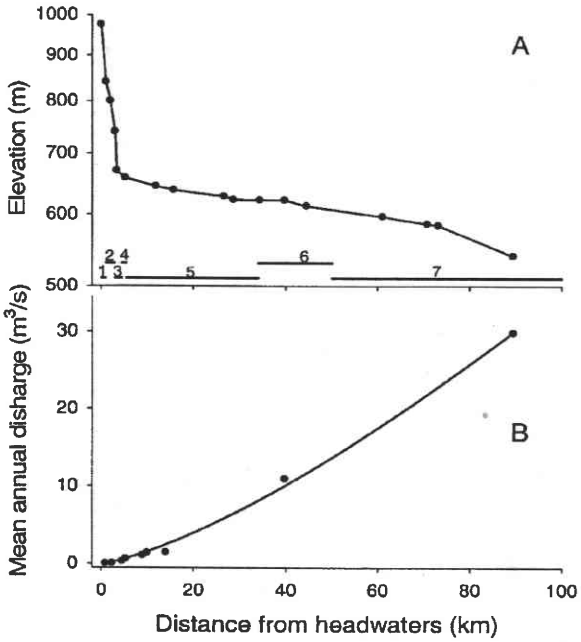

FIG. 1. A.—Gradient of the Little Tennessee River (LTR) based on elevations read from 1:24,000-scale US Geological Survey (USGS) maps. Bars at the bottom of the figure indicate stream order (see text). B.—Average annual discharge in the LTR (data are from US Forest Service, Coweeta Hydrologic Laboratory, Otto, North Carolina, and USGS, http://waterdata.usgs.gov/nc/nwis). Regression line in (B) is a power function ($r^2 = 0.997$).

original RCC paper (Vannote et al. 1980) emphasized a description of a river with its origin in a forested watershed, the authors also postulated that downstream communities are structured to capitalize on inefficiencies of upstream processing. This more fundamental aspect of the river continuum was elaborated in later papers (e.g., Minshall et al. 1985) in which they stated, "Streams are ... longitudinally linked systems in which ecosystem-level processes in downstream areas are linked to those in upstream areas." Understanding the relationships between stream size, energy inputs, and this longitudinal linkage requires a conceptual approach that explicitly recognizes longitudinal transport in streams. The spiraling concept (Webster and Patten 1979) provides this approach, and the spiraling metrics developed by Newbold et al. (1981) and Elwood et al. (1983) give us the tools for evaluating the strength and importance of longitudinal linkage within a river continuum. Spiraling is a metaphor to describe the coupled transformation and transport of materials in stream ecosystems. Materials do not physically move downstream in a spiral, but metaphors such as spiraling are helpful to our understanding of complex ecological processes (Proctor and Larson 2005).

The objective of my study was to develop a spiraling-based model, i.e., one that explicitly recognizes both transport and exchange between benthic and transport system components. I applied this model to the Little Tennessee River (LTR) to synthesize existing data collected as part of the Coweeta Long-Term Ecological Research program, to illustrate our current understanding of organic matter processes in this river, and to show where inadequate information limits this understanding.

Site Description

Physical characteristics

LTR begins in north Georgia (USA) and flows northward into North Carolina and Tennessee where it joins the Tennessee River. Approximately 100 km from the headwaters, it enters Fontana Reservoir, a logical downstream boundary for my study. The watershed of the LTR is ~1200 km^2 upstream of Fontana Reservoir. This area is mountainous with peaks reaching >1500 m asl. Forest covers ~90% of the watershed, with most of the remaining area in pasture agriculture in the valleys (USGS 2002). Small areas of intense row-crop agriculture are along the river in the valley, and ~1% of the area is developed, mostly in the towns of Franklin and Highlands, North Carolina. Much of the forest land is National Forest, and all of the forests were logged in the last century. The forests are dominated by oaks (*Quercus* spp.), hickories (*Carya* spp.), red maple (*Acer rubrum*), and yellow poplar (*Liriodendron tulipifera*).

Based on blue lines on US Geological Survey (USGS) 1:24,000 scale maps, the LTR is a 5^{th}-order river (Strahler 1957); however, based on a more detailed 1:7200 scale map of Coweeta Hydrologic Laboratory (Coweeta), which is in the LTR watershed, Coweeta Creek is 5^{th} order (Grubaugh et al. 1997), making the LTR 7^{th} order. I used the relationship between order and stream distance from the Coweeta map, but I applied it to the Keener Creek headwaters of the LTR in north Georgia. The river drops from 975 m asl at the headwaters to 540 m at the Needmore USGS gage 90 km downstream (Fig. 1A). The gradient is very steep in the headwaters, somewhat less steep as the river meanders through a fairly wide valley, and then steeper again as the river turns northwest and begins its cut through the spine of the Appalachian Mountains. Based on US Forest Service stream gages at Coweeta and USGS gages on the LTR (http://waterdata.usgs.gov/nc/nwis), annual discharge increases predictably with distance (Fig. 1B) and

averages 29.9 m^3/s at the Needmore gage (1944–2005; USGS gage no. 03503000).

Stream width and average depth were measured every 10 m at Coweeta from the headwaters of Ball Creek downstream to the Forest Service boundary (5.25 km; JRW, J. B. Wallace, University of Georgia, J. M. Meyer, University of Georgia, E. F. Benfield, Virginia Polytechnic Institute and State University, and G. D. Grossman, University of Georgia, unpublished data). Grubaugh et al. (1997) reported 3 stream widths and depths in Coweeta Creek from Coweeta to its confluence with the LTR. Widths also were measured at 12 sites in the LTR downstream of Coweeta Creek (Neatrour et al. 2004), but there are only 4 measurements of average depth in this part of the river (McTammany et al. 2003). These measurements indicate that depth increases linearly with distance (Fig. 2A) with a few unusually deep pools at ~5 km. Width measurements (Fig. 2B) were consistent with the observation that between ~20 km and 60 km the river is deeply incised and confined to a relatively narrow channel within a broad floodplain. Downstream, the river is broader and becomes somewhat steeper.

I used the regression lines of annual discharge, width, and depth to estimate velocity along the river (Fig. 2C). Estimated velocity increased downstream in the upper, steep reaches, reached a maximum in the mid-reaches, and then decreased again downstream (Fig. 2C). The estimates are consistent with velocity measurements made with conservative tracer releases (D'Angelo et al. 1993, McTammany et al. 2003).

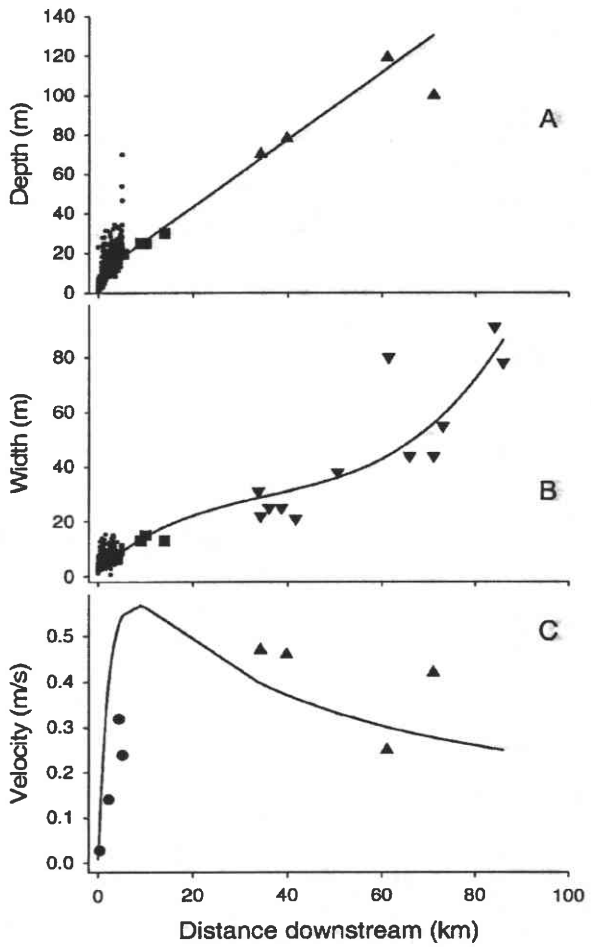

FIG. 2. Depth (A), width (B), and average velocity (C) in the Little Tennessee River. Velocity (line) was calculated from discharge (Fig. 1B), depth, and width. Lines in (A) and (B) are regression lines (depth: linear, $r^2 = 0.80$; width: 3rd-order polynomial, $r^2 = 0.73$). Depth and width data are from JRW, J. B. Wallace, University of Georgia, J. L. Meyer, University of Georgia, E. F. Benfield, University of Georgia, and G. D. Grossman, University of Georgia, unpublished data (circles); Grubaugh et al. 1997 (squares); Neatrour et al. 2004 (triangles down); and McTammany et al. 2003 (triangles up). Data points in (C) are measurements of D'Angelo et al. 1993 (circles) and McTammany et al. 2003 (triangles).

