

Evidence that hyporheic zones increase heterotrophic metabolism and phosphorus uptake in forest streams

*Patrick J. Mulholland and Erich R. Marzolf*¹

Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee 37831-6036

Jackson R. Webster

Department of Biology, Virginia Tech, Blacksburg 24061

Deborah R. Hart

Department of Zoology, Tel Aviv University, Ramat Aviv 69978, Tel Aviv, Israel

Susan P. Hendricks

Hancock Biological Station, 561 Emma Dr., Murray, Kentucky 42071

Abstract

We used nondisruptive, whole-stream methods to measure hydraulic characteristics, ecosystem metabolism, and phosphorus cycling in the west fork of Walker Branch (WB), Tennessee and in Hugh White Creek (HWC), North Carolina. Although similar in many of their hydrological and chemical characteristics, transient storage zone volume in HWC was relatively large (~1.5 times that of the flowing water zone), whereas transient storage zone volume in WB was small (~0.1 times that of the flowing water zone). Both streams were highly heterotrophic (gross primary production:total respiration ratios <0.1), although respiration rate was ~2.4 times greater in HWC than in WB. Phosphorus uptake rate was ~2.6 times greater in HWC than in WB, and P uptake length was 5 times longer in WB than in HWC. Analysis of ³³P:³H ratio profiles from ³³PO₄ and ³H₂O injection experiments indicated that P uptake within the transient storage zone accounted for ~43% of the total P uptake in HWC but was negligible in WB, explaining, in part, the difference in total P uptake rate between these streams. The higher rate of P uptake in the surface zone, shorter P uptake length, and larger ratio of P uptake:respiration in HWC compared with WB suggest that the microbial community in HWC exerts a greater demand for and has a greater affinity for stream-water P, presumably as a result of a greater supply of labile organic matter and/or lower nutrient levels in HWC.

Many studies of metabolism and nutrient uptake in streams have focused on communities on the surface of the stream bottom in direct contact with flowing water (e.g. Newbold et al. 1983; Bott et al. 1985). This focus implicitly

reflects the belief that primarily surficial benthic processes support food webs and alter the chemistry of flowing water.

Recent studies are expanding the view of stream ecosystems, documenting the importance of zones that are partially isolated from flowing surface water, particularly hyporheic zones (zones of stream water within streambed sediments). Bencala and Walters (1983) have shown by applying a hydrodynamic model to data from conservative tracer injections in streams that such zones allow temporary storage of stream water via slow rates of exchange with surface water and have termed these transient storage zones (Bencala and Walters 1983). Using this tracer injection-modeling approach, D'Angelo et al. (1993) and Morrill et al. (1997) showed that transient storage zones are as large as or larger than the flowing surface water in some streams. Other studies involving conservative tracer injections to streams have identified hydrologic connectivity and significant water exchange between surface water and hyporheic zones (Munn and Meyer 1988; Triska et al. 1993). It is clear that the hyporheic zone is a potentially important transient storage zone in some streams.

Findlay (1995) proposed a conceptual framework of streams that emphasizes the role of hyporheic processes in controlling streamwater chemistry. This framework was based on an understanding of the rate of biogeochemical

¹ Present address: Division of Environmental Science, St. Johns Water Management District, P.O. Box 1429, Palatka, Florida 32178-1429.

Acknowledgments

The paper benefited from reviews by Walter Hill and Jeremy Jones.

This research was sponsored by the National Science Foundation's Ecosystem Studies Program through Interagency Agreement DEB-9013883 with the U.S. Department of Energy and the Coweeta Long Term Ecological Research Project. E.R.M. was supported by an appointment to the Oak Ridge National Laboratory Postdoctoral Research Associates Program administered jointly by the Oak Ridge National Laboratory and the Oak Ridge Institute for Science and Education. The work was performed in part on the U.S. Department of Energy's Oak Ridge National Environmental Research Park. Oak Ridge National Laboratory is managed by Lockheed Martin Energy Research Corp. for the U.S. Department of Energy under contract number DE-AC05-96OR22464.

Publication 4620, Environmental Sciences Division, Oak Ridge National Laboratory.

processes in the hyporheic zone and the rate of exchange between surface water and the hyporheic zone. Vervier et al. (1992) proposed that permeability of the hyporheic zone is the characteristic that determines its biogeochemical role in stream ecosystems. The rates and types of processes within the hyporheic zone can be substantially different from those associated with benthic surface communities. For example, anaerobic metabolism and elemental reductions can be much more important in the hyporheic zone than in the surface zone, as indicated by lower concentrations of dissolved oxygen and nitrate, higher concentrations of ammonium and soluble reactive phosphate, and higher rates of denitrification in hyporheic zones (Duff and Triska 1990; Hendricks and White 1991). Respiration in the hyporheic zone can comprise a substantial fraction of whole-stream respiration rate and result in P:R ratios near or below unity even in highly productive streams (Grimm and Fisher 1984). Downwelling of labile dissolved organic carbon supports much of the hyporheic respiration in some streams (Findlay et al. 1993; Jones et al. 1995a).

Most studies of hyporheic biogeochemistry involve measurements at only a few points (wells) or under altered physical or chemical conditions (sediment removal, nutrient amendments) and thus may not accurately reflect the role of the hyporheic zone at the stream ecosystem scale. For example, in a study of Sycamore Creek, Grimm and Fisher (1984) reported rates of ecosystem respiration that were ~25% higher using nondisruptive, whole-stream methods than using sediment incubations in chambers and summing respiration rates. In our study, we used nondisruptive, whole-stream methods in streams with contrasting hydraulic characteristics to determine whether differences in transient storage, presumably derived from differences in the size of hyporheic zones, are associated with differences in ecosystem metabolism and phosphorus cycling. Our results indicate that metabolism and nutrient uptake rates are substantially higher in a stream in which transient storage zones are large than a stream in which they are small.

Methods

Study sites—The study was performed in two small, forested streams: the west fork of Walker Branch, Tennessee, and Hugh White Creek, North Carolina. These streams are relatively similar in many physical and chemical characteristics (Table 1). The west fork of Walker Branch (WB) is a first-order stream on the U.S. Department of Energy's Oak Ridge National Environmental Research Park in the Ridge and Valley Province of eastern Tennessee. The stream arises in several springs that produce a relatively constant baseflow of 5–10 liters s^{-1} . The stream water is slightly basic, moderately alkaline, and low in inorganic nitrogen and phosphorus. A 62-m reach ~30 m downstream from two perennial springs, ~180 m downstream from the headwaters, and ~120 m upstream from a weir was chosen for the study. Dolomitic bedrock was exposed at several locations in this reach, and the cobble, gravel, and fine-grained sediments are generally <10 cm deep throughout the reach. The channel gradient is relatively gentle (0.04 $m m^{-1}$) and major debris

Table 1. Characteristics of the west fork of Walker Branch (WB) and Hugh White Creek (HWC) related to metabolism and nutrient dynamics. Data for WB are from Mulholland (1992, 1997). Data for HWC are from Swank and Waide (1988) and Webster et al. (1990).

