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Longitudinal patterns of metabolism in a southern Appalachian river

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Abstract. We investigated longitudinal patterns of ecosystem metabolism (primary production and respiration) at 4 sites along a 37-km segment of the Little Tennessee River (LTR), North Carolina. These sites corresponded to 4th- to 6th-order reaches in the LTR in an attempt to identify the transition from heterotrophic to autotrophic conditions in this river ecosystem. In addition, we compared autochthonous C production to supply of coarse organic material from direct litter fall and entrainment from the floodplain during floods to determine the contributions of each to river energetics on an annual basis. Metabolism was measured at several times of year at each site using the single-station diel oxygen change method and reaeration estimated by the energy dissipation method. Gross primary production (GPP) ranged from 0.07 to 1.92 g C m^{-2} d^{-1} and increased ~3-fold from upstream to downstream. Respiration (R) ranged from 0.27 to 2.32 g C m^{-2} d^{-1} but did not change along the river continuum. Net ecosystem production (NEP) and P/R consistently showed that metabolism was heterotrophic in upstream sites and became autotrophic in the site furthest downstream. Calculated transitional P/R (i.e., where heterotrophic respiration is supported equally by autochthonous and allochthonous C sources) suggested that this heterotrophy–autotrophy shift occurred further upstream than where P/R = 1. Annual rates of GPP were 3 times higher than litter fall and floodplain inputs of C, but R was higher than total C input suggesting that unmeasured C sources must be important for C dynamics in the LTR. The difference between measured C inputs and R decreased along the river continuum because of a 3-fold increase in GPP with little change in allochthonous input and R. Our results suggest that the LTR changes from heterotrophic to autotrophic along this stretch of river and that autochthonous C sources become more important for respiration and secondary production at downstream sites.

Key words: primary production, respiration, river continuum concept, mid-order river, carbon budget, allochthonous input, southern Appalachians.

Although the contrast between allochthonous and autochthonous C as the energy base of streams has been a fruitful area of research, both C sources can play an important role in stream ecosystem energetics. Ecosystems in which respiratory demand is higher than primary production rely on organic material imported from outside the system. For example, many headwater streams are detritus based, and primary production represents only a minor supply of C (e.g., Fisher and Likens 1973). In contrast, when primary production is higher than respiration, surplus C is either stored or exported to other systems. Primary production in streams with open canopies often exceeds respiration (Minshall 1978). The ratio between primary production (P) and respiration (R) has been used to define ecosystems as heterotrophic ($P/R < 1$) or autotrophic ($P/R > 1$), and these terms have been used to infer the primary C source for ecosystems (originally, Odum 1956). However, the simple balance of primary production and respiration does not necessarily indicate whether autochthonous or allochthonous C is most important to ecosystem respiration or secondary production (Rosenfeld and Mackay 1987, Meyer 1989). Organisms in largely heterotrophic rivers may still rely on autochthonous production (planktonic and benthic) as the primary C source for secondary production (Thorp and Delong 1994, 2002).

Vannote et al. (1980), in their river continuum concept (RCC), suggested that ecosystem metabolism shifts from heterotrophy to autotrophy along a continuum from headwaters to downstream. Many studies have demonstrated support for the RCC, particularly in regions where headwater streams are forested (Bott et al. 1985, Naiman et al. 1987, Minshall et al. 1992). In these regions, mid-sized rivers (4th- to 6th-order) generally represent metabolic transition zones between forested heterotrophic streams

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and open-canopied autotrophic rivers (Vannote et al. 1980, Bott et al. 1985, Naiman et al. 1987, Minshall et al. 1992). By studying metabolism in 4th- to 6th-order stream reaches, we can determine the location of the heterotrophic to autotrophic transition and associated longitudinal changes in C supply and demand.

In addition to the balance between production and respiration, we can compare the amount of C coming from different sources at sites along a river continuum to determine the potential importance of each energy source to ecosystem respiration. Sources of allochthonous organic matter include particulate and dissolved organic matter from upstream and tributaries, litter fall from riparian vegetation (including blow-in), and entrainment of organic matter following floods. The relative importance of direct organic matter input from litter fall decreases as one moves down a river continuum (Conners and Naiman 1984), whereas autochthonous production generally increases (Naiman et al. 1987). However, streams and rivers may receive large amounts of allochthonous organic matter from interaction with the floodplain during floods, and these inputs of organic matter can be important for respiration and secondary production in streams (Cuffney 1988, Meyer and Edwards 1990, Smock 1990, Wallace et al. 1997). Autochthonous production can form the C base for food webs in streams that have open canopies because of a lack of trees or wide channels (Minshall 1978, Rosenfeld and Mackay 1987). Furthermore, light often penetrates to the bottom of mid-sized rivers, adding to their potential to support high rates of primary production (Hill and Webster 1982).

