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Inter-biome comparison of factors controlling stream metabolism

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SUMMARY

1. We studied whole-ecosystem metabolism in eight streams from several biomes in North America to identify controls on the rate of stream metabolism over a large geographic range. The streams studied had climates ranging from tropical to cool-temperate and from humid to arid and were all relatively uninfluenced by human disturbances.
2. Rates of gross primary production (GPP), ecosystem respiration (R) and net ecosystem production (NEP) were determined using the open-system, two-station diurnal oxygen change method.
3. Three general patterns in metabolism were evident among streams: (1) relatively high GPP with positive NEP (i.e. net oxygen production) in early afternoon, (2) moderate primary production with a distinct peak in GPP during daylight but negative NEP at all times and (3) little or no evidence of GPP during daylight and a relatively constant and negative NEP over the entire day.
4. Gross primary production was most strongly correlated with photosynthetically active radiation (PAR). A multiple regression model that included log PAR and stream water soluble reactive phosphorus (SRP) concentration explained 90% of the variation in log GPP.
5. Ecosystem respiration was significantly correlated with SRP concentration and size of the transient storage zone and, together, these factors explained 73% of the variation in R. The rate of R was poorly correlated with the rate of GPP.
6. Net ecosystem production was significantly correlated only with PAR, with 53% of the variation in log NEP explained by log PAR. Only Sycamore Creek, a desert stream in Arizona, had positive NEP (GPP: $R > 1$), supporting the idea that streams are generally net sinks rather than net sources of organic matter.

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7. Our results suggest that light, phosphorus concentration and channel hydraulics are important controls on the rate of ecosystem metabolism in streams over very extensive geographic areas.

Keywords: inter-biome, metabolism, primary production, respiration, stream

Introduction

Primary production and respiration are important determinants of ecosystem biomass and trophic structure as well as important drivers of nutrient cycling and other ecosystem processes. Primary production represents the organic matter supply produced within the ecosystem whereas respiration provides an indication of total consumption of organic matter supplied by sources both within (autochthonous) and outside (allochthonous) the ecosystem. Broad comparison of the patterns of gross primary production (GPP) and respiration exhibited by ecosystems in different biomes is an important approach to the determination of fundamental controls on these processes (Cole, Lovett & Findlay, 1991; Schlesinger, 1997).

Streams present unique challenges for the measurement of GPP and total respiration (R). For example, the use of chambers is problematic because of difficulties in incorporating realistic flow regimes and habitat complexity (Bott, 1996). These problems are particularly challenging in small streams with high spatial heterogeneity in water velocity and sediment types. Open-system oxygen change methods were developed to measure the whole-ecosystem rate of GPP and respiration in running waters (Odum, 1956; Hoskin, 1959; Hall, 1972). The open-system methods circumvent many of the problems associated with high spatial variability but require good estimates of air–water oxygen exchange rates. These methods have been used primarily in streams with a relatively high rate of primary productivity, where diurnal changes in dissolved oxygen are relatively large. Recent refinements to the two-station diurnal oxygen change method by Marzolf, Mulholland & Steinman (1994) and Young & Huryn (1998) have improved the performance of the open-system approach in small, relatively unproductive streams.

This study examines broad-scale controls on the rate of stream metabolism across biomes using the comparative ecosystem approach. We report metabolism measurements made using the open-system method in streams in several different biomes of North America. These measurements were made as part of the lotic intersite nitrogen experiment (LINX), a study of nitrogen uptake and cycling using tracer ^{15}N additions (Peterson *et al*., 2001).

Study sites

We measured metabolism in eight first, second and third order streams across a number of different biomes of North America (Fig. 1) spanning a wide range of physical, chemical and biological conditions (Table 1). All of the streams were relatively undisturbed by current human activities (e.g. dissolved inorganic nitrogen (DIN) concentrations < 0.15 mg L^{-1}). The metabolism measurements were made on one date during the 6-week tracer ^{15}N addition in each stream. The period chosen for the LINX study in each stream was designed to represent one of relatively high rates of N uptake and cycling. Thus, our metabolism measurements presumably represent periods of relatively high biological activity. Further, the metabolism measurements were conducted on a date with generally clear to partly clear weather conditions and, consequently, probably represent values that are higher than the annual mean for most of the streams.

Methods

Whole-stream rates of GPP and R were determined using the upstream–downstream diurnal dissolved

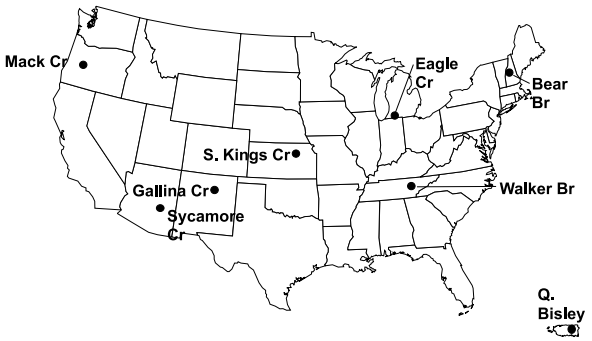

Fig. 1 Map showing location of streams used in study.