Parameter	WB	HWC
Catchment area (ha)	38.4	61.1
Stream order	1	2
Streambed gradient ($m m^{-1}$)	0.04	0.15
Mean annual temperature ($^{\circ}C$)	13	12
Mean annual discharge (liters s^{-1})	12	19
Mean annual litterfall ($g m^{-2}$)*	459	409
Mean coarse benthic organic matter ($g m^{-2}$)*	175	213
Mean fine benthic organic matter ($g m^{-2}$)†	330	166
Streamwater chemistry (mean annual values)		
pH	8.1	6.7
Alkalinity (meq liter $^{-1}$)	2.6	<0.2
NH ₄ ($\mu g N liter^{-1}$)	3	3
NO ₃ ($\mu g N liter^{-1}$)	26	4
SRP ($\mu g P liter^{-1}$)	2	2

* Excluding wood.

† Surficial materials only (measured to a depth of ~10 cm).

dams are absent in the reach. Previous studies involving conservative tracer injections indicated little transient storage in this reach (Hart 1995). A more complete description of WB was reported by Mulholland (1992).

Hugh White Creek (HWC) is a second-order stream at Coweeta Hydrologic Laboratory in the southern Appalachian Mountains of southwestern North Carolina. Stream water is slightly acidic, generally low in alkalinity, and low in inorganic nitrogen and phosphorus. A 78-m reach ~400 m upstream from a weir was chosen for study. Cobble, gravel, and fine-grained sediments are generally <20 cm deep and overlie granitic bedrock. In contrast to WB, the channel gradient of HWC is moderately steep (0.13 $m m^{-1}$), and several large debris dams with relatively deep (20–100 cm) accumulations of fine-grained sediments behind them are found within the study reach. Previous studies involving conservative tracer injections showed relatively large transient storage zones in HWC (Munn and Meyer 1988; D'Angelo et al. 1993). A more complete description of HWC was presented by Webster et al. (1990).

Experimental procedures—Experimental studies were conducted during late-spring/summer baseflow periods in each stream. The experiments were conducted during 15–17 June 1993 in WB and during 11–13 July 1994 in HWC.

Reach-scale measurements of gross primary production (GPP) and community respiration (R) were made using the upstream–downstream diurnal dissolved oxygen change method as modified for use in small streams (Marzolf et al. 1994). Continuous measurements of dissolved oxygen were made at two (WB) or three locations (HWC) at 1-min intervals and 5-min averages recorded over a 40-h period by a datalogger (Campbell Scientific, model CR10). Air–water exchange rates of oxygen were estimated from propane injections to each reach and measurements of the decline in steady-state dissolved propane concentration between sampling stations using gas chromatography. GPP and R were

determined by performing an oxygen mass balance over the stream reach for each 5-min period using measured upstream–downstream changes in dissolved oxygen concentration, discharge rate, and average water travel time (determined from the ^3H injection data), and air–water oxygen flux (determined from the propane evasion rate, scaled to oxygen, and measured dissolved oxygen saturation deficits). Respiration was calculated from the nighttime oxygen mass balance and GPP was calculated as the sum of the daytime mass balance and R. Metabolism in HWC was determined separately for the upper segment (length, 38 m; area, 114 m²) and lower segment (length, 40 m; area, 101.6 m²) of the study reach (defined by the three sampling stations) to reduce the potential error associated with a relatively large inflow of groundwater of unknown dissolved oxygen concentration within the entire reach (26% increase in discharge determined from the ^3H results). Metabolism for the entire reach was calculated as the area-weighted average of the metabolism for each reach. Photosynthetically active radiation was measured at 1-min intervals with a LiCor quantum sensor positioned within the experimental reach and recorded with the datalogger.

Reach-scale measurements of hydraulic characteristics and phosphorus uptake were made using radiotracer injections to stream water (Mulholland et al. 1990). Briefly, ~185 MBq of $^3\text{H}_2\text{O}$ and 56 MBq of carrier-free $^{33}\text{PO}_4$ were mixed in 4 liters of distilled water and pumped at a constant rate into the stream over 2 h. The injection site was located 5–10 m above the upper sampling station on each stream to ensure complete mixing of the injection solution with stream water. Samples of stream water were collected at the upstream and downstream stations in each stream prior to the injections (for background correction) and at intervals ranging from 1 to 5 min over a 4-h period during and after termination of the radiotracer injection. Stream water was filtered (0.45- μm membrane filter) into a small beaker, 5 ml of the filtrate was added to 15 ml of scintillation fluid (Ecolume, Packard), and the samples were returned to the laboratory and assayed for ^3H and ^{33}P by scintillation counting with multiple channels to separate isotopes. No correction for radioisotope decay of ^{33}P was applied because all samples from an experiment were counted at the same time (within a 6-h period, which is short compared to the ^{33}P half-life of 25.4 d), and radioisotope counting efficiency was not determined because all samples were in the same matrix (stream water) and only relative values (comparisons over time or between stations) were required for the analysis. Previous measurements have shown that the counting efficiency for ^3H is ~23% and for ^{33}P ~95% (Mulholland unpubl. data).

Stream-water samples were collected in triplicate from upstream and downstream stations immediately prior to the radiotracer injection for determination of dissolved nutrient concentrations. Stream water was immediately filtered (0.45- μm membrane filter) and samples were placed on ice for return to the laboratory for analysis within 3 d of collection. Concentration of soluble reactive phosphorus (SRP) was determined by the ascorbic acid method with a 10-cm path-length spectrophotometer cell (American Public Health Association 1992). Analytical precision for SRP was $\pm 0.2 \mu\text{g liter}^{-1}$.

Stream reach hydraulic characteristics were determined from analysis of the ^3H concentration data or direct measurements. Average stream width was computed by measuring the wetted width at 1-m intervals within each reach in each stream. Discharge at each station (upstream and downstream ends of each reach) was determined from the injection rate of ^3H , the concentration of ^3H in the injection solution, and the ^3H concentration in stream water after steady state had been achieved. Average stream-water velocity was determined from the time required for the ^3H concentration to reach half of the steady-state value and the distance from the sampling station to the injection site. Average water depth was computed as the average reach discharge divided by the product of the average stream width and average water velocity.