Rivers in the Appalachian Mountains of the eastern United States are ecologically important systems that provide a good opportunity to examine longitudinal patterns in metabolism and organic matter supply. Several rivers in the Appalachians begin in steep forested terrain, flow through low-gradient valleys, and then cut through the mountains (Hack 1973). Headwater streams in the Appalachians are extremely heterotrophic (e.g., Mulholland et al. 2001) and have been intensively studied (see review Wallace et al. 1992), but little research has been done on metabolism in Appalachian river systems (except see Hill and Webster 1982). Mid-order reaches of Appalachian rivers have high macroinvertebrate diversity (Wallace et al. 1992, Grubaugh et al. 1996) and high secondary production (Grubaugh et al. 1997). However, these mid-sized rivers remain poorly studied because of the difficulty in sampling (Wallace et al. 1992) and the focus of stream ecologists on small streams or large rivers (Webster et al. 1995).

Our main objective was to investigate trends in metabolism and C supply along a river continuum from 4th to 6th order. By restricting our study to mid-order reaches, we sought to identify shifts from heterotrophy to autotrophy and from allochthonous-dominated to autochthonous-dominated C supply. We measured metabolism seasonally at 4 sites along a mid-sized river in western North Carolina. We then compared primary production to direct litter fall and floodplain input of organic matter to determine which C source likely supports ecosystem respiration at each site.

Methods

Study sites

Metabolism was measured at 4 sites along a 36.5-km segment of the Little Tennessee River (LTR) in Macon and Swain counties, North Carolina (Fig. 1). Sites 1 and 4 were located ~27 and 63 km downstream of the river source in northern Georgia, respectively (Table 1, based on a 1:150,000 scale map). Elevation decreases from 618 to 586 m along this segment of river (Table 1). The 2 upstream sites (1 and 2) are 4th-order reaches (stream order based on Strahler [1957] using 1:24,000 USGS topographic maps) where the LTR flows through a broad alluvial valley and has a relatively flat, sandy bottom. Two large tributaries join the LTR downstream from site 2 making site 3 a 5th-order reach (Fig. 1) with approximately double the discharge of site 2 (Table 1). In addition, dilution from these tributaries, notably the Cullasaja River, causes reduced specific conductance in downstream sites (>100 μS/cm at sites 1 and 2 to ~65 μS/cm at sites 3 and 4, Table 1). The LTR flows through the town of Franklin and a small reservoir (Lake Emory) between sites 2 and 3. Lake Emory was designed as a surface release hydroelectric facility in 1927 and is now mostly filled with sediment (NCDWQ 2002). Lake Emory likely continues to retain sediment and organic material, but our sites are several km away from Lake Emory (Site 2 is 10 km upstream, and Site

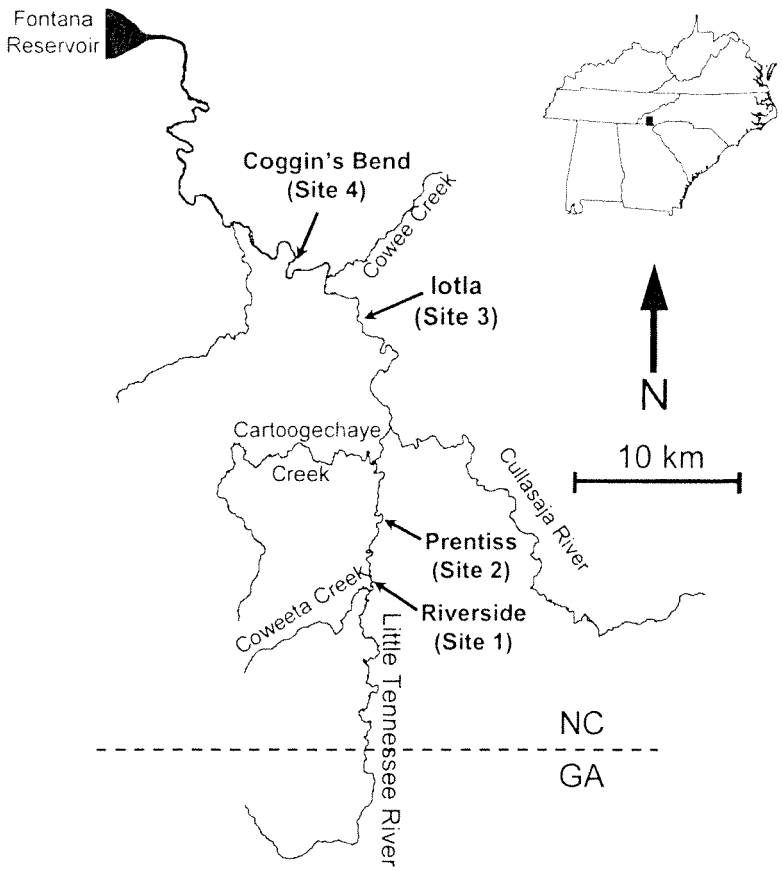

FIG. 1. Study reaches and major tributaries of the Little Tennessee River. Inset shows the southeastern US; the enlarged area is represented by a black rectangle on the inset.