Energy input

Allochthonous inputs of leaf and woody litter from riparian forests to small streams (1st–4th order) have been measured several times at Coweeta using litter traps placed over or adjacent to streams (Webster and Waide 1982, Webster et al. 1990, Wallace et al. 1997, Benfield et al. 2000). Also, Neatrour et al. (2004) estimated litter inputs at 12 sites along the LTR in the 5th- to 7th-order reach. Litter traps were placed on the stream bank, and river input was calculated based on a model with a linear decrease of litterfall out to 10 m from the shoreline. Litter inputs to the small streams in the heavily forested headwaters are very high but decrease rapidly as the river becomes wider (Fig. 3A).

Autochthonous primary production also has been measured several times in small Coweeta streams (Fig. 3B) using either ^{14}C uptake in chambers (Hains 1981) or open-channel O_2 exchange (Mulholland et al. 1997, P. J. Mulholland, Oak Ridge National Laboratory, unpublished data; H. M. Valett, Virginia Polytechnic Institute and State University, S. A. Thomas, University of Nebraska, and JRW, unpublished data; JRW, H. M. Valett, and B. R. Niederlehner, Virginia Polytechnic Institute and State University, unpublished data). McTammany et al. (2003) also measured primary production along the 6th- to 7th-order LTR using open-channel O_2 exchange. All but one of these studies measured whole-stream metabolism and thereby included production by submerged macrophytes and

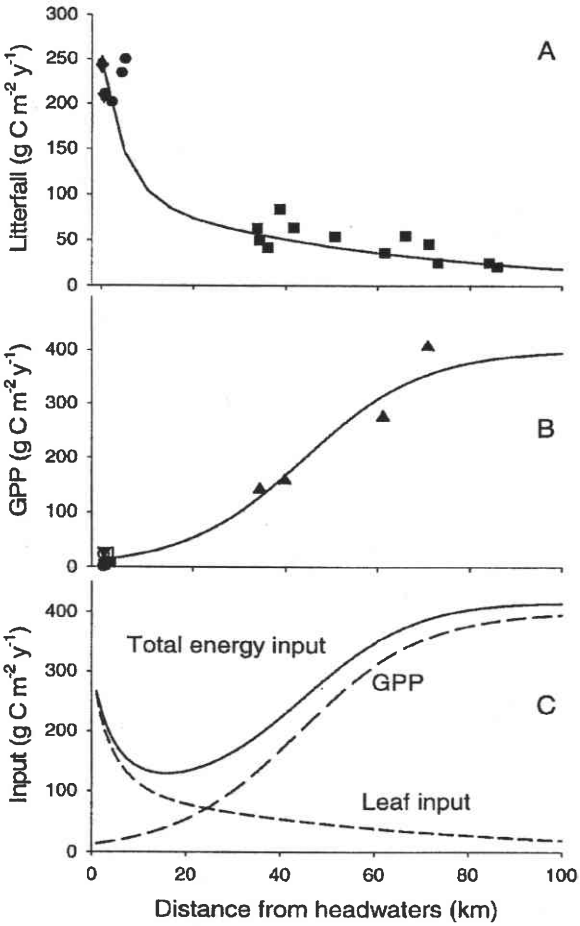

FIG. 3. Litterfall input (A), gross primary production (GPP) (B), and total energy inputs (U-shaped curve) (C) in the Little Tennessee River. Lines in (A) and (B) are regression lines (litterfall: negative exponential, $r^2 = 0.94$; GPP: sigmoid function, $r^2 = 0.97$). All litterfall data are annual estimates as reported by the authors. All GPP values are 1-time measurements except for the annual values reported by McTammany et al. (2003). Leaf input in (C) includes lateral input from Webster and Waide (1982), Webster et al. (1990), and Wallace et al. (1997). Regression line for GPP (sigmoid function, $r^2 = 0.97$) is fit to data of Hains 1981 (circles); Mulholland et al. 1997 (triangle down); McTammany et al. 2003 (triangles up); Webster et al. 2003 (square); H. M. Valett, Virginia Polytechnic Institute and State University, S. A. Thomas, University of Nebraska, and JRW, unpublished data (open circles); JRW, H. M. Valett, and B. R. Niederlehner, Virginia Polytechnic Institute and State University, unpublished data (open squares).

bryophytes. The chamber measurements made by Hains (1981) were in a small stream with no macrophytes and very little bryophyte production. Results of these studies show that primary production is very low in the heavily shaded small streams at Coweeta and much higher downstream. I have chosen to fit these data with a sigmoid curve on the assumption that primary production plateaus in mid-order reaches (Vannote et al. 1980), but statistically a linear or exponential curve would fit the data equally well.

Combining the regression curves for litter inputs (but also including lateral input from Webster and Waide 1982, Webster et al. 1990, and Wallace et al. 1997; Fig. 3A) and gross primary production (GPP) (Fig. 3B) illustrates the U-shaped curve of energy input along this river continuum (Fig. 3C). Minimum energy input occurs in the 5th-order reach, about 17 km downstream of the headwaters.

Model Development

I used a very basic model of biological processes (Fig. 4) with 3 benthic compartments—fine benthic organic matter (FBOM), coarse benthic organic matter (CBOM), and autotrophs—and 1 compartment for suspended particles in transport (seston). I used autotrophs to include attached algae, bryophytes, and the submersed macrophyte *Podostemum ceratophyllum*, which is abundant in downstream areas of the LTR (Grubaugh et al. 1997, Hutchens et al. 2004, Rosi-Marshall and Meyer 2004). Fluxes into and out of these compartments were calculated as follows:

GPP.—I calculated GPP as a function of river distance using the regression in Fig. 3B.

Autotrophic respiration.—I calculated respiration by attached autotrophs as 35% of GPP. Autotrophic respiration (R_A) generally is given as 50% of GPP for terrestrial plants (e.g., Schlesinger 1997), but studies of

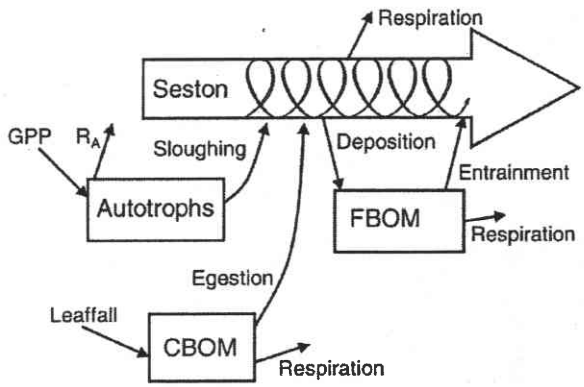

FIG. 4. Compartment model of particulate organic matter dynamics in the Little Tennessee River. GPP = gross primary production, R_A = autotrophic respiration, CBOM = coarse benthic organic matter, FBOM = fine benthic organic matter.

attached algae have suggested a somewhat lower value (Graham et al. 1985, Hill et al. 2001).

Sloughing.—I estimated the sloughing rate of attached autotrophs at 1.3×10^{-2}/d based on the value used by Newbold (1987), but I adjusted the rate to give a stable and reasonable autotroph standing stock. I did not include grazer consumption of algae directly in the model, but I included grazer egestion indirectly in sloughing.

Litter input.—I derived litterfall as a function of river distance from the regression equation in Fig. 3A. I estimated lateral litter input (blow-in) at 55.8 g C m^{-1} y^{-1} to each side of the river, an average from Webster and Waide (1982), Webster et al. (1990), and Wallace et al. (1997). I applied this value throughout the length of the river because no measurements of blow-in have been made downstream. Given the changing vegetation and bank characteristics along the river, blow-in probably varies greatly, but as the stream widens, this input becomes very small on an areal basis.

CBOM breakdown.—I used a breakdown rate of 0.0098/d, which is an average of many measurements made at Coweeta (Webster et al. 1999). No measurements of leaf breakdown have been made in downstream reaches of the LTR, and it is difficult to predict the applicability of this rate downstream. Higher nutrient concentrations, higher sediment transport, and lower abundance of shredders all probably affect downstream breakdown rates, but because of the low abundance of CBOM downstream, any downstream differences in leaf breakdown rate have little effect on the results of the modeling. I apportioned this breakdown into 50% macroinvertebrate egestion, which went directly to seston, and 50% macroinvertebrate and microbial respiration. This apportionment is somewhat arbitrary, but we do know that macroinvertebrates account for a large portion of leaf breakdown in Coweeta streams (Wallace et al. 1982a, Cuffney et al. 1984). I included physical particle generation implicitly in macroinvertebrate egestion, but I did not include dissolved organic C (DOC) leaching.

Seston and FBOM respiration.—I estimated the rate of microbial respiration of benthic and seston particles at 0.0018/d, an average of rates reported by Schaeffer (1993), Peters et al. (1987), and Wojculewski (2006).