Hydraulic characteristics related to the size and exchange rates of transient storage zones were determined by fitting an advection–dispersion–transient storage zone model similar to that of Bencala and Walters (1983) to the ^3H data. Bencala and Walters (1983) found that a simple advection–dispersion model provided a poor fit to data from conservative tracer injections to small streams because of extended tails on the rising and falling limbs of the tracer concentration profile. Addition of a stationary, transient storage compartment to the advection–dispersion model effectively retarded a portion of the tracer movement downstream and allowed for a much better fit to the tracer data. This combined advection–dispersion–transient storage model, which was extensively described by the Stream Solute Workshop (1990), consists of two partial differential equations describing the rate of change in conservative tracer (^3H) concentration over time (t) and distance (x) within the free-flowing water and in the transient storage zone:

$$\frac{\partial C_s}{\partial t} + \frac{Q}{A} \frac{\partial C}{\partial t} = \frac{1}{A} \frac{\partial}{\partial x} \left(AD \frac{\partial C}{\partial x} \right) + k_1(C_s - C) + k_L(C_L - C) \quad (1)$$

$$\frac{\partial C_s}{\partial t} = k_2(C - C_s), \quad (2)$$

where C is the tracer concentration in the free-flowing water, C_s the tracer concentration in the stationary transient storage zone, C_L the tracer concentration in lateral inputs, Q the stream discharge (liters s⁻¹), A the cross sectional area of the flowing water zone (m²), D the dispersion coefficient (m² s⁻¹), k_1 the exchange coefficient from free-flowing water to the transient storage zone (min⁻¹), k_2 the exchange coefficient from the transient storage zone to free-flowing water (min⁻¹), and k_L is the lateral inflow rate coefficient (min⁻¹).

The model was converted to a stochastic process formulation and solved analytically by an efficient, converging infinite series approach (Hart 1995). The parameters D , k_1 , and k_2 were estimated by fitting the model to the ^3H concentration profiles at individual stations as described by Hart (1995). The ratio $k_1:k_2$ gives the size of the transient storage zone relative to the size of the free-flowing water zone and is equivalent to the ratio $A_s:A$ used by Bencala and Walters (1983) and D'Angelo et al. (1993).

Several additional indices were computed from the hy-

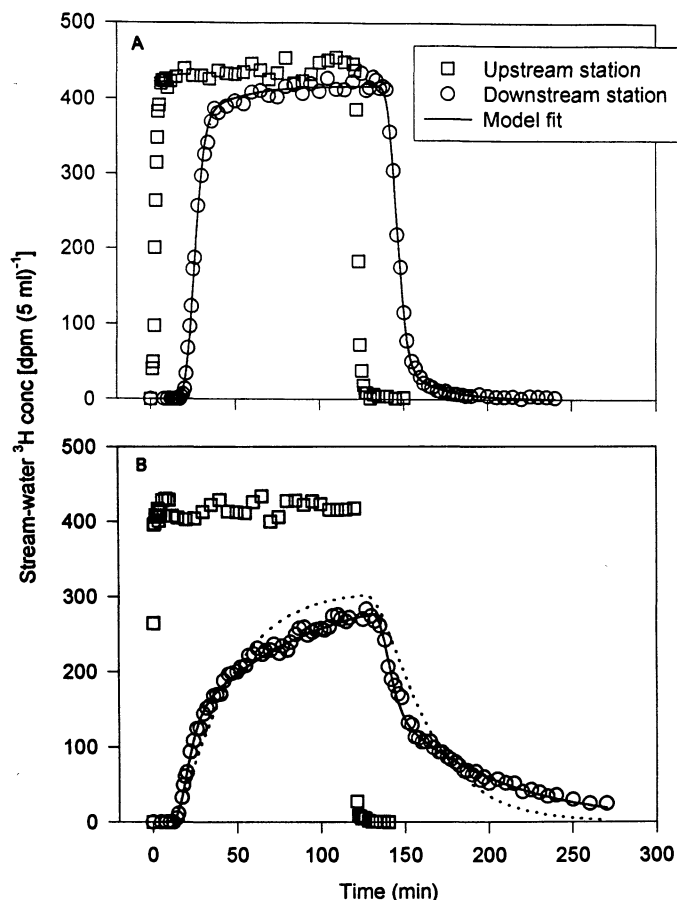


Fig. 1. Profiles of ^3H concentration at upstream and downstream stations during the 120-min radiotracer injection experiments in (A) the west fork of Walker Branch and (B) Hugh White Creek.

hydraulic characteristics determined from the model-fitting process for each stream. The inverse of k_1 and k_2 are the turnover times of water in the free-flowing zone (T_w) and in the transient storage zone (T_s), respectively. The uptake length of water (S_w , average travel distance prior to entry into storage zone) was computed as the product of T_w and the average water velocity and is analogous to the calculation of the uptake length of a nutrient (Newbold et al. 1983). To provide an integrative index of the potential for transient storage zones to effect the concentrations of nonconservative solutes in stream water, we calculated the hydraulic retention factor as proposed by Morrice et al. (1997) as T_s/S_w (units of time distance $^{-1}$). The hydraulic retention factor reflects the fact that potential transient storage zone effect is related to both the time available for transient storage zone processes to occur (T_s) and the likelihood that free-flowing stream water will enter the transient storage zone (inverse of S_w).

Results

Differences in the hydraulic characteristics between the two streams are evident in the shapes of the ^3H concentration profiles (Fig. 1). Whereas ^3H concentration at the downstream station in WB rapidly reached approximate steady

Table 2. Measured physical characteristics and hydraulic parameters determined from model fits to the ^3H data for the study reaches of the west fork of Walker Branch (WB) and Hugh White Creek (HWC) during the experiments.

Parameter	WB	HWC
Average wetted width (m)	2.2	2.8
Discharge (upper station, liters s^{-1})	4.2	4.9
Average surface water velocity (cm s^{-1})	4.5	6.4
Average water depth (cm)	4.3	3.1
Reach water inflow (%)	5	26
Dispersion coefficient (D , $\text{m}^2 \text{min}^{-1}$)	2.8	11.7
Water exchange rate coefficients (min^{-1})		
k_1	0.0042	0.0352
k_2	0.0497	0.0236
Relative transient storage zone size ($k_1:k_2$)	0.09	1.49
Water turnover times (min)		
Free-flowing water (T_w)	238	28.4
Transient storage zone (T_s)	20.1	42.4
Water uptake length (S_w , m)	643	111
Hydraulic retention factor (s m^{-1})	1.9	22.9

state (relatively flat profile after steep ascending limb), ^3H concentration in HWC approached steady state much more slowly. Hydraulic parameters determined from fitting the advection–dispersion/transient storage zone model to the ^3H data for each stream are presented in Table 2. Although mean width, discharge, average water velocity, and water depth were similar between the streams, there were substantial differences in the dispersion coefficients, size of transient storage zones, and exchange rate coefficients between free-flowing water and transient storage zones. The potential importance of transient storage zones for solute dynamics was considerably greater in HWC than in WB as indicated by their larger relative size ($k_1:k_2$ ratio), shorter S_w , and longer T_s in HWC. Thus, the hydraulic retention factor in HWC was about 12 times greater than that in WB.