3 is 5 km downstream). Therefore, we feel that differences in metabolism along the river are a result of increasing river size more than reservoir impacts. The LTR becomes 6th order between sites 3 and 4 after its confluence with Cowee Creek (Fig. 1). At the 2 downstream sites, the river valley is constrained, and the substrate consists of a mix of bedrock, large boulders, and sand. Average temperature increased from 14.7°C at site 1 to 16.0°C at site 4 (Table 1), but temperature range was greater downstream with both the coldest (5.4°C) and warmest (24.8°C) recorded temperatures occurring at site 4. Depth is greater at downstream sites (Table 1), but light appeared to reach the bottom at each site on all sampling dates. Despite the steep gradient at site 1, river gradient is generally greater downstream of Franklin (Grubaugh et al. 1996).

Land use in the basin is predominately Nantahala National Forest in the uplands and pasture/hay fields in the valley. Riparian vegetation consists of mixed deciduous trees dominated by sycamore (*Platanus occidentalis*), black walnut (*Juglans nigra*), American hornbeam (*Carpinus caroliniana*), and red maple (*Acer rubrum*), but these trees are often restricted by agriculture to a narrow strip along the river (Neatrour 1999). The riparian zone is more heavily forested downstream of Franklin, but agriculture is still common in the river valley.

Metabolism

We used a single-station, diel oxygen curve technique to measure gross primary production (GPP), ecosystem respiration (R), net ecosystem production (NEP = GPP − R), and primary production to respiration ratio (P/R). We measured metabolism in 1998 (July, August, and Novem-

Table 1. Physical characteristics of study locations on the Little Tennessee River. Values are means with range in parentheses or ±1 SE. Downstream distance is from the river source based on a 1:150,000 map. Temperature and conductivity were measured concurrently with metabolism. Discharge, width, depth, velocity, and the reaeration coefficient, $k_{2(20°C)}$, were measured during diel oxygen data collection on each date.

	Site			
	1	2	3	4
Latitude	35°05′27.3″N	35°07′19.7″N	35°14′03.1″N	35°15′52.1″N
Longitude	83°22′53.3″W	83°22′26.2″W	83°23′39.9″W	83°26′39.5″W
Downstream distance (km)	27.1	33.1	53.9	63.6
Elevation (m)	618	615	597	586
Temperature (°C)	14.7 (6.1–23.1)	15.0 (6.3–23.2)	15.8 (5.6–24.2)	16.0 (5.4–24.8)
Specific conductance (μS/cm at 25°C)	102.4 ± 12.2	113.6 ± 15.6	65.9 ± 10.1	64.9 ± 8.2
Mean width (m)	18.3 (11.5–23.5)	17.2 (15.8–18.3)	46.3 (43.3–50.2)	40.5 (36.3–49.0)
Mean depth (m)	0.70 (0.51–1.06)	0.78 (0.60–1.09)	1.19 (1.01–1.43)	1.00 (0.71–1.28)
Velocity (m/s)	0.47 (0.34–0.62)	0.46 (0.31–0.76)	0.25 (0.15–0.34)	0.42 (0.21–0.61)
Mean discharge (m^3/s)	7.4 (3.9–11.9)	7.4 (4.1–13.0)	14.8 (6.7–27.5)	18.4 (8.1–31.8)
Gradient (m/km)	1.24	0.49	0.77	1.18
$k_{2(20°C)}$ (/d)	9.26 ± 0.57	3.55 ± 0.38	3.15 ± 0.32	7.55 ± 0.82

ber) at sites 1, 2, and 4, and at all sites in 1999 (March, May, June, July, August, and November) and 2000 (March and May). We took oxygen measurements at 15-min intervals over 24-h periods starting at midnight using air-calibrated Hydrolab MiniSonde 4 units (Hydrolab Corporation, Austin, Texas) equipped with temperature and dissolved oxygen probes. We corrected oxygen values measured with the sondes to dissolved oxygen values from Winkler titration of water samples collected in the early morning and mid-afternoon from each site.