Table 1 List of streams and physical, chemical and biological characteristics at or near the time of metabolism measurements. Although Walker Branch is a forest stream with a closed riparian canopy, it was studied during a period of the year when leaves were absent from the deciduous riparian vegetation. Streams are listed from lowest to highest in latitude

Stream	ID	Date of measure-ment	Riparian canopy	Channel gradient (mm^{-1})	Wetted width (m)	Discharge ($L\ s^{-1}$)	Mean water velocity ($cm\ s^{-1}$)	Mean water depth (m)	PAR ($mol\ m^{-2}\ day^{-1}$)	Mean water temperature (°C)
Quebrada Bisley, Puerto Rico	QBPR	20 January 98	Closed	0.08	4.7	17	4.9	0.12	0.3	21.9
Sycamore Creek, Arizona	SCAZ	27 May 97	Open	0.003	5.8	31	13.8	0.04	50	23
Walker Branch, Tennessee	WBTN	10 April 97	Closed	0.035	3.1	7.8	5.8	0.04	12.6	11.9
Gallina Creek, New Mexico	GCNM	27 August 97	Semi-closed	0.17	1.3	3.1	5.7	0.07	6.8	12.6
South Kings Creek, Kansas	KCKS	22 April 98	Open	0.025	2.4	10.4	4.3	0.10	38	12.1
Eagle Creek, Michigan	ECMI	9 July 98	Closed	0.0025	5.0	198	24	0.19	18	25
Mack Creek, Oregon	MCOR	30 Jul 98	Semi-closed	0.09	5.1	60	9.9	0.11	3.8	13.8
Bear Brook, New Hamphsire	BBNH	27 June 97	Closed	0.13	2.1	2.3	2.2	0.13	2.2	13.8

Table 1 (*Continued*)

Stream	$A_s : A$ ratio, A_s (m^2)	SRP concentration ($\mu g\ L^{-1}$)	DIN concentration ($\mu g\ L^{-1}$)	Autotroph biomass (g AFDM m^{-2}), algal (%)	Detritus standing crop (g AFDM m^{-2}), leaves (%)
Quebrada Bisley, Puerto Rico	0.38, 0.09	14	132	1 (100)	38 (16)
Sycamore Creek, Arizona	0.59, 0.18	14	15	178 (100)	20 (0)
Walker Branch, Tennessee	0.17, 0.02	3	23	41 (3)	385 (20)
Gallina Creek, New Mexico	0.06, 0.004	8	9	42 (2)	120 (6)
South Kings Creek, Kansas	0.16, 0.04	3	5	10 (98)	215 (< 1)
Eagle Creek, Michigan	0.25, 0.22	3	33	0.7 (100)	394 (< 1)
Mack Creek, Oregon	0.29, 0.34	13	61	18 (4)	113 (< 1)
Bear Brook, New Hampshire	0.19, 0.04	4	59	11 (8)	53 (8)

oxygen change technique (Marzolf *et al.*, 1994) with the modification suggested by Young & Huryn (1998) for calculating the air–water exchange rate of oxygen. Measurements of dissolved oxygen concentration and water temperature (Orbisphere Model 2607 (Orbisphere Laboratories, Geneva, Switzerland) dissolved oxygen analyzer or YSI 600 (YSI, yellow Springs, OH, U.S.A.) water quality monitor) were made at 1-min intervals and averages recorded at 5-min intervals over a 24-h period at two stations in each stream. In one stream (Sycamore Creek, Arizona) dissolved oxygen concentration and water temperature were measured at hourly intervals by Winkler titration (APHA, 1992). The distance between stations ranged from 35 to 300 m and, depending on water velocity, water travel time ranged from 9 to 40 min among streams. Exchange of oxygen with the atmosphere was calculated based on the average oxygen saturation deficit or excess within the study reach and the reaeration rate determined from the decline in dissolved propane concentration during steady-state injection of propane and a conservative tracer (to account for dilution of propane caused by groundwater inflow) performed within 1 day of the oxygen measurements. The reaeration rate of propane was converted to oxygen using a factor of 1.39 (Rathbun *et al.*, 1978). The net rate of oxygen change as a result of metabolism (equivalent to net ecosystem production, NEP) was then determined at 5-min intervals from the change in mass flux of dissolved oxygen between stations corrected for air–water exchange of oxygen within the reach. The daily rate of R was calculated by summing the net oxygen change rate measured during the night and the daytime rate of R determined by extrapolating between the net oxygen change rate during the 1-h predawn and postdusk periods. The daily rate of GPP was determined by summing the differences between measured net oxygen change rate and the extrapolated value of R during the daylight period. All metabolism rates were converted to rates per unit area by dividing by the area of stream bottom between the two stations determined from the measurement of wetted channel width at 1-m intervals over each reach.

Groundwater inputs to the study reach, having a dissolved oxygen concentration lower than the stream water, contribute to errors in the measured rate of R in the whole-stream dissolved oxygen balance method (McCutchan, Lewis & Saunders, 1998). Measurable groundwater inputs occurred in five of the eight stream reaches studied (ranging from 3 to 17% of discharge), based on dilution of the injected conservative tracer. For these streams, we corrected R using measurements of dissolved oxygen concentration in groundwater seeps made at the same time of the year as the metabolism measurements. Differences in average dissolved oxygen concentration between surface water and groundwater seeps were multiplied by stream discharge rate to compute the groundwater seepage contribution to R in each stream. The largest correction was for South Kings Creek, Kansas, which amounted to a 33% reduction in R (from 3.6 to 2.4 $gO_2\ m^{-2}\ day^{-1}$); corrections to R for the other four streams with groundwater inputs were < 15%. The daily rate of NEP was calculated as the difference between the daily rate of GPP and groundwater-corrected R.