Seston deposition and FBOM entrainment.—I based seston deposition on a deposition velocity of 1.7 m/d. FBOM entrainment rate (resuspension rate, Newbold et al. 2005) was 1.7×10^{-2}/d. I started with values from Newbold (1987) but adjusted them to give stable and reasonable values of seston concentration and FBOM standing stock.

Groundwater and tributary input.—I modeled the increase in flow along the river as a continuous function using the regression equation from Fig. 1B. At Coweeta, ~50% of flow entering the streams can be accounted for as tributaries and the rest comes from ground water (Webster 1983). Based on a groundwater particulate C concentration of 0 and a tributary concentration equal to the mainstream concentration at the point of entry, new water enters the stream with a seston concentration of 50% of the mainstream concentration.

Model Implementation

I set up the model as a single partial differential equation for the downstream advection of seston and 100 sets of 3 differential equations for benthic compartments, 1 set for each kilometer along the river. I made the approximation that within each 1-km reach benthic compartments do not change with distance.

$$\begin{cases} \dfrac{\partial X_1}{\partial t} = -u\dfrac{\partial X_1}{\partial x} + \dfrac{X_L}{A}\dfrac{\partial Q}{\partial x} + \dfrac{(SX_2) + (FX_3) + (EX_4) - (DX_1)}{z} - (R_1 X_1) \\ \left[\dfrac{dX_2}{dt} = GPP - R_A - (SX_2)\right]_{1-100} \\ \left[\dfrac{dX_3}{dt} = L_F + \dfrac{2L_M}{w} - (FX_3) - (R_3 X_3)\right]_{1-100} \\ \left[\dfrac{dX_4}{dt} = (DX_1) - (EX_4) - (R_4 X_4)\right]_{1-100} \end{cases} \quad [1]$$

Symbols used in these equations are given in Table 1.

I solved these equations numerically using a Lagrangian approach with the Runge–Kutta technique to integrate the seston compartment over distance at 100-s intervals and the Euler method to integrate the benthic compartments over time at daily intervals. I programmed the model in C++ and executed it using ABSOFT software (version 5.32, ABSOFT Editor; ABSOFT Corporation, Rochester Hills, Michigan) with a DISLIN user interface (version 7.6, DISLIN Scientific Plotting Software; Max Planck Institute for Solar System Research, Lindau, Germany).

I ran the model for >600 d (simulation time) to ensure that all compartments were at steady state. I used these steady-state values as initial conditions for subsequent simulations. There is strong seasonal variation in this system, and Wallace et al. (1995) suggested that Coweeta streams undergo long-term cycles of litter accumulation and losses. However, for the purposes of this article, I have approximated the LTR as a steady-state system.

I calculated linear and nonlinear regressions with

TABLE 1. Terms and symbols used in the model. In the model, all units were converted to s (time), m (distance), and g (mass of C) but are given here in more conventional units for convenience. Terms with no value in the 3rd column are terms that were determined by model simulation. CBOM = coarse benthic organic matter, FBOM = fine benthic organic matter.

Symbol	Explanation	Value	Dimensions
X_1	Seston concentration		Mass C/volume
X_2	Autotroph standing stock		Mass C/area
X_3	CPOM standing stock		Mass C/area
X_4	FPOM standing stock		Mass C/area
x	Distance from headwaters	0–100 km	Distance
t	Time	0–1 y	Time
u	Velocity	Calculated from discharge, width, and depth (Fig. 2)	Distance/time
X_L	Lateral input concentration	$0.5(X_1)$ at that distance	Mass C/volume
A	Cross-sectional area	Width × depth	Area
Q	Discharge	Fig. 1	Volume/time
z	Depth	Fig. 2	Distance
S	Sloughing rate	1.3×10^{-2}/d	1/time
F	Egestion rate	0.0049/d	1/time
E	Entrainment rate	1.7×10^{-2}/d	1/time
D	Deposition velocity	1.7 m/d	Distance/time
R_1	Seston respiration	0.0018/d	1/time
L_F	Litterfall	Fig. 3	Mass C area^{-1} time^{-1}
L_M	Lateral litter input	55.8 g C m^{-1} y^{-1}	Mass C length^{-1} time^{-1} (to each side of stream)
w	Stream width	Fig. 2	Distance
R_3	CBOM respiration rate	0.0049/d	1/time
R_4	FBOM respiration	0.0018/d	1/time

SigmaStat (version 3.1; SYSTAT Software, Richmond, California). Throughout the article, I converted values originally reported as ash-free dry mass (AFDM) to C on the basis of 0.5 g C/g AFDM.

Results

Compartment values

Simulated standing stocks for all compartments illustrate various levels of agreement with measured values (Fig. 5A–C). These simulations are not validations of the model because some model parameters for seston, FBOM, and autotrophs were adjusted to achieve reasonable fits of simulations to data. However, CBOM parameters were determined independent of the standing-stock data.

Simulated CBOM was generally lower than measured values in the first kilometer and higher than measured values for the next 4 km (Fig. 5A). Simulated FBOM also was lower than measured values in the first kilometer but then was very similar to measured values for the next 4 km (Fig. 5B). Total BOM (CBOM + FBOM) was consistently higher than measured values beyond the first kilometer (Fig. 5C). The ratio of simulated CBOM to FBOM declined exponentially downstream (Fig. 6A). Near the headwaters, CBOM was nearly 2× FBOM, but FBOM began to exceed CBOM ~15 km from the headwaters. This change was attributable to a decrease in CBOM inputs (litterfall) and an increase in FBOM, primarily from autotroph sloughing. This general trend is as predicted by Vannote et al. (1980), although the pattern differs from RCC predictions to some degree.

Measurements of autotroph standing crop showed considerable variability along the LTR (Fig. 6B); however, the simulation generally reflected the pattern of low values through the first 20 km and higher values downstream. The sigmoid pattern of the simulation was a direct result of the sigmoid curve used for GPP (Fig. 3B).

Simulated seston concentration was lower than measured values (Fig. 6C). After trying many combinations of model parameters, I was unable to raise the seston concentration without changing parameters or benthic compartment simulations beyond reasonable values.

Ecosystem variables

Simulated ecosystem respiration (R_E) reflected inputs of particulate organic matter (Fig. 7A). Near the headwaters, R_E was primarily heterotrophic based on allochthonous materials. Downstream, R_A became increasingly important. Using the model, I estimated the fractions of heterotrophic respiration (R_H) attributable to allochthonous and autochthonous material. Near the headwaters, most R_H was based on alloch-

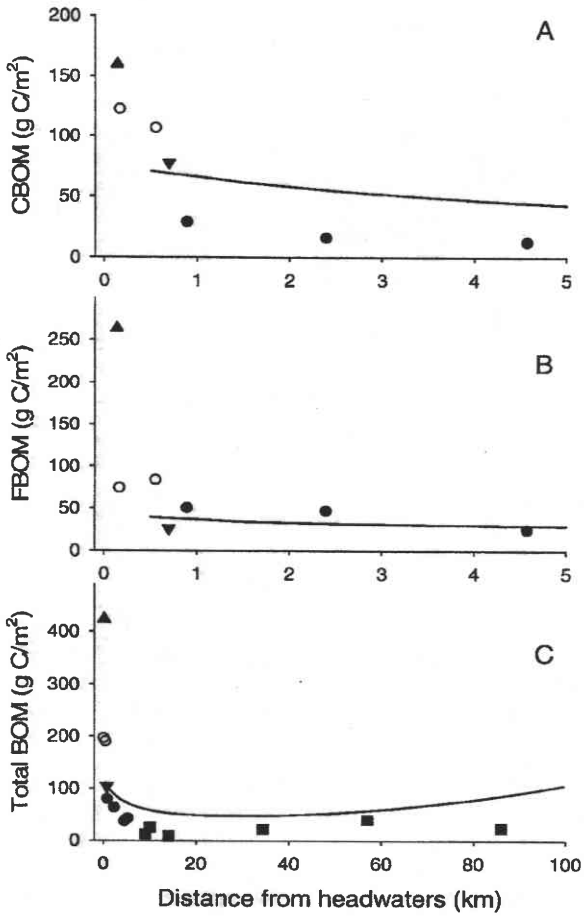

FIG. 5. Coarse benthic organic matter (CBOM) (A), fine benthic organic matter (FBOM) (B), and total benthic organic matter (BOM) (C) standing crops in the Little Tennessee River. CBOM and FBOM are shown only for the first 5 km to illustrate the major changes occurring in the upper reaches of the river. Lines are results of model simulations. All data are annual averages as calculated by the authors. Data from Grubaugh et al. (1997) are based on BOM in depositional areas and % depositional area of the river. Data points are from Grubaugh et al. 1997 (squares), Huryn and Wallace 1987 (triangles down), Golladay et al. 1989 (open circles), Wallace et al. 1997 (triangles up), and Benfield et al. 2000 (solid circles).