To estimate metabolism from diel oxygen curves, we corrected for changes in oxygen caused by physical reaeration. We estimated the reaeration coefficient (k_2) using the energy dissipation method, which uses water velocity and river gradient to determine k_2 (Tsivoglou and Neal 1976, Bott 1996). On each oxygen sampling date, we measured water velocity using slug chloride injections to determine travel time through a 300-m reach at each study site. We measured the gradient over each 300-m study reach using a transit and stadia rod. To determine oxygen exchange across the water surface, we multiplied k_2 (at ambient stream temperature) by saturation deficit. The saturation deficit is the difference between measured oxygen values and equilibrium oxygen concentrations at stream temperature and ambient barometric pressure (APHA 1998). We monitored barometric pressure continuously at Coweeta Hydrologic Laboratory (within 25 km of each site) using a Vaisala pressure transmitter equipped with a Campbell data logger. We corrected barometric pressure values for elevation differences between Coweeta and each site.

We calculated GPP by integrating the difference between reaeration-corrected dissolved oxygen changes and estimated daytime R. R was calculated using reaeration-corrected dissolved oxygen change and a 2-point linear regression between dawn and dusk. We assumed daytime R to be equal to nighttime R. We established transects every 50 m within a 300-m reach at each site and measured depth at several points along each transect on each sampling date. We multiplied GPP and R by average depth to convert from volumetric to areal units. We converted GPP from oxygen to C units by multiplying by the atomic ratio of C to O_2 and dividing by a photosynthetic quotient of 1.2 (Hill et al. 2001). We then converted GPP to NPP (NPP = GPP × 0.556; Westlake 1974, Likens 1975) for compari-

son to other studies. We converted R to C units by multiplying by the atomic ratio of C to O_2 and a respiratory quotient of 0.85 (Wetzel 1983). We determined mean GPP, R, NEP, and P/R for each site by averaging data from all sampling dates. We determined longitudinal trends in metabolism by regressing the mean of each metabolic parameter against position of study sites along the river continuum. We performed all statistical analyses using SAS (version 8, SAS Institute, Cary, North Carolina).

Neatrour (1999) quantified allochthonous input of coarse particulate organic matter (CPOM) to the LTR from direct litter fall and entrainment from the floodplain during floods. We used data from his sites closest to our metabolism sampling sites to estimate annual allochthonous C load of CPOM to these reaches of the LTR. We compared annual C supply from autochthonous (GPP) and allochthonous (direct litter fall and floodplain interaction) sources to determine longitudinal patterns in C supply. In addition, we calculated the annual C deficit by subtracting total C input (GPP + allochthonous CPOM) from annual R to determine how these inputs contribute to the energetics of the LTR. We obtained annual GPP and R values by multiplying average daily values by 365.

Results

Mean GPP ranged from 0.39 g C m^{-2} d^{-1} at site 1 (upstream) to 1.11 g C m^{-2} d^{-1} at site 4 (downstream). GPP increased significantly with distance downstream (Fig. 2; linear regression, $r^2 = 0.947$, $p = 0.027$). Mean R ranged from 1.05 g C m^{-2} d^{-1} at site 3 to 1.43 g C m^{-2} d^{-1} at site 1 but did not exhibit a significant longitudinal trend. Mean NEP was negative at all sites and ranged from −1.04 g C m^{-2} d^{-1} at site 1 to −0.09 g C m^{-2} d^{-1} at site 4. NEP increased with distance downstream (linear regression, $r^2 = 0.921$, $p = 0.040$). Mean P/R ranged from 0.32 at site 1 to 1.01 at site 4 and increased with distance downstream (linear regression, $r^2 = 0.953$, $p = 0.024$).

C supply (CPOM and GPP) to the LTR averaged 312.9 g C m^{-2} y^{-1} with 23.8% from allochthonous CPOM sources and 76.2% from autochthonous production (Table 2). The relative contribution of allochthonous C sources of CPOM decreased from 36.3% to 13.6% over the length of river studied. Direct litterfall input to the river decreased per unit area as the river got larger. Flood input of CPOM ranged from 16.2 g C m^{-2} y^{-1} at site 2 to 26.8 g C m^{-2} y^{-1} at site 1, but input varied dramatically because of differential inundation and entrainment (Neatrour 1999). Annual respiratory loss of C was highest at site 1 (522.7 g C m^{-2} y^{-1}) and lowest at site 3 (384.5 g C m^{-2} y^{-1}). Annual respiratory loss was greater than C input for the LTR indicating a C deficit of 124.0 g C m^{-2} y^{-1}, but this value varied among sites. The annual C deficit (respiration > input) was 299.7 g C m^{-2} y^{-1} at site 1, but there was an annual C surplus (respiration < input) at site 4 of 30.1 g C m^{-2} y^{-1}.