To permit a comparison of the reaeration rate determined experimentally using propane injections with that determined from physical characteristics of the stream channel, the reaeration rate was also estimated using the energy dissipation model (Tsivoglou & Neal, 1976) as follows:

$$k_{20} = K' \times (\Delta H/\Delta X) \times V \quad (1)$$

where k_{20} is the oxygen reaeration rate at 20 °C (day^{-1}), K' is an empirical constant equivalent to 28.3×10^3 s m^{-1} day^{-1} for streams with discharge values < 280 L s^{-1}, $\Delta H/\Delta X$ is the channel slope (m m^{-1}) and V is water velocity (m s^{-1}). The estimated rate was compared with that determined directly from propane injections and corrected to oxygen as described above and to 20 °C according to:

$$k_{20} = \frac{k_T}{1.0241^{T-20}} \quad (2)$$

where k_T is the reaeration rate measured at temperature T (Elmore & West, 1961). Although there are a number of physically based methods for estimating reaeration rate (Genereux & Hemond, 1992), we chose to compare our experimentally derived values with the energy dissipation method because the latter has been recommended for use in open-system methods for determining stream metabolism (APHA, 1992).

We measured a number of physical, chemical and biological characteristics in each stream to identify possible causal relationships with stream metabolism. We determined average stream discharge and water

velocity from conservative tracer additions performed within 1 day of the oxygen measurements. We monitored photosynthetically active radiation (PAR) within 20 cm of the stream water level at one streamside location in the experimental reach during the period of oxygen measurements using a quantum sensor (LiCor 190SA; LI-COR, Lincoln, NB, U.S.A.) and data logger (LiCor 1000). We characterized channel hydraulic conditions by applying a transient storage model to data from conservative tracer injections performed 2–3 weeks prior to the metabolism measurements under similar flow conditions in each stream (Stream Solute Workshop, 1990; Webster & Ehrman, 1996). We pumped a sodium chloride (NaCl) or sodium bromide (NaBr) solution into the stream until a steady-state was reached across a 100–300-m stream reach (2–6 h). We monitored either Cl^- concentration (Orion model 9417 (Orion Instruments, Beverley, MA, U.S.A.) B ion specific electrode), Br^- concentration (ion chromatography) or specific conductance (YSI Model 30) at intervals ranging from one to several minutes at the downstream station during and for several hours after the injection. We then fit a two-compartment transient storage zone model (Bencala & Walters, 1983; Hart, 1995) to the ion or specific conductance data to determine the rate of exchange between flowing and stationary water zones within the stream channel. From the model output, we computed the cross-sectional area of the stationary transient storage zone (A_s), the ratio of the cross-sectional areas of the transient storage zone and the surface flowing zone ($A_s : A$), the average travel distance of a water molecule prior to uptake into a transient storage zone (water uptake distance) and a hydraulic retention factor. The hydrologic retention factor is the ratio of the water residence time in the transient storage zone to the water uptake distance (Morrice *et al*., 1997).

We measured concentrations of ammonium, nitrate and soluble reactive phosphorus (SRP) on three to five dates within 3 weeks of the metabolism measurements using standard colorimetric methods (APHA, 1992). We calculated DIN as the sum of ammonium and nitrate concentration.

We measured the standing crop of detrital benthic organic matter (BOM) 2–3 weeks prior to the metabolism measurements according to methods described by Mulholland *et al*. (2000). We placed an open-ended metal cylinder (0.07 m^2) into the stream bottom at 10 locations and collected coarse particulate organic matter (CPOM, > 1 mm diameter) and separated it into leaves and wood. To estimate fine particulate organic matter (FPOM), we vigorously agitated the sediments within the cylinder to a depth of about 10 cm, pumped the slurry through a 1-mm screen into a container of known volume and subsampled the pumped slurry. Material was returned to the laboratory, dried (60 °C), weighed, combusted (500 °C) and reweighed to determine ash-free dry mass (AFDM) per unit area sampled. We calculated total benthic detritus as the sum of CPOM (leaves and wood) and FPOM.

We measured epilithon standing crop by collecting rocks randomly from five to six locations in the stream, scraping the rock surfaces and washing the material into a container with stream water. We then filtered this slurry (Whatman GFF; Whatman, Maidstone, U.K.), extracted the filters in 90% acetone overnight and analysed spectrophotometrically for chlorophyll *a*, using the method of Lorenzen (1967). We measured the area of each rock scraped to determine chlorophyll *a* per unit area. We estimated the biomass of the algal component of the epilithon as 100 × chlorophyll *a* mass per unit area of rock surface (Reynolds, 1984). We determined the areal coverage of filamentous algae and bryophytes by establishing transects across the stream every 5 m along the study reach and determining presence/absence every 10–20 cm across the transects. We estimated biomass by scraping or coring material from known areas of substratum with 100% coverage of filamentous algae or bryophytes and determining AFDM as the difference between dry mass (60 °C) and ash mass (500 °C). We calculated the biomass of filamentous algae and bryophytes as the product of average per cent cover and biomass per unit area in areas of 100% cover. We calculated total autotroph biomass as the sum of epilithon, filamentous algae and bryophyte biomass.

Statistical analysis

We analysed the data using bivariate correlation and stepwise multiple regression (SAS, 1985). Correlation analysis was used to identify relationships between single factors and metabolism rates, whereas multiple regression was used to determine whether predictive relationships for the rate of metabolism could be developed using more than one environmental factor.