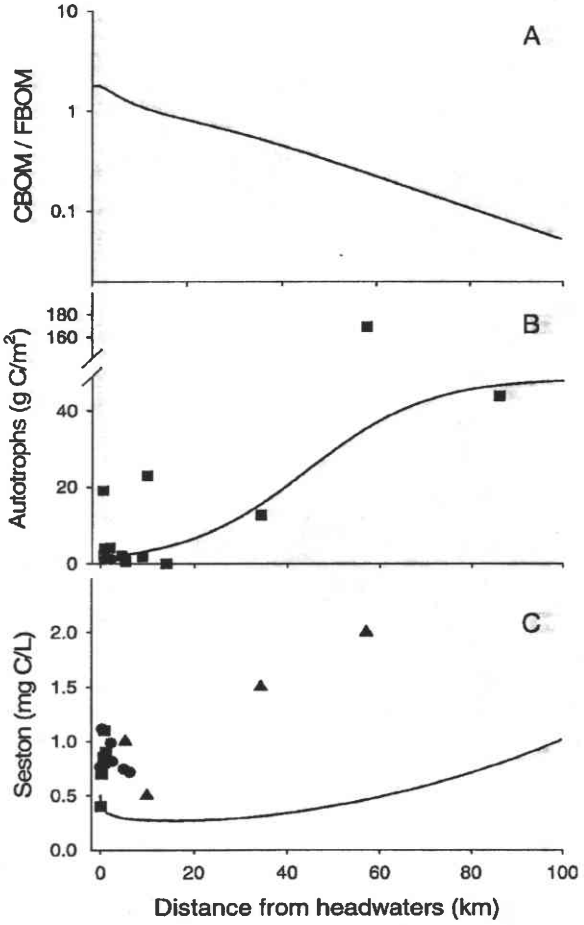

FIG. 6. Coarse benthic organic matter (CBOM)/fine benthic organic matter (FBOM) ratio (A) and autotroph (B) and seston (C) standing crops in the Little Tennessee River. Lines are results of model simulations. Data from Grubaugh et al. 1997 (squares) and JRW, E. F. Benfield, Virginia Polytechnic Institute and State University, and J. L. Tank, University of Notre Dame, unpublished (circles) are annual averages calculated from seasonal samples. The data from JRW, H. M. Valett, Virginia Polytechnic Institute and State University, and B. R. Niederlehner, Virginia Polytechnic Institute and State University, unpublished (open squares) are single measurements. Data from Grubaugh et al. (1997) are weighted averages from the various sampled habitats. All seston data are annual averages as reported by the authors. Seston data are from Wallace et al. 1982b (circles); Webster and Golladay 1984 (squares); and Rosi-Marshall and Meyer 2004 (triangles).

thonous material, but R_H of autochthonous material became increasingly important downstream (Fig. 7B).

Model-generated estimates of R_E were consistently lower than measured values (Fig. 7C); this trend was especially true in the headwaters where predicted R_E was, in some cases, an order of magnitude lower than measured values. The measured R_E values, all of which were obtained by the open-channel O_2 exchange method, also were much higher than measured total inputs (Fig. 3C). Based on the model, the river was heterotrophic, i.e., R_E > GPP, through ~25 km and was autotrophic from there downstream (Fig. 8A). The production (P)/respiration (R) graph (Fig. 8B) showed

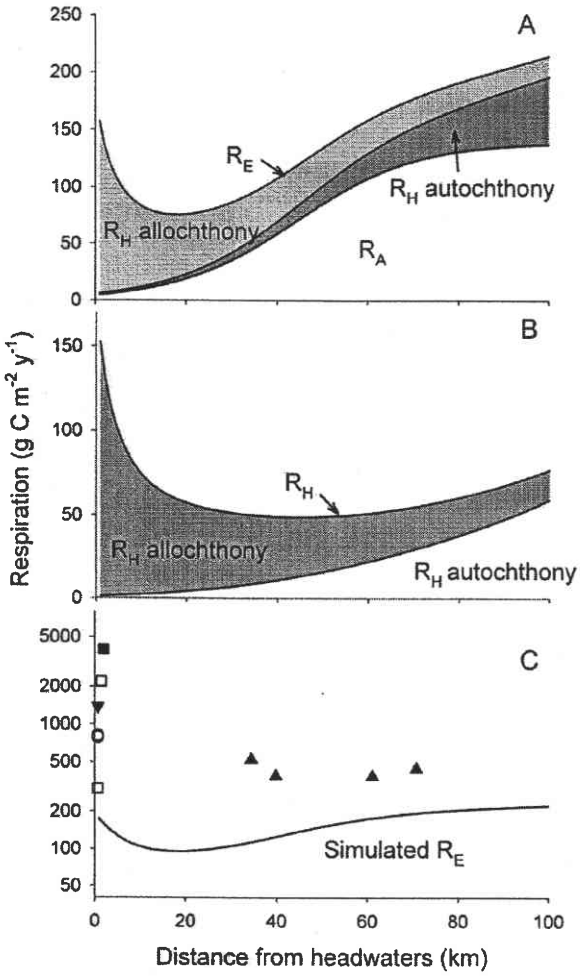

FIG. 7. A.—Simulated components of respiration in the Little Tennessee River are autotrophic respiration (R_A), ecosystem respiration (R_E, upper line), and heterotrophic respiration (R_H, shaded area). R_H is divided into respiration of allochthonous material and autochthonous material. B.—The U-shaped curve of R_H. C.—Simulated and measured values of R_E. All values are one-time measurements except for the annual values reported by McTammany et al. (2003). Measurements of ecosystem respiration are from Mulholland et al. (1997, triangle down); McTammany et al. (2003, triangles up); Webster et al. (2003, solid square); H. M. Valett, Virginia Polytechnic Institute and State University, S. A. Thomas, University of Nebraska, and JRW, unpublished data (open circle); and JRW, H. M. Valett, and B. R. Niederlehner, Virginia Polytechnic Institute and State University, unpublished data (open square).

a slight decline after ~75 km, which resulted from R_H of autochthonously generated detritus.

From the model, I estimated budgets for the LTR system (Fig. 9). For the whole system, i.e., the whole

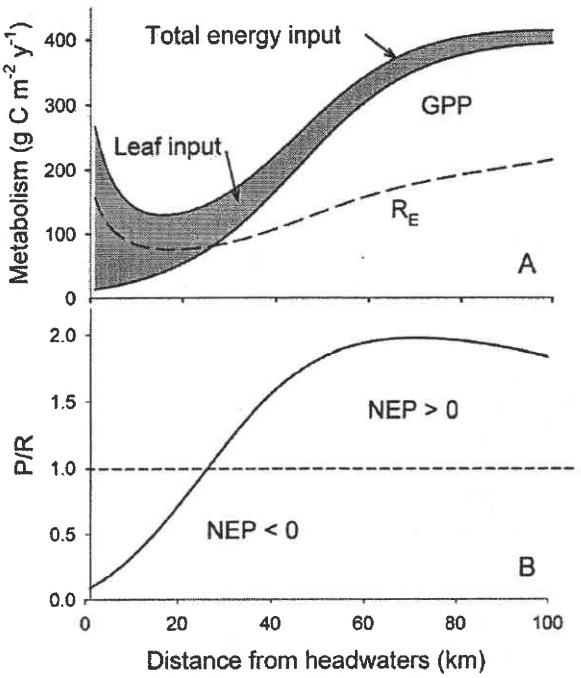

FIG. 8. A.—Simulated metabolism in the Little Tennessee River. The top solid line is total input and the lower solid line is gross primary production (GPP). The shaded area between the solid lines is leaf input. The dashed line is ecosystem respiration (R_E). B.—Production (P)/respiration (R) ratio corresponding to the simulated metabolism results. Dashed line shows $P/R = 1$ for reference. Where GPP > R_E, net ecosystem production (NEP) > 0 and where GPP < R_E, NEP < 0.

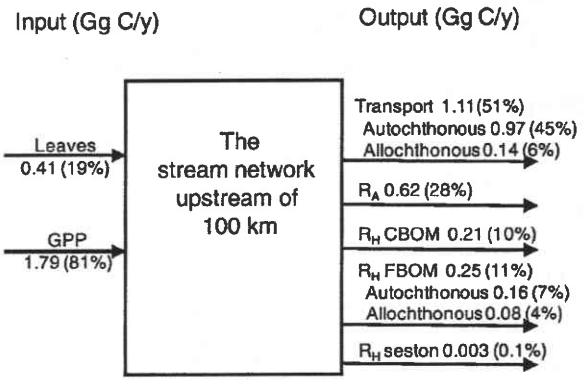

FIG. 9. Particulate organic matter budget for the Little Tennessee River network upstream of 100 km. Transport and heterotrophic respiration (R_H) of fine benthic organic matter (FBOM) are separated based on the allochthonous or autochthonous source of the material. Percentages shown in parentheses are based on % of total inputs or outputs. Gg = 10^9 g, CBOM = coarse benthic organic matter, R_A = autotrophic respiration.