Discussion

Comparisons to other studies

Metabolism in the LTR was similar to values reported in other studies of mid-sized rivers in the eastern United States (Table 3). NPP at our upstream sites was lower than reported for other 4th-order streams, but several of those streams were in agricultural regions of the midwest where primary production was high because of high nutrients and light (Flemer 1970, Wiley et al. 1990). Walker Camp Prong, in the Great Smoky Mountain National Park, Tennessee, had the lowest NPP of streams compared here (Mulholland et al. 1986). Although NPP at our upstream sites was low, our downstream sites had NPP values that were higher than other eastern US streams (Hoskin 1959, Hornberger et al. 1977, Sumner and Fisher 1979, Hill and Webster 1982, Bott et al. 1985) but lower than streams from the midwest (Bott et al. 1985, Wiley et al. 1990). NPP at our most downstream site was very similar to the New River, Virginia, another mid-sized southern Appalachian river (Hill and Webster 1982).

R in our 4th-order sites was within the range reported for other small rivers (0.26–6.09 g C m^{-2} d^{-1}) and was higher than chamber R estimates (Brown and King 1987, Naimo et al. 1988). Despite the impact of humans on the LTR from impoundment and agriculture, the Raritan River, New Jersey (Flemer 1970) and Vermilion River, Illinois (Wiley et al. 1990) had much higher R as a result of nutrient loading from agricultural or municipal sources. R in our downstream reaches was similar to other rivers in the Appalachians (Hornberger et al. 1977) but was

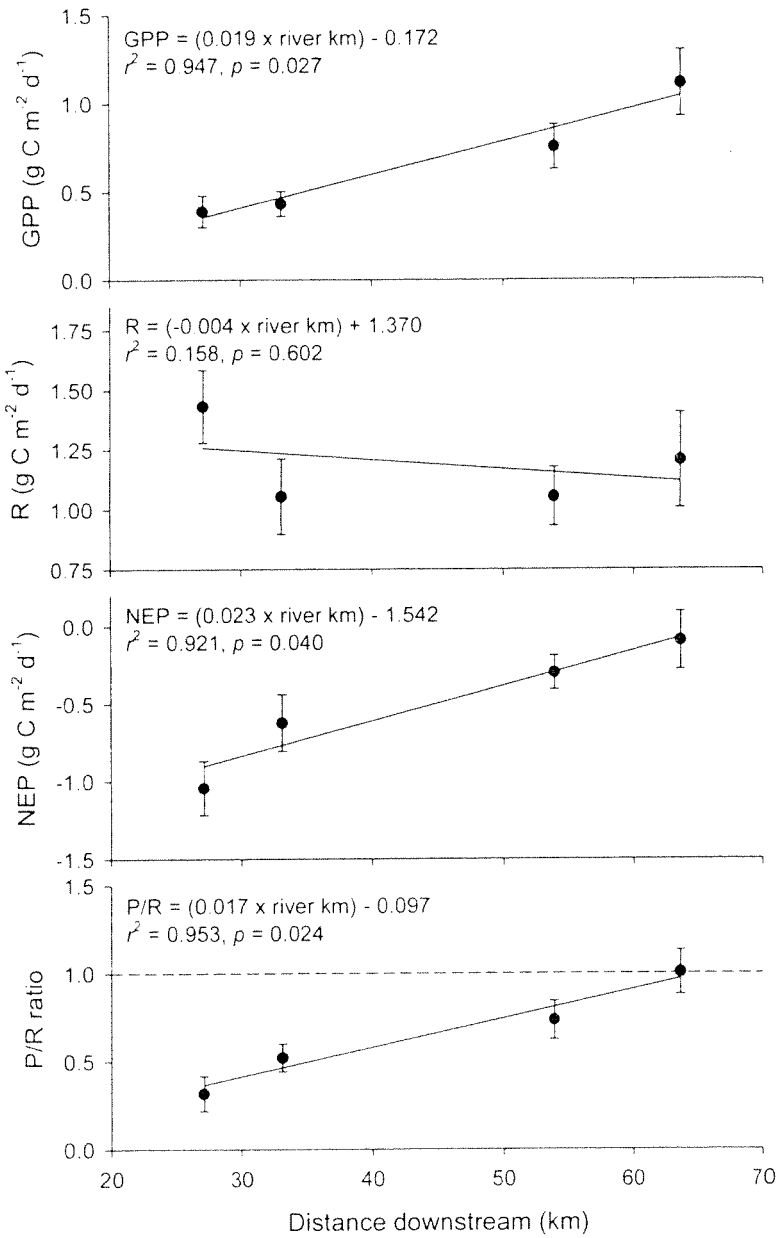

FIG. 2. Relationships between gross primary production (GPP), respiration (R), net ecosystem production (NEP), and primary production to respiration (P/R) ratio and distance downstream from the headwaters of the Little Tennesse River. Values are means (±1 SE) of each site. The dashed line represents P/R = 1.

lower than agricultural (Wiley et al. 1990) and blackwater rivers (Edwards and Meyer 1987).