Variation among values for several of the variables was considerable (> 20-fold) and data were normalized by log-transformation of these values. For stepwise multiple regression, we used $P = 0.05$ as the criterion for entry into the model, and an analysis of collinearity was performed for all variables entering the regression model.

Results

Diurnal profiles of metabolism rate varied considerably among streams. Three general patterns were evident. Streams with little canopy cover and high PAR, such as South Kings Creek, had a relatively high rate of GPP and a positive rate of NEP, peaking in the afternoon (Fig. 2a). Sites with somewhat greater shading and lower PAR, such as Walker Branch, Tennessee, in early spring, had an intermediate rate of GPP but NEP rate remained negative throughout the day (Fig. 2b). Heavily shaded sites with low PAR, such as Quebrada Bisley, Puerto Rico, showed no evidence of GPP and the rate of NEP was highly negative and somewhat variable with no clear diurnal pattern (Fig. 2c).

The daily rate of metabolism also varied considerably among streams. The GPP ranged from < 0.1–15 $gO_2\ m^{-2}\ day^{-1}$, with Quebrada Bisley having the lowest and Sycamore Creek having the highest rate (Fig. 3a). There was substantially lower variation in R than GPP, with values ranging from 2.4 $gO_2\ m^{-2}\ day^{-1}$ in South Kings Creek to 11 $gO_2\ m^{-2}\ day^{-1}$ in Mack Creek, Oregon (Fig. 3b). The NEP was negative and P : R ratios were < 1 for all streams except Sycamore Creek (Fig. 3c). Six of the eight streams were strongly heterotrophic, with P : R ratios < 0.25.

Relationships between the instantaneous rate of GPP and PAR were variable among streams (Fig. 4). For South Kings Creek and Walker Branch, light saturation of GPP appeared to occur at PAR values > 200–500 μmol $m^2\ s^{-1}$. However, there was no evidence of light saturation of GPP in Sycamore Creek. In the streams with the highest light levels and greatest algal biomass (Sycamore and South Kings Creeks), GPP was consistently higher in the afternoon than in the morning under the same PAR. This might reflect a delay in oxygen diffusion from within the algal mat to the overlying water in streams with thick algal mats. Relationships between GPP and PAR were more variable in Mack Creek, Gallina Creek and Bear Brook, although GPP appeared to become light-saturated at relatively low PAR in these streams.

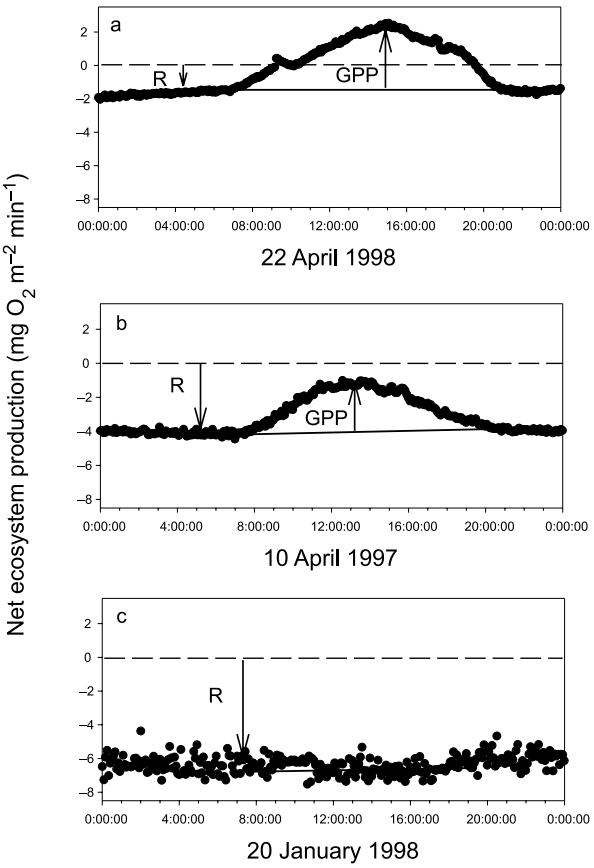

Fig. 2 Diurnal patterns of net ecosystem production (net oxygen change corrected for reaeration) for South Kings Creek, Kansas (a), Walker Branch, Tennessee (b), and Quebrada Bisley, Puerto Rico (c). The line extending from the predawn to postsunset period in each plot is the extrapolated respiration rate during daylight. Sycamore Creek, Arizona, also fit the pattern shown in (a). Other streams fitting the pattern in (b) were: Eagle Creek, Michigan, and Mack Creek, Oregon, and to a lesser extent, Gallina Creek, New Mexico. Bear Brook, New Hampshire, also fits the pattern in (c).

The daily rate of GPP was significantly correlated with daily PAR (Fig. 5a). The correlation between GPP and other physical and chemical characteristics (water temperature, discharge, water velocity, DIN concentration and SRP concentration) was not significant ($P > 0.05$). Gross primary production was marginally correlated with total algal biomass (epilithon plus filamentous algae, $r = 0.66$, $P = 0.077$). Multiple regression analysis indicated that 90% of the variation in log GPP could be explained by a model that included log PAR and SRP concentration (Table 2).