The dissolved oxygen mass balance data showed that metabolism was dominated by R in both streams. In WB there was a distinct GPP pulse during daylight (Fig. 2), but in HWC, GPP was very low in both reaches (Fig. 3). Metabolism was dominated by respiration in both streams (P:R ratios ≤ 0.1), but R was ~ 2.4 times greater in HWC than in WB (Table 3). These differences were not related to temperature differences, because water temperatures were similar in these streams at the time of the measurements. The difference in GPP between streams was probably due to a difference in light regimes, although we do not have comparative measures of photosynthetically active radiation for both streams because the quantum sensor failed at HWC. Canopy shading is substantially greater in HWC due to the dense understory of *Rhododendron*, which is absent in WB. Also, GPP in HWC was measured under overcast conditions, whereas the GPP measurements in WB were made under relatively clear skies. Photosynthetically active radiation at the stream surface totaled $1.39 \text{ mol m}^{-2} \text{ d}^{-1}$ on the day of the GPP measurements in WB.

Differences in phosphorus uptake between the streams were considerable (Fig. 4, Table 3). Phosphorus uptake rate per unit distance was ~ 5 times greater and P uptake length

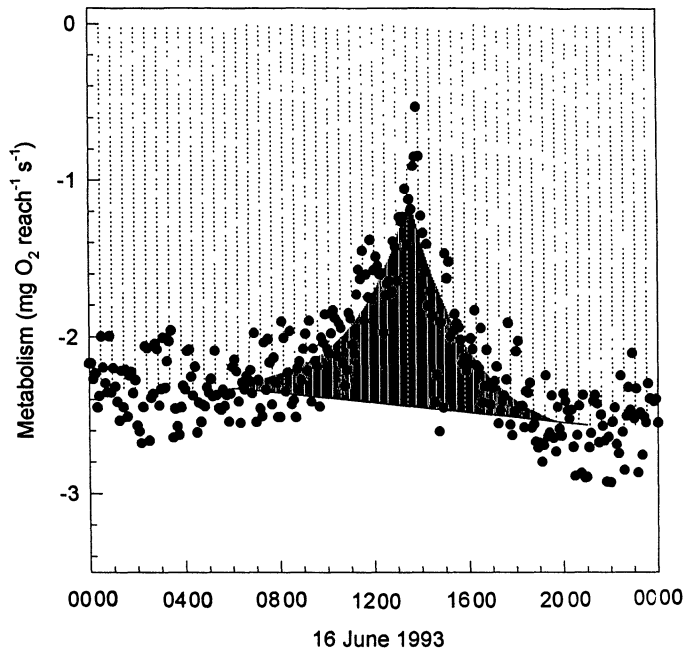


Fig. 2. Metabolism data for Walker Branch calculated from the dissolved oxygen mass balance over the study reach for 5-min periods. Total respiration (R) is the sum of the region indicated by the vertical dashed lines (negative to denote oxygen consumption). Gross primary production (GPP) is the sum of the region indicated by the dark shading (difference between the metabolism data and the line that estimates respiration during daylight).

was ~5 times shorter in HWC than in WB. Mass rate of P uptake was 2.6 times greater in HWC than in WB, despite the twofold lower SRP concentration in HWC. In both streams, there was little change in SRP concentrations from upstream to downstream (no change in WB, $0.2 \mu\text{g liter}^{-1}$ increase in HWC), indicating that remineralization of P was approximately in balance with P uptake.

Inspection of the streamwater $^{33}\text{P} : ^3\text{H}$ ratio profiles for each stream provides evidence of several other differences in phosphorus uptake between the streams. The increase in the $^{33}\text{P} : ^3\text{H}$ ratio at the downstream station in WB after 145 min (during the declining limb of the radiotracer pulse as shown by the ^3H data; Fig. 1A) suggests a rapid release of ^{33}P , probably a result of isotopic exchange within adsorbed pools of phosphate on the stream bottom (Fig. 4A). There was no evidence of a similar rapid release of ^{33}P on the declining limb of the radiotracer pulse in HWC (Fig. 4B). This apparent difference in adsorbed pools of P between the streams is likely a result of differences in bedrock type. In WB, which is underlain by dolomite, concentrations of Ca are moderately high ($25\text{--}30 \text{ mg liter}^{-1}$ at baseflow; Mulholland 1992). During summer when water temperatures and pH are highest, stream water is occasionally saturated with respect to CaCO_3 and precipitation likely occurs (Mulholland unpubl. data). Thus, the sediments of WB likely contain CaCO_3 particles and an associated pool of adsorbed phosphate. In contrast, HWC is underlain by granitic bedrock and Ca concentrations are very low ($<1 \text{ mg liter}^{-1}$; Swank and Waide 1988). The apparent isotopic exchange of ^{33}P in WB