Longitudinal trends in metabolism

GPP increased 3-fold from site 1 to site 4, and other studies have shown increases of similar magnitude along river continua. Minshall et al. (1983) observed longitudinal increases of similar magnitude in GPP, but these were measured across larger changes in stream size. Meyer and Edwards (1990) showed a remarkably similar increase from 4th-order Black Creek, Georgia, to 6th-order Ogeechee River, Georgia, sites with

TABLE 2. Annual C input and output (g C m^{-2} y^{-1}) from different sources to the Little Tennessee River. Allochthonous inputs were measured by Neatrour (1999) at sites near river metabolism sites. Percent of total input is in parentheses below input values. Total allochthonous is the sum of direct litter fall and flood input of coarse particulate organic matter. Net C deficit is calculated from respiration (R) minus total input. Values for allochthonous inputs were converted from ash-free dry mass (AFDM) to g C using g C = 0.5 g AFDM (Meyer and Edwards 1990). GPP = gross primary production.

	Direct litter fall	Flood input	Total allochthonous	GPP	Total C input	R	Net C deficit
Site 1	54.2	26.8	81.0	142.0	223.0	522.7	+299.7
	(24.3)	(12.0)	(36.3)	(63.7)			
Site 2	74.2	16.2	90.4	157.9	248.3	385.0	+136.7
	(29.9)	(6.5)	(36.4)	(63.6)			
Site 3	45.2	19.5	64.7	275.3	340.0	384.5	+44.5
	(13.3)	(5.7)	(19.0)	(81.0)			
Site 4	44.3	19.7	64.0	406.0	470.0	439.9	−30.1
	(9.4)	(4.2)	(13.6)	(86.4)			
Average input to river	53.4	21.1	74.5	238.4	312.9	436.9	+124.0
	(17.1)	(6.7)	(23.8)	(76.2)			

values that were almost identical to mean GPP for our sites in the LTR. Vannote et al. (1980) predicted a decline in GPP downstream of 6th-order rivers because of increased turbidity. However, mid-sized rivers in the southern Appalachians (e.g., New River, French Broad, Pigeon, LTR) are clear, wide, and shallow as they cut across the mountains.

Longitudinal trends of R are difficult to predict because studies have shown different results. The LTR did not exhibit a significant longitudinal trend and Vannote et al. (1980) did not predict longitudinal changes in R. Furthermore, Minshall et al. (1983) showed that longitudinal R dynamics were variable and depended on season. However, several studies have demonstrated longitudinal increases in R. Minshall et al. (1992) attributed longitudinal increases in R to autotrophic activity in the highly autotrophic Salmon River, Idaho. Meyer and Edwards (1990) attributed downstream increases in R to heterotrophic activity supported by high allochthonous C input from riparian swamps in a blackwater stream system in Georgia. R in Hugh White Creek (Mulholland et al. 1997 as corrected by Mulholland et al. 1999), a headwater tributary of the LTR at Coweeta Hydrologic Laboratory, greatly exceeded LTR estimates. If we include this headwater stream as part of our continuum, then R appears to decrease downstream through 6th order.

NEP and P/R increased significantly along the stretch of river studied, indicating a general tendency for the river to become less heterotrophic in downstream reaches. This result is similar to other studies of forested streams (Minshall et al. 1983, Naiman 1983, Bott et al. 1985); however, metabolism in grassland rivers has generally indicated little longitudinal trend in net metabolism because of high GPP in upstream river reaches where there is no gallery forest (Wiley et al. 1990, Young and Huryn 1996). Meyer and Edwards (1990) suggested that NEP was a more useful indicator of organic matter transitions than P/R when considering C budgets in stream systems because NEP demonstrates the amount of C deficit or surplus. In Meyer and Edwards (1990), NEP and P/R had opposite downstream trends (NEP decreased while P/R increased longitudinally) because of the magnitude of difference between GPP and R. Although Meyer and Edwards (1990) demonstrated the need for caution when interpreting net metabolism, both NEP and P/R increased with distance downstream in the LTR.