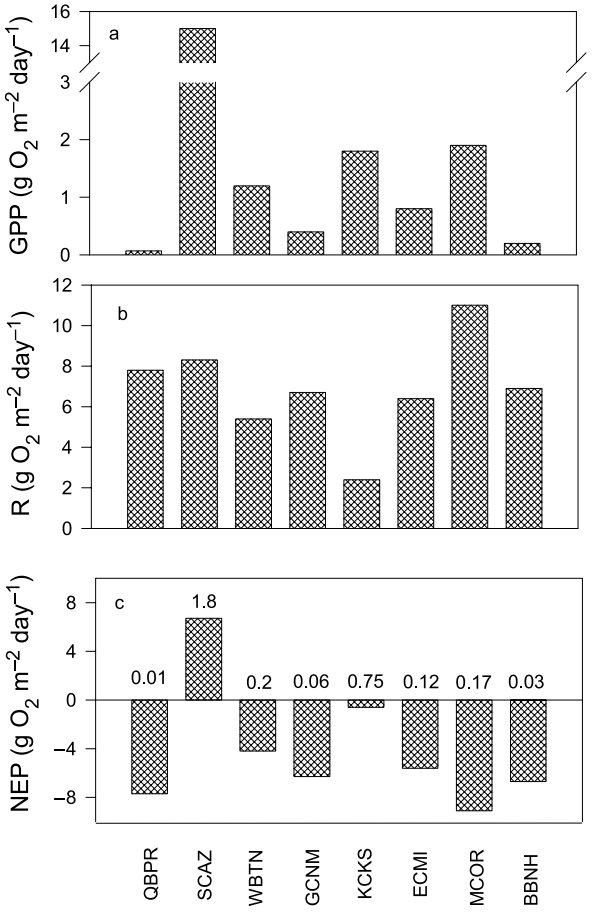

Fig. 3 Daily rates of gross primary productivity (GPP), total respiration (R) and net ecosystem production (NEP). Streams are listed using the codes in Table 1 and are ordered from lowest (left) to highest latitude. Values on bars in (c) are GPP : R ratios.

The daily rate of R was significantly correlated with SRP concentration and the size of the transient storage zone, A_s (Fig. 5b & c). Correlations between R and several other physical and chemical characteristics (water temperature, discharge, water velocity, DIN concentration, $A_s : A$ ratio, water uptake distance and hydraulic retention factor) were not significant ($P > 0.05$). In addition, R was not significantly correlated with total detritus standing crop ($P > 0.05$). Multiple regression analysis indicated that only SRP was a significant predictor of R using a model entry criterion of $P = 0.05$ (Table 2). Relaxation of the model entry criterion to $P = 0.15$ resulted in the addition of A_s as a significant predictor in the multiple regression analysis, with 73% of the variation in R explained by the model containing both variables (Table 2).

The daily rate of NEP was significantly correlated only with PAR (Fig. 5d). Multiple regression analysis indicated that 53% of the variation in log(NEP + 10) could be explained by a model that included log PAR, with no other variables significantly improving the model (Table 2).

The reaeration rate measured directly from the propane injections was generally higher than estimates from the energy dissipation method (Fig. 6a). The differences in the reaeration rate between methods appeared to be related to average water depth by an exponentially declining function (Fig. 6b). For average water depth > 6 cm, the reaeration rate measured using direct propane injections was < 25%, higher than that calculated using channel physical features for five of seven data points.

Discussion

Methodology

Estimates of whole-ecosystem rates of GPP and R in streams have been made for many years by measuring diurnal changes in dissolved oxygen in open systems (e.g. Odum, 1956; Hoskin, 1959; Hall, 1972; Meyer & Edwards, 1990; Young & Huryn, 1996; Uehlinger & Naegeli, 1998), although most previous studies have been of unshaded, relatively productive streams. Refinements to the two-station diurnal oxygen change method by Marzolf *et al.* (1994) and Young & Huryn (1998) have improved the performance of this open-system approach in small streams with relatively low rates of GPP. Most of the streams studied here were of this type.

Open-system methods offer some advantages over chamber methods for determining the rate of stream metabolism because they do not suffer from enclosure artefacts (e.g. nutrient and oxygen depletion), difficulties in transferring all components of the stream ecosystem in correct proportions (e.g. fine sediments, hyporheic sediments) and scaling problems (e.g. accounting for spatial variability) associated with chamber measurements. Because of these problems, open-system methods should result in higher estimates of whole-ecosystem metabolism, particularly respiration, than chamber studies. Comparison of our results with those from several previous studies seems to confirm this. Respiration rates determined from chamber measurements reported by Bott *et al.*