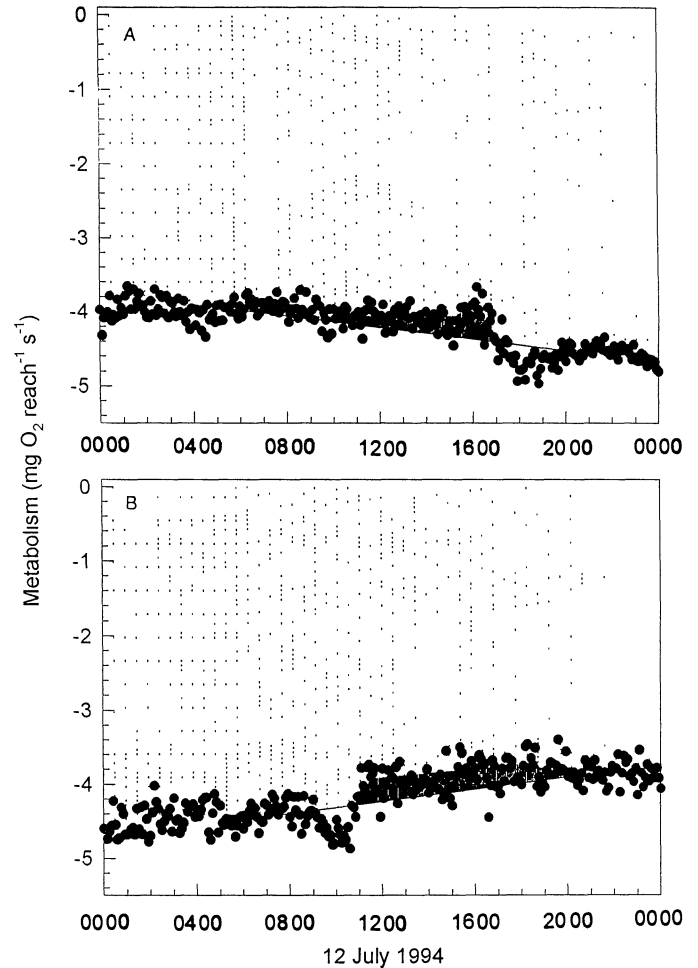


Fig. 3. Metabolism data for Hugh White Creek for (A) upper reach (38 m) and (B) lower reach (40 m). R and GPP are denoted as in Fig. 2.

Table 3. Water temperature, SRP concentrations, and whole-reach measurements of metabolism and phosphorus uptake in the west fork of Walker Branch (WB) and Hugh White Creek (HWC) during the periods 15–17 June 1993 and 11–13 July 1994, respectively.

Parameter	WB	HWC
Average water temperature ($^{\circ}\text{C}$)	14.8	15.0
Average SRP concentrations ($\mu\text{g liter}^{-1}$)	4.6	2.2
Metabolism ($\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$):		
Gross primary production rate	0.14	0.07*
Respiration rate	1.45	3.41†
P:R ratio	0.1	0.02
Phosphorus uptake:		
Uptake rate per unit distance (m^{-1})	0.0064	0.0334
Uptake length (m)	156	30
Mass uptake rate ($\mu\text{g m}^{-2} \text{ h}^{-1}$)	204	534

* Area-weighted average of rates for the upper ($0.073 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) and lower ($0.069 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) segments.

† Area-weighted average of rates for the upper ($3.25 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) and lower ($3.59 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$) segments.

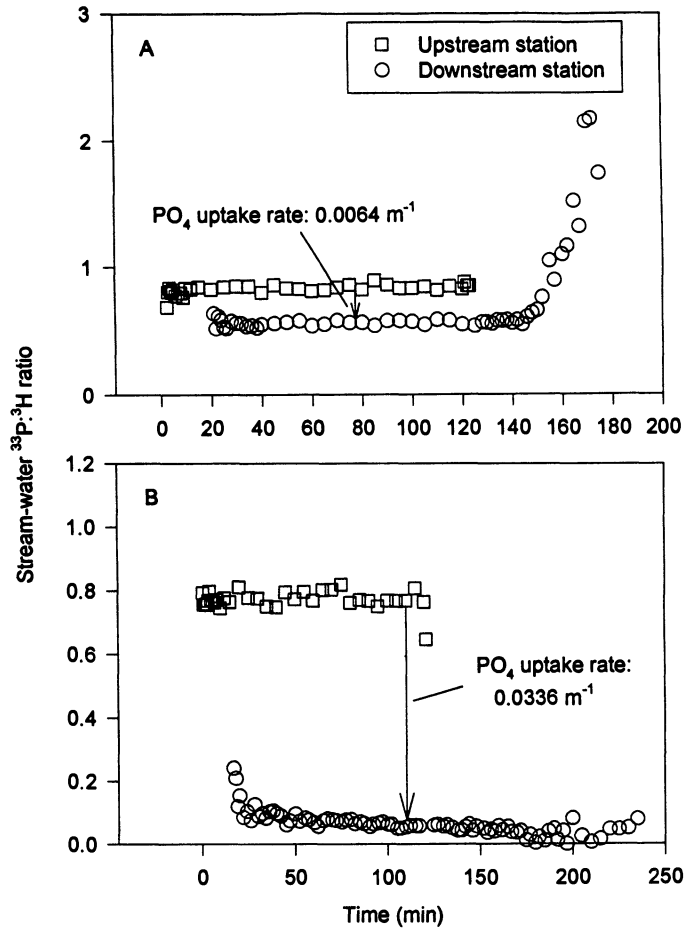


Fig. 4. Profiles of $^{33}\text{P}:^3\text{H}$ concentration ratio at upstream and downstream stations during the radiotracer injection experiments in (A) the west fork of Walker Branch and (B) Hugh White Creek. The PO_4 uptake rate per unit distance was computed as the difference in the mean $\ln(^{33}\text{P}:^3\text{H})$ at steady state between upstream and downstream stations divided by the distance between the stations, and the PO_4 uptake length is the inverse of uptake rate (after Newbold et al. 1983).

was only a small portion of the total uptake of the radiotracer in this stream, however. The excess ^{33}P flux in stream water at the downstream station (^{33}P concentration in excess of that expected based on a constant $^{33}\text{P}:^3\text{H}$ ratio multiplied by discharge) during the first hour of the declining limb of the radiotracer pulse (145–205 min) amounted to $\sim 6\%$ of the total ^{33}P uptake within the reach during the experiment.

The $^{33}\text{P}:^3\text{H}$ ratio at the downstream WB station was constant during the steady-state period (Fig. 4A), but the downstream $^{33}\text{P}:^3\text{H}$ ratio in HWC declined throughout the period (Fig. 4B). Expanding the vertical scale of the plot for HWC shows this decline more clearly (Fig. 5), indicating increasing ^{33}P uptake rates throughout the experiment. One explanation to account for this behavior is significant uptake of P in the transient storage zone. Uptake of ^{33}P by organisms in direct contact with free-flowing water should produce approximately steady $^{33}\text{P}:^3\text{H}$ ratios at the downstream station throughout the experiment (as was the case in WB). However, uptake of ^{33}P by organisms in transient storage zones