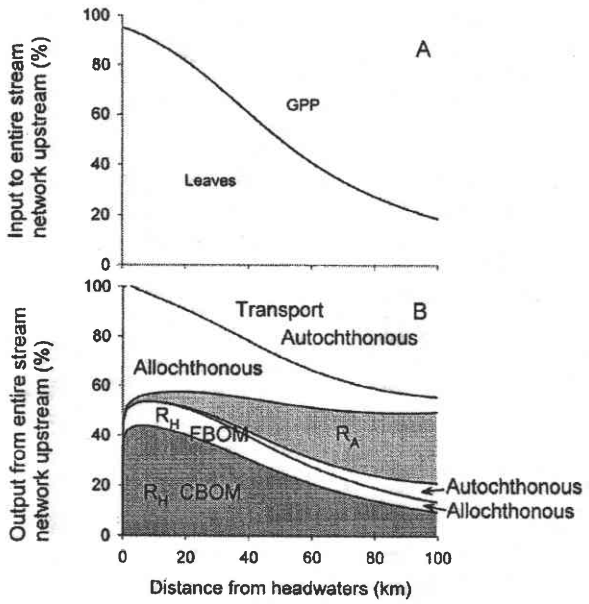

FIG. 10. Changes in the particulate organic matter budget along the Little Tennessee River. At each point along the length of the stream, the estimates of input (A) and output (B) are for the stream network upstream of that point. Respiration is divided into 3 components: autotrophic respiration (R_A), heterotrophic respiration (R_H) of coarse benthic organic matter (CBOM), and R_H of fine benthic organic matter (FBOM). Transport and R_H of FBOM are also separated based on the allochthonous or autochthonous source of the material. GPP = gross primary production.

network of streams draining the watershed upstream of 100 km, allochthonous leaf inputs accounted for 19% of the inputs, and the remainder was from autochthonous GPP. Just >½ (51%) of this input was exported, 28% was R_A, and R_H was split between respiration of CBOM and FBOM. Respiration of material in transport was very small.

These budget numbers changed considerably depending on the extent of the network considered (Fig. 10A, B). Near the headwaters, inputs were clearly dominated by allochthonous leaves. The switch to autochthonous dominance of the network did not occur until ~50 km downstream (Fig. 10A). Except for some initial changes in the headwaters, respiration accounted for 50 to 60% of particulate C loss throughout the system (Fig. 10B), with CBOM respiration being replaced by R_A downstream. FBOM respiration was ~10% all along the system, and, for any location in the network, 40 to 50% of all inputs were transported downstream. Near the headwaters, nearly all FBOM respiration and transport were from allochthonous sources, but autochthonous sources to these outputs increased downstream.

I calculated ecosystem efficiency as R_E divided by total inputs (Fisher and Likens 1973). This measure of efficiency depends on the stream length (Fisher 1977, Webster and Meyer 1997), but using the model, we can look for patterns in ecosystem efficiency downstream (Fig. 11A). R_E as a % of outputs is also ecosystem efficiency because this model is a steady-state model with inputs equal to outputs. Ecosystem efficiency changes little along the 100-km length of the LTR. It changes from ~40% at the headwaters to near 60% at ~20 km and then declines to ~50%. Relative to discharge (Fig. 11B), ecosystem efficiency in the LTR is generally higher than that reported for other streams compiled by Webster and Meyer (1997), perhaps in part because the model does not include storm transport. For example, ecosystem efficiencies for the 2 Coweeta headwater streams included in Fig. 11B (Satellite Branch and Hugh White Creek) are based on total annual export including storms and are somewhat lower than model estimates for the headwaters of the LTR. Also, the model does not include DOC. If I were to include DOC input and assume little direct

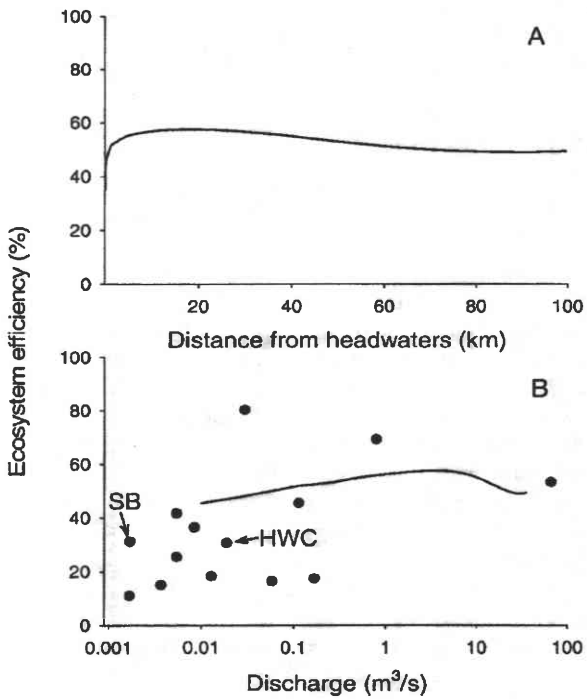

FIG. 11. A.—Ecosystem efficiency along the Little Tennessee River. B.—Comparison of model-estimated ecosystem efficiency (solid line) and stream efficiencies estimated by Webster and Meyer (1997; watershed budgets only, outliers identified by Webster and Meyer 1997 are not included). Satellite Branch (SB) and Hugh White Creek (HWC) are streams at Coweeta.

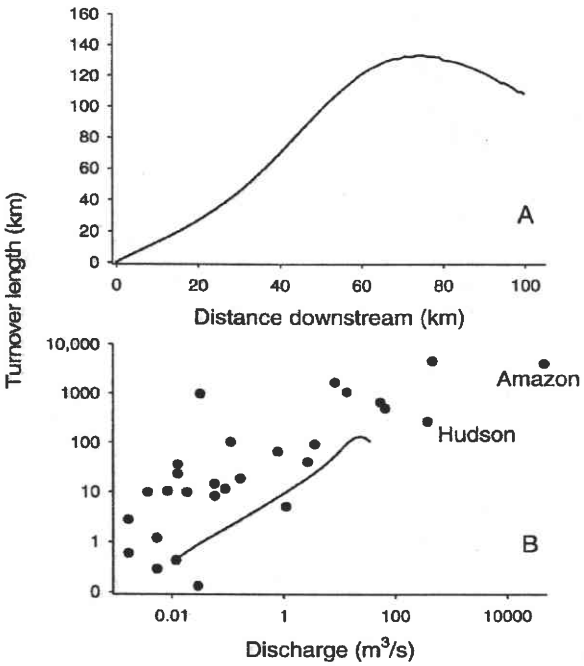

FIG. 12. A.—Turnover length along the Little Tennessee River. B.—Comparison of model-estimated turnover length (solid line) and turnover lengths estimated by Webster and Meyer (1997), Richey et al. (1990; Amazon River), and Howarth et al. (1996; Hudson River).

respiration of DOC, ecosystem efficiency would be reduced to values more similar to measured values that included DOC.

Turnover length is the average distance a particle of C travels between entering the stream (either allochthonously or by instream photosynthesis) and being respired to CO_2 (Newbold et al. 1982); it is calculated as the downstream flux of particulate C divided by respiration. Turnover length increased with distance downstream until ~70 km (Fig. 12A), although it was fairly long, even in the headwaters. Turnover length began to decrease after 70 km as respiration of autochthonously generated particulates became increasingly important. Relative to discharge, turnover length in the LTR was generally shorter than values reported for other streams (Webster and Meyer 1997), and again this difference is probably a result of not including DOC and storm transport (Fig. 12B).

Discussion

Modeling is not the final step of research, but rather it is part of the normal cycle of research known as the hypothetico-deductive approach (e.g., Fretwell 1972). A model is an hypothesis, that is, an attempt to explain how the real system works. From the model, we generate predictions that can be tested by field and laboratory research. Models are not correct or incorrect but, rather, more or less useful. A major contribution of modeling comes in making the necessary simplifications to construct the model and in identifying the limitations of existing knowledge. For example, in developing this model, I identified discrepancies between whole-stream measurements of respiration and substrate-based measurements (Fig. 7B) and between whole-stream measured respiration and measured organic inputs (Figs 3C, 7B), although these discrepancies had been noted earlier (McTammany et al. 2003, Webster et al. 2003). A 2nd major contribution of this model type comes from predictions that are not supported by data rather than from predictions that are correct. For example, a comparison of simulated seston concentration with data (Fig. 10B) suggests that there are significant, unidentified sources of particulate organic C. Another contribution of this model is that it is a bookkeeping device that enables us to make complex calculations of system properties, such as those illustrated in Figs 7 and 10.

Caveats

This model is based on observed data, but it portrays an idealized picture of the LTR system. The biological data are primarily from the small, forested streams at Coweeta and include only 1 study of Coweeta Creek downstream of Coweeta (Grubaugh et al. 1997) and 4 studies of the larger river (Grubaugh et al. 1997, McTammany et al. 2003, Neatrour et al. 2004, Rosi-Marshall and Meyer 2004). It does not account for higher primary production (e.g., McTammany 2004) and modified leaf litter breakdown (Hagen et al. 2006) in small streams draining agricultural land.