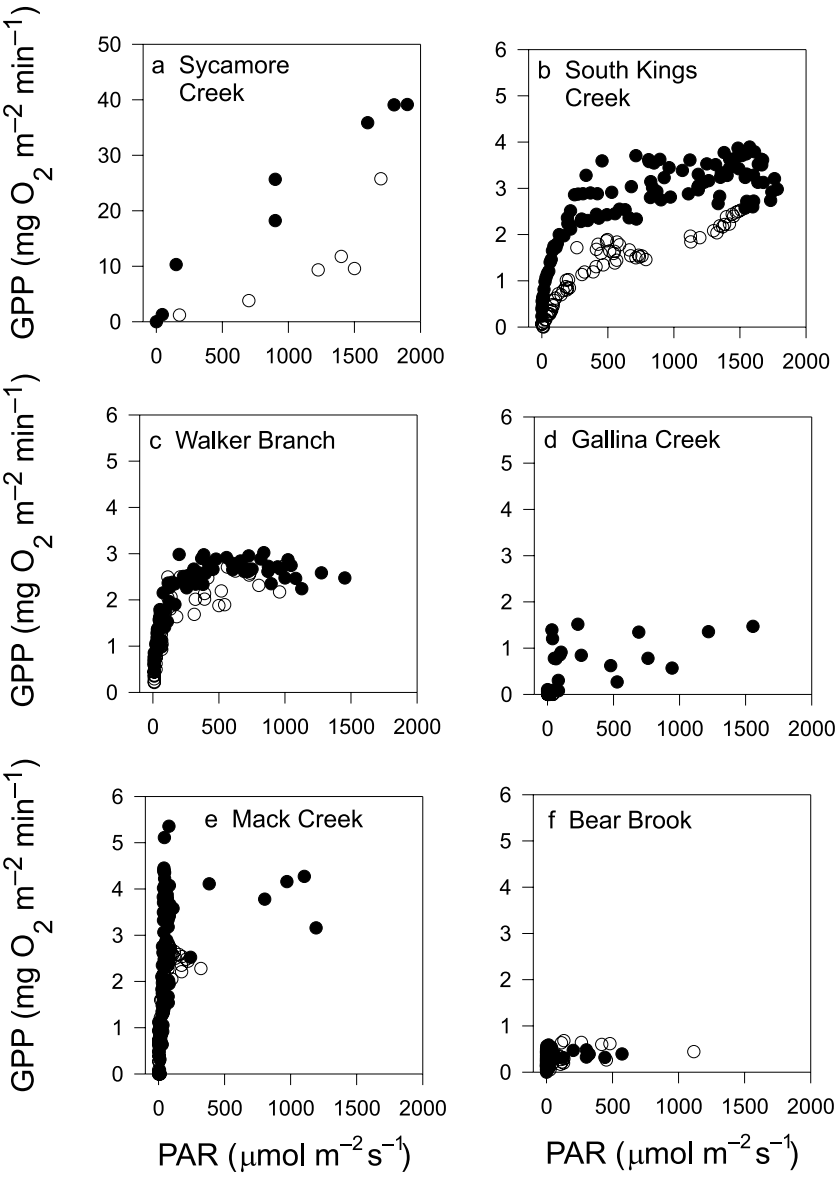

Fig. 4 Relationships between rate of gross primary productivity (GPP) and photosynthetically active radiation (PAR) for six of the eight streams. Eagle Creek is not shown because only daily PAR value was recorded, and Quebrada Bisley is not shown because GPP remained very low throughout the day. Open circles denote measurements made in the morning and closed circles measurements made in the afternoon.

(1985) for small streams in Pennsylvania, Michigan and Oregon (0.6–2.1 gO_2 m^{-2} day^{-1}) are considerably lower than respiration rates measured in our study (2.4–11 gO_2 m^{-2} day^{-1}). Respiration rates for streams in the Hubbard Brook Experimental Forest, New Hampshire, reported by Hedin (1990) for summer and autumn (0.1–0.8 gO_2 m^{-2} day^{-1}), were considerably lower than our value of R in summer for Bear Brook (6.7 gO_2 m^{-2} day^{-1}), also located in the Hubbard Brook Experimental Forest. In a previous study, in Walker Branch, Marzolf *et al.* (1994) compared open-system measurements with chamber measurements and found that chamber measurements underestimated GPP by about 20% and R by about 300%. Chamber measurements of R for Sycamore Creek (2–5 gO_2 m^{-2} day^{-1}) by Grimm (1987) also were lower than the respiration rate measured in our study for the same stream (8.3 gO_2 m^{-2} day^{-1}). Comparing chamber and open-system measurements on the same date in Sycamore Creek, Grimm & Fisher (1984) argued that chamber measurements were lower because they do not include the hyporheic component of respiration. Webster, Wallace & Benfield (1995) summarized stream metabolism measurements made in over 30 streams in the eastern U.S.A. and found that estimates of mean primary production and respiration rate were