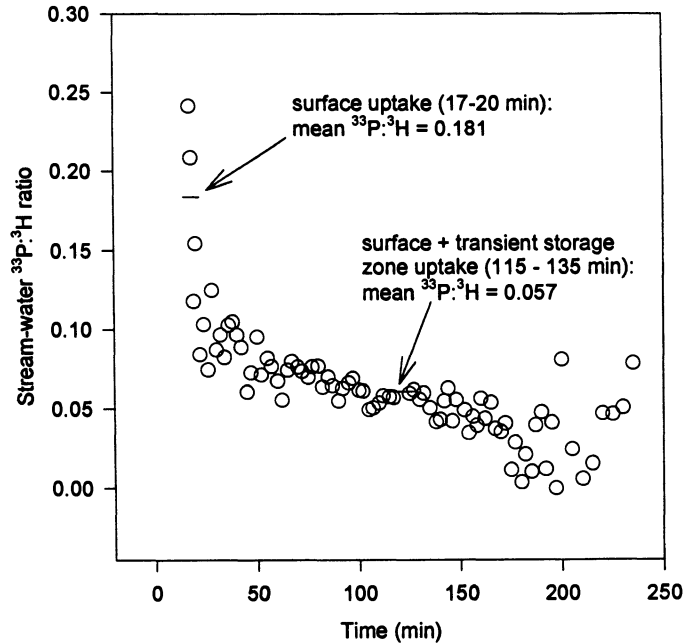


Fig. 5. Plot of the $^{33}\text{P}:^3\text{H}$ concentration ratio at the downstream station in Hugh White Creek showing the decline in $^{33}\text{P}:^3\text{H}$ ratio during the experiment. Average $^{33}\text{P}:^3\text{H}$ ratios over the period when the radiotracer pulse first arrives (17–20 min, defined as the time when ^3H first exceeds $2\times$ the background level to the time when water traveling at the average water velocity arrives) and for the latter portion of the radiotracer pulse (115–135 min) are shown and used for calculations of surface P uptake and total P uptake, respectively (see text).

(e.g. hyporheic zone sediments) would not be reflected in lower $^{33}\text{P}:^3\text{H}$ ratios at the downstream station until a portion of the radiotracer-labeled water entering transient storage zones reemerged as surface flow. Turnover time of water in the transient storage zone in HWC, estimated from the model fit to the ^3H data ($1/k_2$), was 42 min (Table 2). Therefore, if uptake within the transient storage zone was important, we would expect to observe declining $^{33}\text{P}:^3\text{H}$ ratios at the downstream station in HWC for a period at least two to three times the transient storage zone water residence time after the initial portion of the radiotracer pulse arrived.

Separate estimates of P uptake rate by organisms in direct contact with the flowing surface water (presumably on the surface of the stream bottom) and organisms within the transient storage zone were made for HWC. Average $^{33}\text{P}:^3\text{H}$ ratios at the downstream station during the period when the radiotracer pulse first arrived (from 17 min, when ^3H concentration first exceeded $2\times$ background levels, to 20 min, when water traveling at the average water velocity arrived) were assumed to reflect P uptake by the surface community only. The $^{33}\text{P}:^3\text{H}$ ratios during the latter portion of the radiotracer pulse (115–135 min) were assumed to include P uptake by both the surface and transient storage zone communities (Fig. 5). By using these early and late phase downstream $^{33}\text{P}:^3\text{H}$ ratios and the average $^{33}\text{P}:^3\text{H}$ ratio at the upstream station during the experiment (0.778), we estimated the P uptake rate by the surface community to be 0.0187 m^{-1} ($303 \mu\text{g P m}^{-2} \text{ h}^{-1}$) or 57% of the total P uptake. There-

fore, P uptake in the transient storage zone of HWC was $\sim 231 \mu\text{g P m}^{-2} \text{h}^{-1}$ or 43% of total P uptake.

Total P uptake was also separated into autotrophic and heterotrophic components by assuming that P demand by autotrophic organisms was a constant function of GPP. If we use the Redfield C:P ratio (106:1) and a productivity quotient of 1 (to convert GPP from O_2 to C units), autotrophic P uptake in WB was $\sim 53 \mu\text{g m}^{-2} \text{h}^{-1}$ and in HWC it was $\sim 26 \mu\text{g m}^{-2} \text{h}^{-1}$. These values represented about 26 and 5% of the total P uptake in WB and HWC (Table 3). Subtracting autotrophic P uptake from the total P uptake yielded heterotrophic P uptake rates of $151 \mu\text{g m}^{-2} \text{h}^{-1}$ in WB and 508 in HWC. To estimate heterotrophic respiration rate in each stream we assumed that autotrophic respiration was half of GPP and subtracted this value from the total respiration rate measured (converted from O_2 to C using a respiratory quotient of 1). Dividing the calculated heterotrophic P uptake rate by the calculated heterotrophic respiration rate for each stream yielded the stoichiometric ratios for heterotrophic P demand (moles P taken up per mole C respired by heterotrophs) of 1:370 in WB and 1:267 in HWC.

Discussion

Our results show that despite the similarity in some physical (flow, temperature) and ecological (organic matter inputs and benthic storage) characteristics in these two small, forested streams, there were substantial differences in hydraulic characteristics, metabolism, and phosphorus uptake rates. Specifically, the size of the transient storage zone, total respiration rate, and phosphorus uptake rate were all considerably larger in HWC compared with WB. Analysis of $^{33}\text{P}:^{3}\text{H}$ ratios during radiotracer injections in these streams suggests that the difference in P uptake rate between streams was at least partly a result of P uptake in the larger transient storage zone of HWC.

The relatively large transient storage zone in HWC compared to that in WB was probably the result of differences in sediment depths (hyporheic zones). Sediments in WB are shallow (depth to bedrock is generally <10 cm) and $\sim 10\%$ of the reach studied is exposed bedrock. Sediment depths in HWC are variable but generally deeper than in WB. Also, the HWC study reach contained several debris dams with sediment accumulations of >50 cm depth behind them. Although surface water pools (backwaters) that exchange with the flowing water very slowly might contribute to transient storage zones identified from the model, large backwater pools were visibly absent in the HWC study reach.

Our measurements of the sizes of transient storage zones in these streams agree well with previous measurements. D'Angelo et al. (1993) reported that transient storage zones were ~ 1.8 times as large as the flowing surface water zone in another reach of HWC in summer, compared to the relative transient storage zone size of 1.5 times the surface water zone in this study. Hart (1995) reported a relative transient storage zone size of 0.08 for WB in June 1993, and several other experiments have indicated a range from 0.07 to 0.14 in WB under different flow conditions (P. J. Mulholland and D. R. Hart unpubl. data). Thus, the difference

in transient storage zone sizes determined in this study appear to be representative of a consistent difference in hydrodynamics between these streams.