This model also does not account for the known large effects of changing discharge on particle transport (e.g., Webster 1983). Inclusion of these processes would require considerably more information on the effects of discharge on particle entrainment and deposition than currently exists. Certainly any inclusion of storm effects would show higher transport, longer transport distances, and budgets influenced more strongly by transport and less strongly by respiration.

Also, I have not included DOC in this model. DOC inputs from soils and leaf leaching represent a major C input, and the more labile forms probably are used rapidly by bacteria. However, most soil-derived DOC is fairly refractory (e.g., Battin et al. 2003, McDowell et al. 2006), and its respiration probably contributes little to stream C budgets. For example, Battin et al. (2003) estimated that DOC contributed only ~16% of annual respiration to White Clay Creek.

As a final caveat, I have not included seasonal changes. Varying temperature, plant transpiration, day length, and leaf fall dramatically affect streams in deciduous forests in regions with strong seasonal climates. However, this variability was not included to enable the examination of more general patterns.

Why are model-predicted seston concentrations low?

The model simulations indicated seston concentrations that were generally less than measured values (Fig. 6B). Therefore, I tried various ways to increase seston concentration. A 1-y simulation that increased shredder contribution to CBOM breakdown from 50% to 90% resulted in an increase of FBOM from an average of 47.4 g C/m^2 over the length of the river to 60.9 g C/m^2, but seston concentration increased only from 0.54 mg C/L to 0.67 mg C/L. Doubling the CBOM breakdown rate had even less effect, increasing FBOM to 49.6 g C/m^2 and seston to 0.57 mg C/L. I increased entrainment, and doing so initially increased seston, but eventually FBOM, followed by seston, decreased. I also tried decreasing deposition velocity, but this change depleted FBOM and seston decreased. It is clear that other sources of organic matter to the stream must be included in the model if predicted seston concentrations are to track measured values more closely.

There are various additional sources of organic matter that have been identified for streams. DOC uptake and sloughing by biofilms or DOC ingestion and production of fecal or psuedofecal pellets by invertebrates (Wotton 2006) may be important in some streams. If the metabolism of DOC is significant, it also could account for high levels of measured ecosystem metabolism. I ran a simulation with a DOC input of 1 mg C/L for all entering water (e.g., Brookshire et al. 2005), immediate conversion of ½ of the DOC to seston, and subsequent deposition as FBOM. This change raised seston concentration to ~0.6 mg C/L through 25 km with an increase to 1.3 mg C/L at 100 km—still below most measured values. R_H increased 25% at most, far less than needed to account for the very high rates of measured metabolism in the upstream reaches of the LTR. However, it is certainly true that some DOC is being metabolized directly and contributing somewhat to total heterotrophic metabolism.

Another possible source that I have not accounted for in the model is erosion of soil organic C. Sollins et al. (1985) found that soil was a major source of FPOM to streams in Oregon, but at Coweeta, leaves appear to be the major source of particulate organic C. As noted previously, elimination of invertebrate shredders greatly reduced seston. Also, eliminating leaf input to a stream resulted in decreased seston concentrations (Wallace et al. 1999). Wallace et al. (1999) estimated that bank runoff contributed 22.8 g AFDM m^{-2} y^{-1} compared to a normal litter input (litterfall + lateral movement) of >600 g AFDM m^{-2} y^{-1}. However, after 8 y of leaf exclusion and removal of all wood from the stream, annual seston export was reduced to only 48% of pre-exclusion amounts relative to a control stream (J. B. Wallace, University of Georgia, S. Eggert, University of Georgia, J. L. Meyer, University of Georgia, and JRW, unpublished data). This finding suggests that wood removal may have accelerated erosion from the streambed and banks.

Another potentially significant C source is entrainment from the floodplain. Neatrour et al. (2004) estimated that floodplain input to the main stem of the LTR was slightly <½ of direct litterfall. The addition of floodplain inputs would have little effect on total inputs because direct litterfall is a relatively small input to this part of the river. Also, floodplain entrainment would add very little to upper reaches of the river where riparian vegetation extends over most or all of the stream. In the upper reaches, floodplain areas extend very little beyond bankfull width, the width I used to estimate litterfall inputs. Wallace et al. (1995) suggested that the riparian zone immediately adjacent to small streams may be more important in retaining leaves than as a source of leaves.

Why are model-predicted respiration rates lower than measured values?

Accurate measurement of respiration in small streams with high rates of reaeration is difficult. The rate of reaeration can be measured with tracer gases such as propane or SF_6, but application of this rate to calculate respiration is sensitive to absolute measurement of dissolved O_2 concentration. When reaeration is very high, small errors in dissolved O_2 concentration measurements can lead to large errors in estimated respiration (McCutchan et al. 1998). Also, respiration can be significantly overestimated in reaches with significant inputs of ground water with low dissolved O_2 unless proper measurements and corrections are made (McCutchan et al. 2002, Hall and Tank 2005). Both of these problems affect measurements of whole-stream respiration at Coweeta. The model-generated rates of R_H, which are based on measured rates of substrate respiration or breakdown, may be closer to actual values. Whole-stream measurements of respiration greatly exceed inputs, but the substrate-based rates are somewhat lower than inputs, allowing for reasonable estimates of downstream transport.

TABLE 2. Various estimates of the location of the transition from heterotrophy to autotrophy in the Little Tennessee River. The first 4 estimates are based on data at a single location in the river, and the other 3 are based on data for the whole river network upstream of the location. P = production, R = respiration, GPP = gross primary production, NPP = net primary production, R_H = heterotrophic respiration.

Method of estimating transition	Distance from headwaters (km)
River	
P/R = 1 (Fig. 8)	27
GPP = allochthonous inputs (Fig. 3)	25
NPP = allochthonous inputs	30
R_H from autochthony = R_H from allochthony (Fig. 7B)	67
River network	
GPP = allochthonous inputs (Fig. 10A)	50
NPP = allochthonous inputs	62
R_H from autochthony = R_H from allochthony (Fig. 10B)	>100

Where does the transition from heterotrophy to autotrophy occur?

The U-shaped curve of energy inputs to streams occurs because of the upstream input of allochthonous material and the downstream increase in autochthonous production. Various indices have been used to quantify the transition from heterotrophy to autotrophy that is a result of the U-shaped curve of inputs (Table 2). If I use the traditional P/R = 1 as the transition from heterotrophy to autotrophy, this transition occurs in the LTR ~27 km downstream from the headwaters where the river is 5th order (Fig. 8B). For ecosystems without transport and completely autochthonous, i.e., with no allochthonous inputs, heterotrophy (respiration) equals autotrophy (primary production) at steady state. So a more useful point of transition occurs when a system goes from being dominated by allochthonous inputs to one dominated by autochthonous inputs. Based on where GPP exceeds allochthonous inputs, this point would be slightly upstream of the P/R = 1 transition, at ~25 km (Fig. 3C). Alternatively, using the input to heterotrophs, the point where net primary production (NPP = GPP – R_A) exceeds allochthonous input is at 30 km. Rosenfeld and Mackay (1987) and Meyer (1989) suggested that a more appropriate point of division than those just described should be determined from the basis of secondary production, i.e., one should ask whether allochthonous or autochthonous C is supporting secondary production. I do not have secondary production estimates, but the model does calculate the basis of R_H. R_H is the energy used by the whole assemblage of heterotrophs. From an ecosystem perspective, the basis of R_H is a useful indicator of the importance of allochthonous and autochthonous inputs to the stream. Using R_H, heterotrophic respiration becomes predominantly autochthonous-based ~67 km from the headwaters in the 7th-order reach of the river (Fig. 7A). If I base the transition on the input of allochthonous vs autochthonous material to the entire stream network upstream of that point, the transition occurs at ~50 km based on GPP (Fig. 10A) or at ~62 km based on NPP. Last, using the basis of R_H for the entire network, the transition would be beyond the 100-km limit of my simulations. At 100 km, 62% of heterotrophic respiration in the network was still based on allochthonous inputs.

These different transition points illustrate spiraling. The U-shaped curve of energy inputs indicates a transition in the upper reaches of the river (Fig. 3C), whereas the U-shaped curve of R_H shows the transition much further downstream (Fig. 7B). As the fixed C inputs to the river are used and metabolized to CO_2, they also are subject to downstream transport. The distance between these points depends on the turnover length and the retentive characteristics of the river. Riparian forest cutting, river channelization, wood removal from river channels, and nearly total elimination of beavers undoubtedly have increased the distance between these transitions. On the other hand, damming and water removal have just the opposite effects—they increase retention and shorten the distance between input and respiration.