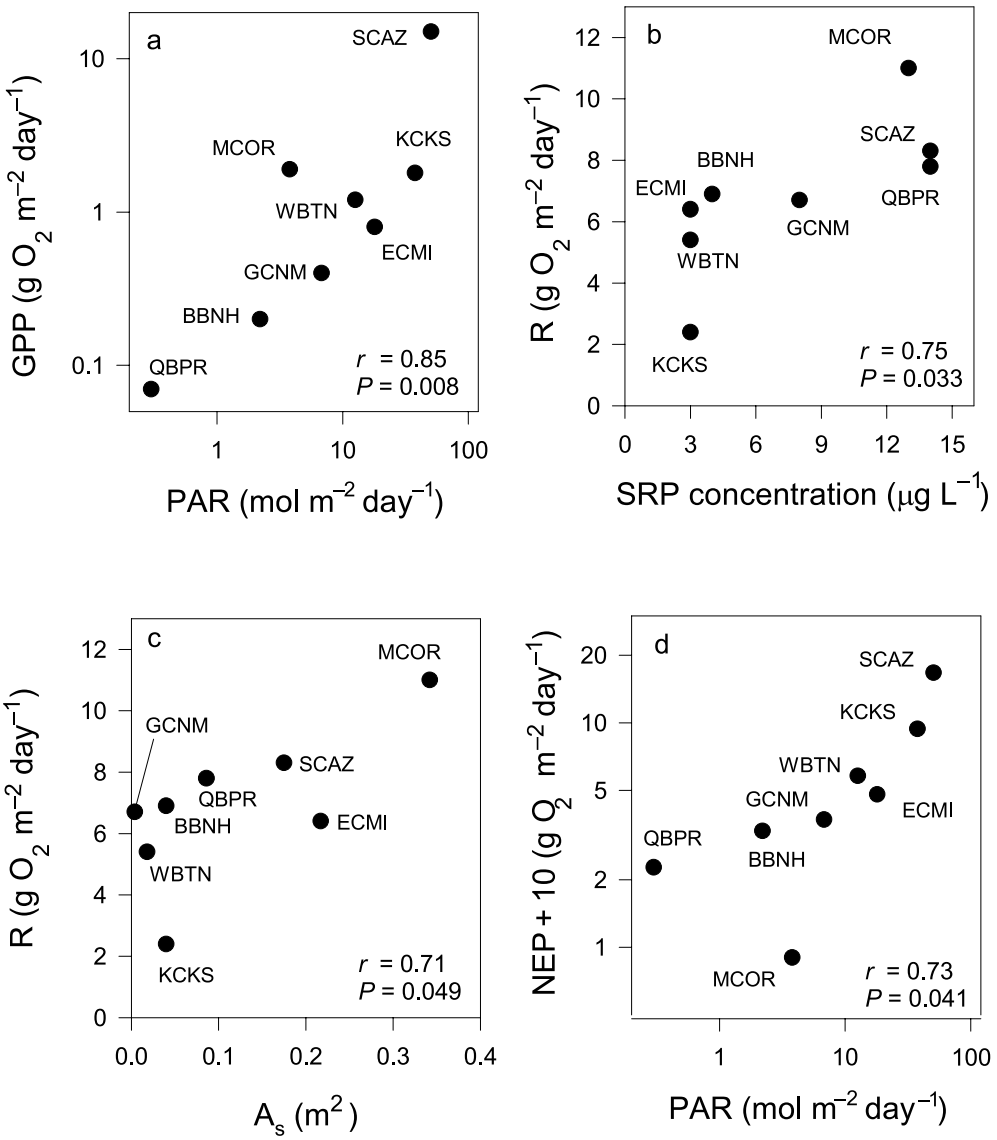

Fig. 5 Significant correlations between gross primary productivity (GPP), total respiration (R) and net ecosystem production (NEP) and various physical and chemical characteristics.

significantly higher in studies where open-system methods were used than those using chamber methods. As they have pointed out, however, their comparison was confounded by the fact that open-system methods were generally used where a higher rate of metabolism might be expected (larger, more nutrient-rich streams). Our range in respiration rates was similar to that reported for New Zealand streams (1–8 gO_2 m^{-2} day^{-1}) by Young & Huryn (1999) and that reported over a 2-year period for a Swiss river (1–13 gO_2 m^{-2} day^{-1}) by Uehlinger & Naegeli (1998), also using open-system oxygen change methods.

Limitations of the open-system method include the need for accurate measurements of dissolved oxygen concentration and saturation deficit as well as good estimates of reaeration rates. Accurate dissolved oxygen measurements require high-precision instruments, accurate field calibration and frequent checks on calibration. McCutchan *et al*. (1998), in a detailed analysis of uncertainties associated with open-system methods, demonstrated that estimates of R are subject to greater uncertainty than estimates of GPP, particularly in high gradient streams. Reaeration rates were > 100 day^{-1} in five of our eight

Table 2 Results of stepwise multiple regression analysis for rates of gross primary production (GPP), respiration (R) and net ecosystem production (NEP) ($n = 8$ for each regression)

Dependent variable	Independent variable	Parameter estimate (SE)	r^2	Prob > F
log GPP	Intercept	−1.737 (0.349)		0.0042
	log PAR	0.994 (0.147)	0.720	0.0011
	SRP	1.027 (0.338)	0.181	0.0288
	Full model		0.901	0.003
R	Intercept	4.104 (1.175)		0.013
	SRP	0.356 (0.129)	0.561	0.033
R ($P = 0.15$)	Intercept	3.775 (1.031)		0.0146
	SRP	0.255 (0.125)	0.560	0.0966
	A_s	9.572 (5.463)	0.167	0.1401
	Full model		0.73	0.0387
log(NEP + 10)	Intercept	0.298 (0.164)		0.1195
	log PAR	0.381 (0.150)	0.529	0.0437

Criterion for entry into the model was $P = 0.05$, except for R where results for a relaxed entry criterion ($P = 0.15$) are also given.

streams, a level that could result in uncertainties in metabolism rates of > 30% according to McCutchan *et al*. (1998).