The values reported here for GPP are somewhat lower and for R somewhat higher (particularly in HWC) than those reported by others for first or second-order forested streams in summer. For example, Bott et al. (1985) reported GPP values of $0.1\text{--}2.0 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ and R values of $0.6\text{--}2.1 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ for such streams in Pennsylvania, Michigan, and Oregon, and Hedin (1990) reported R of $\sim 0.1\text{--}0.8 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ (converted from C units) for streams at the Hubbard Brook Experimental Forest. However, all of these studies used chamber techniques to measure metabolism, and these techniques may not provide accurate estimates of metabolism for the ecosystem as a whole because some stream components (e.g. patchy plant distributions, fine-grained or deeper sediments) may be poorly represented. In particular, ecosystem respiration is likely to be underestimated by chamber techniques. There are a few whole-system measurements of metabolism using diurnal oxygen change techniques, but these are primarily from larger, more open-canopy streams. Meyer and Edwards (1990) reported summer GPP values of $0.5\text{--}1.5 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ and R of $3\text{--}6 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ in Black Creek, a fourth-order Coastal Plain stream in Georgia. Grimm and Fisher (1984) reported GPP of $9.4\text{--}10.3 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ and R of $10.1\text{--}10.9 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ in August in Sycamore Creek, a fourth-order Arizona stream. Rand et al. (1992) reported summer GPP of $0.9\text{--}10.2 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ and R of $5.0\text{--}14.0 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ in Little Sandy Creek, a third- to fourth-order stream in New York. Previous whole-stream measurements of metabolism in WB in summer indicated a range in GPP of $0.1\text{--}0.2 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ and a range in R of $1.4\text{--}2.6 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ (Marzolf et al. 1994, unpubl. data).

The relatively high rate of ecosystem respiration in HWC compared with WB despite similar surficial organic matter standing stocks suggests that the larger transient storage zone (presumably due to a larger hyporheic zone) in HWC may be an important factor. In streams in the Hubbard Brook Experimental Forest, R was found to be related positively to the total amount of benthic organic matter and accumulations of organic-rich sediments in areas such as debris dams produced "hot spots" of respiration (Hedin 1990). In their study of Sycamore Creek, Grimm and Fisher (1984) determined that respiration in hyporheic sediments accounted for at least half of the total ecosystem respiration. Consideration of hyporheic respiration and use of whole-stream diurnal O_2 change methods in computing the metabolism budget of Sycamore Creek resulted in P:R ratios $0.9\text{--}1$, whereas use of chamber methods that included only the surface sediment metabolism resulted in P:R ratios of ~ 2 in this highly productive stream. The size of the hyporheic zone seems to be an important determinant of stream ecosystem respiration, and nondisruptive, whole-stream methods, such as the diurnal O_2 change technique, must be used to accurately determine stream ecosystem respiration rates. Recent improvements in diurnal O_2 change methodology have made this technique more amenable for use in small streams (Marzolf et al. 1994).

Although the larger phosphorus uptake rate in HWC compared with WB seems to be related to the larger transient

Table 4. Calculation of phosphorus uptake rate by the surface and transient storage zone communities in Hugh White Creek, based on the differences in the $^{33}\text{P} : ^3\text{H}$ ratios at the upstream station (mean $^{33}\text{P} : ^3\text{H} = 0.778$) and downstream station as the radiotracer pulse first arrived (surface uptake, calculated using the mean $^{33}\text{P} : ^3\text{H}$ ratio at the downstream station at 17–20 min, *see Fig. 5*) and during the latter stages of the radiotracer pulse (surface + transient storage zone uptake).

P uptake	Surface zone	Surface + transient storage zone
Uptake rate per unit distance (m^{-1})	0.0187	0.0334
Mass uptake rate ($\mu\text{g P m}^{-2} \text{h}^{-1}$)	303	534

storage zone in HWC, P uptake in the transient storage zone does not account entirely for the larger P uptake rate in this stream. The P uptake rate in the surface zone only of HWC ($303 \mu\text{g m}^{-2} \text{h}^{-1}$) was ~ 1.5 times larger than the total P uptake rate in WB ($204 \mu\text{g m}^{-2} \text{h}^{-1}$), despite the twofold higher SRP concentration in WB. The higher surface zone P uptake rate and the shorter P uptake length in HWC suggest that the benthic community in HWC is considerably more P deficient and has much higher affinity for streamwater P than the benthic community in WB.

The larger rate of P uptake in HWC was probably the result of greater availability of labile organic matter and greater microbial demand for streamwater P in this stream. Uptake of P by heterotrophs was considerably higher than uptake by autotrophs in both of these streams, as is expected for forest streams with low P : R ratios. Although the process of respiration probably does not exert a demand for P, respiration rate should be positively related to production rate of microbial heterotrophs and the latter would require P. The higher rate of heterotrophic P uptake per unit respiration in HWC suggests that either more labile organic matter is available for growth in HWC (resulting in higher microbial production per unit respiration) or that a greater portion of the microbial P demand is met by uptake from stream water in HWC, caused perhaps by a lower availability of P in the benthic organic matter used as a substrate for growth. Thus, our results point to the importance of organic carbon supply and quality in stream nutrient cycles. Alternatively, the difference in the heterotrophic P uptake : respiration ratios between streams might reflect differences in the requirements for P by different species or groups of microbes. It is difficult to evaluate this possibility because there is little information on the P content of microbes in aquatic environments and we have no data on possible differences in composition of the microbial communities of these streams.

The P uptake rates measured in this study were similar to previous measurements of P uptake in these streams. Previous summer studies of P uptake in HWC using short-term additions of phosphate also indicated that P uptake length was short (< 50 m) and was controlled primarily by biotic processes (Webster et al. 1991). The P uptake length measured in WB is within the range of previous summer measurements (98–164 m) and has also been previously shown to be controlled primarily by biotic processes (Newbold et al. 1983; Mulholland et al. 1990). Thus, the difference in P

uptake reported here appears to reflect consistent differences in the biotic demand for P in these streams.

Cycling of P in these streams is rapid, as indicated by the lack of change in SRP concentrations from upstream to downstream despite relatively high rates of P uptake. Phosphorus cycling is most rapid in HWC where the uptake flux of P in the study reach (116.6 mg h^{-1}) was considerably greater than the flux in stream water (43.8 mg h^{-1}). In WB, the uptake flux in the study reach (27.8 mg h^{-1}) was only $\sim 40\%$ of the streamwater P flux (71.3 mg h^{-1}), but nonetheless should have produced a 40% decline in streamwater SRP concentration in the absence of regeneration. These results highlight the importance of using in situ tracer additions to determine nutrient uptake rates in streams when regeneration rates are also high. These results also suggest that nutrient cycling (uptake and remineralization) is intensified in streams with larger transient storage zones.