Final points

CBOM is broken down close to where it enters streams (e.g., Webster et al. 1999), but the ultimate metabolism of much of the organic C to CO_2 might occur a considerable distance downstream because of the recalcitrance and transportability of the small particles produced by CBOM breakdown. Cole and Caraco (2001) and Mayorga et al. (2005) suggested that much of the respiration in large rivers is from C of terrestrial origin. Whether organic C enters streams allochthonously or autochthonously, much of it probably ends up in lakes, reservoirs, and near-shore marine systems (e.g., Biddanda and Cotner 2002). My model estimates of turnover length (Fig. 12) and the % of loss resulting from transport (Figs 9 and 10) are undoubtedly low because the data suggest the simulated seston concentrations are low and because storm transport and DOC are not included. However, despite the many approximations of the model and limited length of the LTR, my estimates of ecosystem efficiency (~50%; Fig. 11) are remarkably similar to

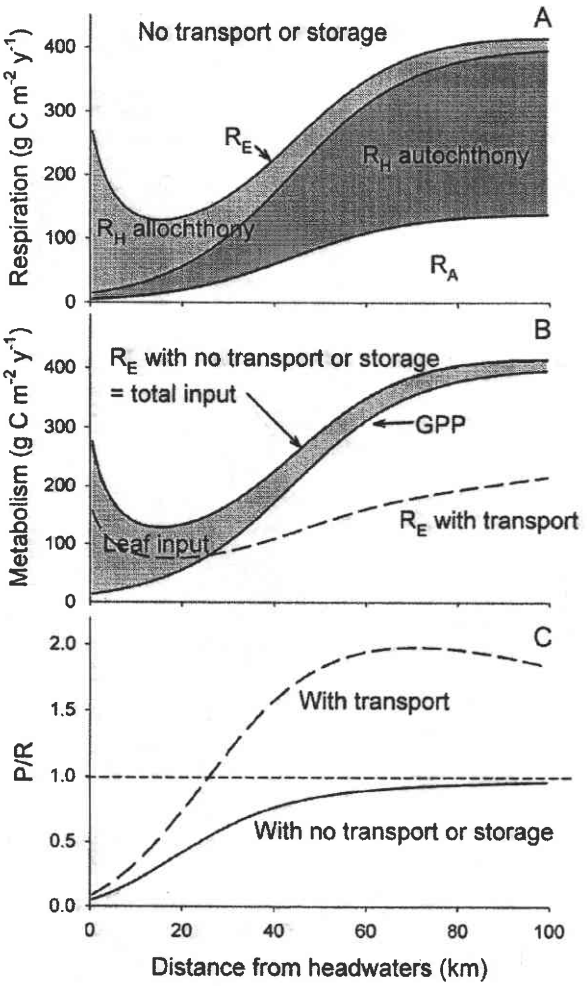

FIG. 13. A.—Simulated respiration in the Little Tennessee River (LTR) with no transport and no storage. Components of respiration are autotrophic respiration (R_A), ecosystem respiration (R_E, upper line), and heterotrophic respiration (R_H, shaded area). R_H is divided into respiration of allochthonous material and autochthonous material. B.—Simulated metabolism in the LTR. The top solid line is total input, which is equal to R_E in this simulation, and the lower solid line is gross primary production (GPP). The shaded area between the solid lines is leaf input. For comparison, the dashed line is ecosystem respiration (R_E) in the normal simulation with transport. C.—Comparison of production (P)/respiration (R) ratios with and without transport.

that estimated by Cole and Caraco (2001) for 45 large rivers located throughout the world. They calculated that the loss of CO_2 from rivers is similar to the transport of organic C in rivers to the sea.

A consequence of the downstream displacement of metabolism is that the nutrients bound in the organic particles also are mineralized downstream. If seston has a concentration of 1 mg C/L and a C:N ratio (by mass) of 20 (Wojculewski 2006), the N concentration associated with particles would be 50 μg N/L, ~½ or less of the dissolved inorganic N concentrations in the LTR (JRW, H. M. Valett, B. R. Niederlehner, unpublished data), but still represents a considerable downstream displacement of N. If storm transport is included, the downstream transport of particle-bound nutrients may be much greater because storms typically increase particle concentrations more than dissolved concentrations.

Leaves are important to metabolism in the LTR. Based on inputs to the river at any point, leaves become less important than GPP at ~25 km downstream (Table 2). However, based on their contribution to secondary metabolism, this transition is much further downstream (Table 2). For the whole river network, nearly 62% of R_H was still based on the input of leaves.

The downstream transport of particulate organic C is a strong linkage along the river continuum. What would happen without any transport? The river would act as a lake or wetland, and all particulate C eventually would be stored (i.e., buried in the sediments) or metabolized where it entered the river, resulting in much higher R_E (Fig. 13A). Without transport or storage, R_E would equal total inputs (Fig. 13B), and P/R would be <1 throughout the length of the river (Fig. 13C). The river would be heterotrophic everywhere because of allochthonous inputs and no transport (Fig. 13C). The observation that rivers can, at some points, be autotrophic, i.e., GPP can exceed R_E on an annual basis (e.g., Fig. 8A), occurs only as a result of downstream transport.

Without transport the river continuum would simply be a gradient, a series of changes that occur primarily as a result of changes in stream size, such as the U-shaped curve of inputs. Organic C transport provides a linkage along the gradient that is fundamental to the nature of river ecosystems. The spiraling approach to stream ecology enables us to conceptualize rivers as they are, systems continuously linked by the downstream transport of organic materials.

Acknowledgements

Research on the LTR has been supported primarily by National Science Foundation grants to the Coweeta Long-Term Ecological Research project (BSR-90116611, DEB-9632854, and DEB-02218001). I thank the many students and colleagues who provided the data I used in my study, and I particularly thank Judy Meyer, Bruce Wallace, and Fred Benfield for our many years of

collaborative research at Coweeta. Denis Newbold, Alan Steinman, Bobbie Niederlehner, and an anonymous referee provided very helpful comments on the manuscript.

Literature Cited

BATTIN, T. J., L. A. KAPLAN, J. D. NEWBOLD, AND S. P. HENDRICKS. 2003. A mixing model analysis of stream solute dynamics and the contribution of a hyporheic zone to ecosystem function. Freshwater Biology 48:995–1014.

BENFIELD, E. F., J. R. WEBSTER, J. J. HUTCHENS, J. L. TANK, AND P. A. TURNER. 2000. Organic matter dynamics along a stream-order and elevational gradient in a southern Appalachian stream. Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie 27:1341–1345.

BIDDANDA, B. A., AND J. B. COTNER. 2002. Love handles in aquatic ecosystems: the role of dissolved organic carbon drawdown, resuspended sediments, and terrigenous inputs in the carbon balance of Lake Michigan. Ecosystems 5:431–445.

BROOKSHIRE, E. N. J., H. M. VALETT, S. A. THOMAS, AND J. R. WEBSTER. 2005. Coupled cycling of dissolved organic nitrogen and carbon in a forest stream. Ecology 86:2487–2496.

COLE, J. J., AND N. F. CARACO. 2001. Carbon in catchments: connecting terrestrial carbon losses with aquatic metabolism. Marine and Freshwater Research 52:101–110.

CUFFNEY, T. F., J. B. WALLACE, AND J. R. WEBSTER. 1984. Pesticide manipulation of a headwater stream: invertebrate responses and their significance for ecosystem processes. Freshwater Invertebrate Biology 3:153–171.

D'ANGELO, D. J., J. R. WEBSTER, S. V. GREGORY, AND J. L. MEYER. 1993. Transient storage in Appalachian and Cascade mountain streams as related to hydraulic characteristics. Journal of the North American Benthological Society 12: 223–235.

ELWOOD, J. W., J. D. NEWBOLD, R. V. O'NEILL, AND W. VANWINKLE. 1983. Resource spiralling: an operational paradigm for analyzing lotic ecosystems. Pages 3–27 *in* T. D. Fontaine and S. M. Bartell (editors). Dynamics of lotic ecosystems. Ann Arbor Science, Ann Arbor, Michigan.

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. 1973. Energy flow in Bear Brook, New Hampshire: an integrative approach to stream ecosystem metabolism. Ecological Monographs 43:421–439.

FRETWELL, S. D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton, New Jersey.

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

GRAHAM, J. M., J. A. KRANZFELDER, AND M. T. AUER. 1985. Light and temperature as factors regulating seasonal growth and distribution of *Ulothrix zonata* (Ulvophyceae). Journal of Phycology 21:228–234.

GRUBAUGH, J., B. WALLACE, AND E. HOUSTON. 1997. Production of benthic macroinvertebrate communities along a southern Appalachian river continuum. Freshwater Biology 37:581–596.

HAGEN, E. M., J. R. WEBSTER, AND E. F. BENFIELD. 2006. Are leaf breakdown rates a useful measure of stream integrity along an agricultural landuse gradient? Journal of the North American Benthological Society 25:330–343.

HAINS, J. J. 1981. The response of stream flora to watershed perturbation. PhD Dissertation, Clemson University, Clemson, South Carolina.