Annual C budget

GPP, allochthonous CPOM, and respiratory losses of C were used to construct a C budget for each reach in our study. Although allochthonous input of CPOM was substantial, in-stream primary production was 3× greater than direct litter fall and floodplain inputs. However,

Table 3. Comparison of metabolic parameters (net primary production [NPP] and respiration [R]) in streams of similar size from the eastern United States (Webster et al. 1995). OSDO = open system dissolved oxygen, CHDO = chamber dissolved oxygen, CHC14 = chamber ^{14}C. For our study (bolded), NPP = 0.556 × GPP (Westlake 1974, Likens 1975). – = no data.

Stream	Order	Method	NPP (g C m^{-2} d^{-1})	R (g C m^{-2} d^{-1})	Reference
Black Creek, GA	4	OSDO	–	1.31	Meyer and Edwards 1990
Buttahatchie River, MS	4	CHDO	–	0.26	Naimo et al. 1988
Chippewa River A, MI	4	CHDO	0.38	0.38	Brown and King 1987
Chippewa River C, MI	4	CHDO	0.33	0.32	Brown and King 1987
Fort River, MA	4	OSDO	–	1.15	Fisher and Carpenter 1976
LTR 1, NC	**4**	**OSDO**	**0.20**	**1.37**	**This study**
LTR 2, NC	**4**	**OSDO**	**0.21**	**0.98**	**This study**
Raritan River 2, NJ	4	OSDO	1.53	2.33	Flemer 1970
Raritan River 3, NJ	4	OSDO	2.19	3.12	Flemer 1970
Vermilion River, IL	4	OSDO	2.97	6.09	Wiley et al. 1990
Walker Camp Prong, TN	4	CHC14	0.09	–	Mulholland et al. 1986
Buck Run PA	5	CHDO	0.28	0.70	Bott et al. 1985
Fort River, MA	5	CHDO	0.38	–	Sumner and Fisher 1979
Kalamazoo River, MI	5	CHDO	0.63	0.92	Bott et al. 1985
Little River, NC	5	OSDO	0.21	1.79	Hoskin 1959
LTR 3, NC	**5**	**OSDO**	**0.45**	**1.07**	**This study**
Mechums River, VA	5	OSDO	0.24	0.92	Hornberger et al. 1977
Rivanna River, VA	5	OSDO	0.33	1.63	Hornberger et al. 1977
South Fork Rivanna River, VA	5	OSDO	0.33	1.08	Hornberger et al. 1977
South River, VA	5	OSDO	0.32	1.69	Hornberger et al. 1977
Vermilion River, IL	5	OSDO	1.65	5.71	Wiley et al. 1990
LTR 4, NC	**6**	**OSDO**	**0.62**	**1.20**	**This study**
Middle Oconee River, GA	6	OSDO	0.03	–	Nelson and Scott 1962
New River, VA	6	CHC14	0.55	–	Hill and Webster 1982
Ogeechee River, GA	6	OSDO	–	2.14	Edwards and Meyer 1987
Vermilion River, IL	6	OSDO	0.95	5.42	Wiley et al. 1990
Eno River, NC	7	OSDO	0.38	1.79	Hoskin 1959
Neuse River 1, NC	7	OSDO	0.29	0.77	Hoskin 1959
Neuse River 2, NC	7	OSDO	0.05	0.54	Hoskin 1959
Rappahannock River, VA	7	OSDO	0.97	2.33	Hornberger et al. 1977
Tombigbee River, MS	7	CHDO	–	0.83	Naimo et al. 1988
Vermilion River, IL	7	OSDO	0.68	2.65	Wiley et al. 1990

the combined sources of C were not large enough to account for R in the LTR. The annual C deficit indicated that respiratory demand was ~30% (~124 g C m^{-2} y^{-1}) higher than measured C input to the LTR, but the size of the C deficit was not constant among sites. Respired C was ~60% higher than measured C sources at site 1 and ~7% lower at site 4. Allochthonous inputs decreased longitudinally in the LTR, suggesting that the longitudinal increase in GPP accounted for more of R in downstream reaches.

The C deficit of the LTR indicates that C must be reaching the river from some sources other than GPP, direct litter fall, and floodplain interaction. Researchers have attributed similar discrepancies between C supply and R to floodplain organic matter inputs (Meyer and Edwards 1990), import from upstream reaches (Young and Huryn 1996), and dissolved organic C (DOC; Edwards and Meyer 1987, Cole and Caraco 2001). The C deficit of Hugh White Creek was 787.3 g C m^{-2} y^{-1} based on values derived from other studies (DOC: Meyer and Tate 1983; litter fall and transport: Webster et al. 1990; FPOM: Golladay 1997; GPP and R: Mulholland et al. 1997 as corrected by Mulholland

et al. 1999). Although several additional sources of C were estimated for Hugh White Creek, its annual C deficit was over twice the observed LTR deficit. Further research into the possible impact of each of these sources on energetics in the LTR should enable us to fill in the missing components of our C budget.