Microbial processes in the hyporheic zone of streams can substantially modify the nutrient and organic carbon concentrations in groundwater inputs to streams (Ford and Naiman 1989). Our results contribute to a growing body of literature (e.g. Grimm and Fisher 1984; Triska et al. 1993; Findlay 1995) suggesting that hyporheic zones are also important sites of metabolism and nutrient cycling in stream ecosystems. Previous studies have identified the hyporheic zone as an important site of nutrient remineralization and supply to surface communities (Hendricks and White 1991; Jones et al. 1995b). Our results expand this view, indicating that hyporheic zones can also be important sites of nutrient uptake and at least temporary retention of surface water nutrients in stream ecosystems.

References

- AMERICAN PUBLIC HEALTH ASSOCIATION. 1992. Standard methods for the examination of water and wastewater, 18th ed. APHA.
- BENCALA, K. E., AND R. A. WALTERS. 1983. Simulation of solute transport in a mountain pool-and-riffle stream: A transient storage model. *Water Resour. Res.* **19**: 718–724.
- BOTT, T. L., AND OTHERS. 1985. Benthic community metabolism in four temperate stream systems: An inter-biome comparison and evaluation of the river continuum concept. *Hydrobiologia* **123**: 3–45.
- 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. *J. North Am. Benthol. Soc.* **12**: 223–235.
- DUFF, J. H., AND F. J. TRISKA. 1990. Denitrification in sediments from the hyporheic zone adjacent to a small forested stream. *Can. J. Fish. Aquat. Sci.* **47**: 1140–1147.
- FINDLAY, S. 1995. Importance of surface–subsurface exchange in stream ecosystems: The hyporheic zone. *Limnol. Oceanogr.* **40**: 159–164.
- , D. STRAYER, C. GOUMBALA, AND K. GOULD. 1993. Metabolism of streamwater dissolved organic carbon in the shallow hyporheic zone. *Limnol. Oceanogr.* **38**: 1493–1499.
- FORD, T. E., AND R. J. NAIMAN. 1989. Groundwater–surface water relationships in boreal forest watersheds: Dissolved organic carbon and inorganic nutrient dynamics. *Can. J. Fish. Aquat. Sci.* **46**: 41–49.
- GRIMM, N. B., AND S. G. FISHER. 1984. Exchange between inter-

- stitial and surface water: Implications for stream metabolism and nutrient cycling. *Hydrobiologia* **111**: 219–228.
- HART, D. R. 1995. Parameter estimation and stochastic interpretation of the transient storage model for solute transport in streams. *Water Resour. Res.* **31**: 323–328.
- HEDIN, L. O. 1990. Factors controlling sediment community respiration in woodland stream ecosystems. *Oikos* **57**: 94–107.
- HENDRICKS, S. P., AND D. S. WHITE. 1991. Physicochemical patterns within a hyporheic zone of a northern Michigan river, with comments on surface water patterns. *Can. J. Fish. Aquat. Sci.* **48**: 1645–1654.
- JONES, J. B., JR., S. G. FISHER, AND N. B. GRIMM. 1995a. Vertical hydrologic exchange and ecosystem metabolism in a Sonoran desert stream. *Ecology* **76**: 942–952.
- , ———, AND ———. 1995b. Nitrification in the hyporheic zone of a desert stream ecosystem. *J. North Am. Benthol. Soc.* **14**: 249–258.
- MARZOLF, E. R., P. J. MULHOLLAND, AND A. D. STEINMAN. 1994. Improvements to the diurnal upstream–downstream dissolved oxygen change technique for determining whole-stream metabolism in small streams. *Can. J. Fish. Aquat. Sci.* **51**: 1591–1599.
- MEYER, J. L., AND R. T. EDWARDS. 1990. Ecosystem metabolism and turnover of organic carbon along a blackwater river continuum. *Ecology* **71**: 668–677.
- MORRICE, J. A., H. M. VALETT, C. N. DAHM, AND M. E. CAMPANA. 1997. Alluvial characteristics, groundwater–surface water exchange and hydrologic retention in headwater streams. *Hydrol. Processes* **11**: 253–267.
- MULHOLLAND, P. J. 1992. Regulation of nutrient concentrations in a temperate forest stream: Roles of upland, riparian, and in-stream processes. *Limnol. Oceanogr.* **37**: 1512–1526.
- . 1997. Organic matter dynamics in the west fork of Walker Branch, Tennessee, USA. *J. North Am. Benthol. Soc.* **16**: 61–67.
- , A. D. STEINMAN, AND J. W. ELWOOD. 1990. Measurement of phosphorus uptake length in streams: Comparison of radiotracer and stable PO₄ releases. *Can. J. Fish. Aquat. Sci.* **47**: 2351–2357.
- MUNN, N. L., AND J. L. MEYER. 1988. Rapid flow through the sediments of a headwater stream in the southern Appalachians. *Freshwat. Biol.* **20**: 235–240.
- NEWBOLD, J. D., J. W. ELWOOD, R. V. O'NEILL, AND A. L. SHELDON. 1983. Phosphorus dynamics in a woodland stream ecosystem: A study of nutrient spiraling. *Ecology* **64**: 1249–1265.
- RAND, P. S., C. A. S. HALL, W. H. MCDOWELL, N. H. RINGLER, AND J. G. KENNEN. 1992. Factors limiting primary productivity in Lake Ontario tributaries receiving salmon migrations. *Can. J. Fish. Aquat. Sci.* **49**: 2377–2385.
- STREAM SOLUTE WORKSHOP. 1990. Concepts and methods for assessing solute dynamics in stream ecosystems. *J. North Am. Benthol. Soc.* **9**: 95–119.
- SWANK, W. T., AND J. B. WAIDE. 1988. Characterization of baseline precipitation and stream chemistry and nutrient budgets for control watersheds, p. 57–79. In W. T. Swank and D. A. Crossley, Jr. [eds.], *Forest hydrology and ecology at Coweeta*. Springer.
- TRISKA, F. J., J. H. DUFF, AND R. J. AVANZINO. 1993. Patterns of hydrological exchange and nutrient transformation in the hyporheic zone of a gravel-bottom stream: Examining terrestrial–aquatic linkages. *Freshwater Biol.* **29**: 259–274.
- VERVIER, P., J. GIBERT, P. MARMONIER, AND M.-J. DOLE-OLIVIER. 1992. A perspective on the permeability of the surface freshwater–groundwater ecotone. *J. North Am. Benthol. Soc.* **11**: 93–102.
- WEBSTER, J. R., D. J. D'ANGELO, AND G. T. PETERS. 1991. Nitrate and phosphate uptake in streams at Coweeta Hydrologic Laboratory. *Int. Ver. Theor. Angew. Limnol. Verh.* **24**: 1681–1686.
- , 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. *J. North Am. Benthol. Soc.* **9**: 120–140.

Received: 17 April 1996

Accepted: 7 September 1996

Amended: 2 January 1997