HALL, R. O. J., AND J. TANK. 2005. Correcting whole-stream estimates of metabolism for groundwater input. Limnology and Oceanography 3:222–229.

HILL, W. R., P. J. MULHOLLAND, AND E. R. MARZOLF. 2001. Stream ecosystem responses to forest leaf emergence in spring. Ecology 82:2306–2319.

HOWARTH, R. W., R. SCHNEIDER, AND D. SWANEY. 1996. Metabolism and organic carbon fluxes in the tidal freshwater Hudson River. Estuaries 19:848–865.

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

HUTCHENS, J. J., J. B. WALLACE, AND E. D. ROMANISZYN. 2004. Role of *Podostemum ceratophyllum* Michx. in structuring benthic macroinvertebrate assemblages in a southern Appalachian river. Journal of the North American Benthological Society 23:713–727.

MAYORGA, E., A. K. AUFDENKAMPE, C. A. MASIELLO, A. V. KRUSCHE, J. I. HEDGES, P. D. QUAY, J. E. RICHEY, AND T. A. BROWN. 2005. Young organic matter as a source of carbon dioxide outgassing from Amazonian rivers. Nature 436: 538–541.

MCCUTCHAN, J. H., W. M. LEWIS, JR, AND J. F. SAUNDERS. 1998. Uncertainty in the estimation of stream metabolism from open-channel oxygen concentrations. Journal of the North American Benthological Society 17:155–164.

MCCUTCHAN, J. H., J. F. SAUNDERS, W. M. LEWIS, JR, AND M. G. HAYDEN. 2002. Effects of groundwater flux on open-channel estimates of stream metabolism. Limnology and Oceanography 47:321–324.

MCDOWELL, W. H., A. ZSOLANY, J. A. AITKENHEAD-PETERSON, E. G. GREGORICH, D. L. JONES, D. JÖDEMANN, K. KALBITZ, B. MARSCHNER, AND D. SCHWESIG. 2006. A comparison of methods to determine the biodegradable dissolved organic carbon from different terrestrial sources. Soil Biology and Biochemistry 38:1933–1942.

MCTAMMANY, M. E. 2004. Recovery of southern Appalachian streams from historical agriculture. PhD Dissertation, Virginia Polytechnic Institute and State University, Blacksburg, Virginia.

MCTAMMANY, M. E., J. R. WEBSTER, E. F. BENFIELD, AND M. A. NEATROUR. 2003. Longitudinal patterns of metabolism in a southern Appalachian river. Journal of the North American Benthological Society 22:359–370.

MEYER, J. L. 1989. Can P/R ratio be used to assess the food base of stream ecosystems? A comment on Rosenfeld and Mackay (1987). Oikos 54:119–121.

MINSHALL, G. W., K. W. CUMMINS, R. C. PETERSEN, C. E. CUSHING, D. A. BRUNS, J. R. SEDELL, AND R. L. VANNOTE. 1985. Developments in stream ecosystem theory. Canadian Journal of Fisheries and Aquatic Sciences 42:1045–1055.

MULHOLLAND, P. J., E. R. MARZOLF, J. R. WEBSTER, D. R. HART, AND S. P. HENDRICKS. 1997. Evidence that hyporheic zone increase heterotrophic metabolism and phosphorus uptake in forest streams. Limnology and Oceanography 42:443–451.

NAIMAN, R. J., J. M. MELILLO, M. A. LOCK, T. E. FORD, AND S. R. REICE. 1987. Longitudinal patterns of ecosystem process-

es and community structure in a subarctic river continuum. Ecology 68:1139–1156.

NEATROUR, M. A., J. R. WEBSTER, AND E. F. BENFIELD. 2004. The role of floods in particulate organic matter dynamics of a southern Appalachian river-floodplain ecosystem. Journal of the North American Benthological Society 23:198–213.

NEWBOLD, J. D. 1987. Phosphorus spiralling in rivers and river-reservoir systems: implications of a model. Pages 303–327 *in* J. F. Craig and J. B. Kemper (editors). Regulated streams. Plenum, New York.

NEWBOLD, J. D., J. W. ELWOOD, R. V. O'NEILL, AND W. VANWINKLE. 1981. Measuring nutrient spiralling in streams. Canadian Journal of Fisheries and Aquatic Sciences 38:860–863.

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., S. A. THOMAS, G. W. MINSHALL, C. E. CUSHING, AND T. GEORGIAN. 2005. Deposition, benthic residence, and resuspension of fine organic particles in a mountain stream. Limnology and Oceanography 50:1571–1580.

PETERS, G. T., J. R. WEBSTER, AND E. F. BENFIELD. 1987. Microbial activity associated with seston in headwater streams: effects of nitrogen, phosphorus and temperature. Freshwater Biology 18:405–413.

PROCTOR, J. D., AND B. M. H. LARSON. 2005. Ecology, complexity, and metaphor. BioScience 55:1065–1068.

RICHEY, J. E., J. I. HEDGES, A. H. DEVOL, P. D. QUAY, R. VICTORIA, L. MARTINELLI, AND B. R. FORSBERG. 1990. Biogeochemistry of carbon in the Amazon River. Limnology and Oceanography 35:352–371.

ROSENFELD, J. S., AND R. J. MACKAY. 1987. Assessing the food base of stream ecosystems: alterations to the P/R ratio. Oikos 50:141–147.

ROSI-MARSHALL, E. J., AND J. L. MEYER. 2004. Quality of suspended fine particulate matter in the Little Tennessee River. Hydrobiologia 519:29–37.

SCHAEFFER, M. A. 1993. Effects of land use on oxygen uptake by microorganisms on fine benthic organic matter in two Appalachian Mountain streams. MS Thesis, Virginia Polytechnic Institute and State University, Blacksburg, Virginia.

SCHLESINGER, W. H. 1997. Biogeochemistry: an analysis of global change. Academic Press, San Diego, California.

SOLLINS, P., C. A. GLASSMAN, AND C. N. DAHM. 1985. Composition and possible origin of detrital material in streams. Ecology 66:297–299.

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

USGS (US GEOLOGICAL SURVEY). 2002. Multi-Resolution Land Characteristics (MRLC) consortium land-cover dataset. US Geological Survey, US Department of the Interior, Washington, DC.

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., 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.

WALLACE, J. B., S. L. EGGERT, J. L. MEYER, AND J. R. WEBSTER. 1999. Effects of resource limitation on a detrital-based ecosystem. Ecological Monographs 69:409–442.

WALLACE, J. B., D. H. ROSS, AND J. L. MEYER. 1982b. Seston and dissolved organic-carbon dynamics in a southern Appalachian stream. Ecology 63:824–838.

WALLACE, J. B., J. R. WEBSTER, AND T. F. CUFFNEY. 1982a. Stream detritus dynamics: regulation by invertebrate consumers. Oecologia (Berlin) 53:197–200.

WALLACE, J. B., M. R. WHILES, S. EGGERT, T. F. CUFFNEY, G. J. LUGTHART, AND K. CHUNG. 1995. Long-term dynamics of coarse particulate organic matter in three Appalachian Mountain streams. Journal of the North American Benthological Society 14:217–232.

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., E. F. BENFIELD, T. P. EHRMAN, M. A. SCHAEFFER, J. L. TANK, J. J. HUTCHENS, AND D. J. D'ANGELO. 1999. What happens to allochthonous material that falls into streams? A synthesis of new and published information from Coweeta. Freshwater Biology 41:687–705.

WEBSTER, J. R., AND S. W. GOLLADAY. 1984. Seston transport in streams at Coweeta Hydrologic Laboratory, North Carolina, U.S.A. Verhandlungen 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. 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.

WEBSTER, J. R., P. J. MULHOLLAND, J. L. TANK, H. M. VALETT, W. K. DODDS, B. J. PETERSON, W. B. BOWDEN, C. N. DAHM, S. FINDLAY, S. V. GREGORY, N. B. GRIMM, S. K. HAMILTON, S. L. JOHNSON, E. MARTÍ, W. H. MCDOWELL, J. L. MEYER, D. D. MORRALL, S. A. THOMAS, AND W. M. WOLLHEIM. 2003. Factors affecting ammonium uptake in streams—an inter-biome perspective. Freshwater Biology 48:1329–1352.

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., AND J. B. WAIDE. 1982. Effects of forest clearcutting on leaf breakdown in a southern Appalachian stream. Freshwater Biology 12:331–344.

WINTERBOURN, M. J., J. S. ROUNICK, AND B. COWIE. 1981. Are New Zealand stream ecosystems really different? New Zealand Journal of Marine and Freshwater Research 15: 321–328.

WOJCULEWSKI, C. A. 2006. Influence of land use on the quality of seston in southern Appalachian stream ecosystems. MS Thesis, Virginia Polytechnic Institute and State University, Blacksburg, Virginia.

WOTTON, R. S. 2006. Have we underestimated the role of faeces in aquatic systems? Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie 29:1212–1214.

Received: 8 September 2006
Accepted: 23 February 2007