Heterotrophic–autotrophic transition

Vannote et al. (1980) predicted that the transition from heterotrophic to autotrophic metabolism should occur in 3rd-order reaches of streams in regions with deciduous vegetation, based on the definition of $P/R < 1$ for heterotrophic systems and $P/R > 1$ for autotrophic systems. In our study, P/R was ~1 in the 6th-order reach of the LTR. Other studies have also demonstrated metabolic transitions downstream of RCC predictions (e.g., Bott et al. 1985, Meyer and Edwards 1990). Downstream metabolic transition shifts could be explained by hydrologic factors (Young and Huryn 1996) or floodplain contributions of organic matter (Meyer and Edwards 1990). In the LTR, hydrologic influences, such as turbidity, were likely not an important determinant of observed metabolic patterns because our study was done at baseflow in a river that is not greatly affected by sediment. However, the metabolic transition could be shifted downstream in the LTR by allochthonous inputs of organic matter and unsuitable substrate for algae in upstream reaches. Bott (1983) mentioned geomorphic factors, such as substrate, as potentially important determinants of primary production in streams. Shifting, sandy substrate upstream of Franklin may have limited benthic algal production. Local geomorphology (Hack 1973) and sediment retention in Lake Emory (NCDWQ 2002) likely result in more stable substrate for primary producers downstream of Franklin and could help autotrophic production in lower LTR reaches.

The application of P/R to indicate the heterotrophic–autotrophic transition in streams has been criticized (e.g., Fisher and Likens 1973, Minshall 1978) because this index does not indicate which C source (allochthonous or autochthonous) supports secondary production (Rosenfeld and Mackay 1987, Meyer and Edwards 1990). To clarify the C sources of secondary producers in streams, Meyer (1989) evaluated the "transitional P/R" proposed by Rosenfeld and Mackay (1987). Transitional P/R is "the P/R ratio above which the heterotrophic community is primarily dependent on autochthonous organic matter and below which it is primarily dependent on allochthonous organic matter" (Meyer 1989). Meyer (1989, equation 4) simplified the transitional P/R equation to:

$$\text{Transitional } P/R = 1 \div (a + 4k - 4ak - 2k^2 + 2ak^2)$$

where a is the fraction of GPP respired by primary producers and k is the fraction of NPP respired in a reach (Rosenfeld and Mackay 1987). Reported values of a range from as low as 0.1 to as high as 0.5 and depend on the type of plants present (Meyer 1989). However, the transitional P/R is fairly insensitive to a (Meyer 1989). We used a value of 0.44 because of the abundance of submerged vascular plants in the LTR (Grubaugh et al. 1996). Using this value and a k of 0.5 based on the physical properties of the LTR and suggestions by Rosenfeld and Mackay (1987), we calculated a transitional P/R of 0.78. Based on our regression of P/R with longitudinal position in the river, the LTR shifts from allochthonous-based to autochthonous-based (i.e., $P/R = 0.78$) ~52 km downstream from the river source where the stream is 5th order. Our annual C budget estimation also indicates that R is heavily supported by primary production at sites 3 and 4. The annual C budget in the LTR switches from a deficit to a surplus near this reach, providing further support of the longitudinal position of the allochthonous–autochthonous transition. Rosi-Marshall and Wallace (2002) found that relative amounts of autochthonous material in benthic macroinvertebrate guts in the LTR increased downstream to our 5th-order reach (site 3), indicating that autochthonous C likely supports secondary production. Stable isotope data indicate that autochthonous production may be the primary source of C for higher trophic levels, even in heterotrophic rivers larger than 4th order (Thorp and Delong 1994, 2002).

In conclusion, streams exhibit changes in organic matter production and balance as they flow from headwaters to rivers. Mid-sized streams (small rivers) in temperate deciduous forests represent transition zones from highly heterotrophic headwater streams to autotrophic rivers. We demonstrated longitudinal patterns

of metabolism over a 4th- to 6th-order range of streams to locate the transition from heterotrophy to autotrophy along a river continuum. This transition was ~60 km from the river source where the LTR is 6th order. However, estimates of the transitional P/R suggest that secondary production is supported by autochthonous C sources where the LTR is 5th order, 10 km upstream of the heterotrophic–autotrophic transition. Autochthonous C supply was higher than input of coarse organic material from direct litter fall and floodplain interaction in the LTR, and the importance of primary production increased at downstream sites. However, GPP, litter fall, and floodplain inputs do not account for all the C required to support ecosystem respiration at most sites in the river. Many other possible sources of C have not been studied in this river, and future research will quantify these C fluxes and their importance to the LTR.

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