Reaeration rate is often the most problematic component of open system methods. For direct measurements, using injections of volatile gas tracers, achieving complete mixing can be difficult, particularly in larger streams. Several predictive equations have been developed to estimate reaeration rate from more readily determined physical characteristics of streams (channel slope, water velocity and depth); however, these indirect methods for determining oxygen reaeration rate were generally developed for larger rivers with less turbulent flow. Genereux & Hemond (1992) compared a number of these indirect estimates with direct measurements of reaeration made using propane injections in Walker Branch and found poor agreement, with most of the indirect methods underestimating reaeration rate by 25% or more. Young & Huryn (1999) made a similar comparison between reaeration rates determined by propane injections and those estimated by indirect methods for streams in New Zealand and found that the indirect methods substantially underestimated reaeration rates, particularly for rates > 50 day^{-1} as determined by the direct propane method. Our comparison of direct and indirect measurements indicates that the underestimation of reaeration rate

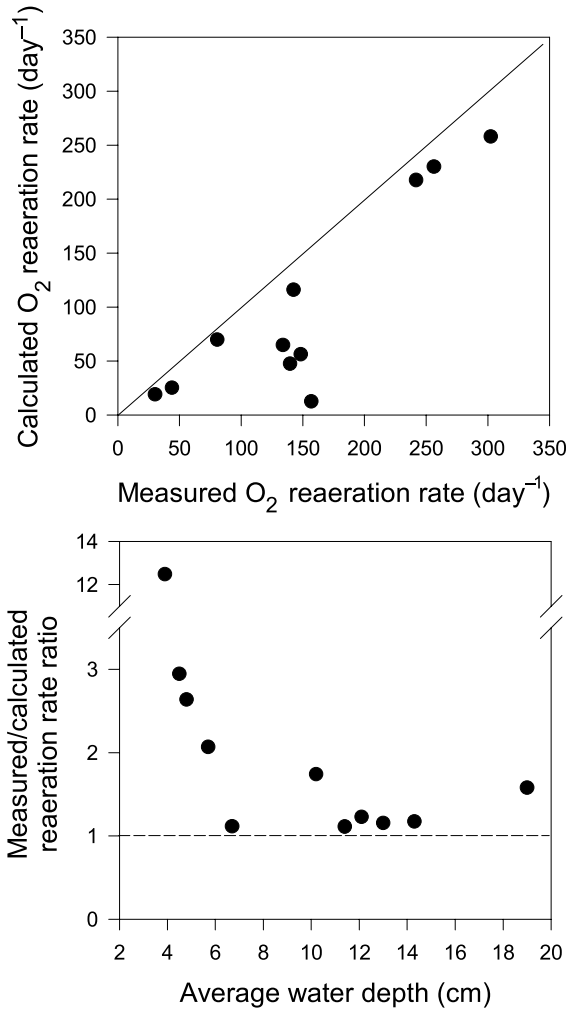

Fig. 6 Comparison of reaeration rates measured using propane injections with rates calculated using the energy dissipation model of Tsivoglou & Neal (1976) (a) and measured : calculated rate ratios as a function of average water depth (b). Included in the plot are data from measurements on three different dates in Walker Branch (Mulholland *et al*., 2000) and data from measurements in Upper Ball Creek, North Carolina.

by the energy dissipation method declines with an increase in average water depth. In streams with a water depth > 6 cm, the energy dissipation method may provide acceptable estimates of reaeration rate for use in open-channel measurements of stream metabolism in many cases.

Gross primary production rate

Our results indicate that light (PAR) is the dominant control on stream GPP. Other multi-stream comparison studies have also shown that available light, as

indicated by canopy cover, is a strong determinant of primary production rate (Naiman, 1983; Bott *et al*., 1985; Webster *et al*., 1995; Young & Huryn, 1999). In these studies light availability was primarily a function of stream size or land use, with larger streams or those in grazed pasture having more open canopies (higher light) and higher rates of primary productivity. The streams we studied were all relatively small (average width ranging from 0.8 to 5.8 m) and high PAR values were primarily the result of the lower density of riparian trees found in more arid climates (e.g. South Kings Creek and Sycamore Creek). In addition, PAR was moderately high in Walker Branch because the period of measurement was prior to spring leaf emergence in the surrounding deciduous forest. In a previous paper, Mulholland *et al*. (2000) showed that PAR values declined by about 85% between early April and the middle of May as the leaves emerged and shaded the stream. A 75% reduction in GPP and a sharp decline in the rate of nitrate uptake accompanied the reduction in PAR, demonstrating that the phenology of riparian vegetation is an important determinant of light availability and, consequently, of GPP. Our study did not address such seasonal changes in GPP in the other streams.

Although we observed a saturating effect of light on the instantaneous rate of GPP in most streams over the course of the day, we did not observe light saturation of daily GPP across streams. With the exception of Sycamore Creek, which showed no evidence of light saturation, our GPP–PAR relationships for individual streams were generally consistent with results from chamber studies of stream periphyton showing light saturation of photosynthesis at an irradiances above 200–400 μmol m^{-2} s^{-1} (Hill & Boston, 1991; Hill, Ryon & Schilling, 1995). Our results were also consistent with those of Young & Huryn (1996), who measured whole-system GPP using the open-system oxygen change method in New Zealand streams, and commonly found evidence of light saturation at PAR of 250–500 μmol m^{-2} s^{-1}. However, several other stream studies using the open-system oxygen change method have shown no evidence of saturation at high irradiance (Duffer & Dorris, 1966; Kelly, Hornberger & Cosby, 1974; Hornberger, Kelly & Fuller, 1976). Uehlinger, Konig & Reicher (2000) monitored GPP at 3-day intervals in a small, mostly unshaded Swiss river using the open-system method and reported that light saturation was restricted to the winter months only. It is not surprising that light saturation of GPP would be observed less frequently when open-system, whole-stream measurements of GPP are used than in chamber studies because the latter include only one component of the stream autotroph community. The lack of evidence for light saturation of daily rates of GPP observed across streams in our study also suggests long-term adaptation to high light levels. Thus, it would appear that, although individual communities at specific sites can sometimes become light saturated, patterns of whole-ecosystem GPP across biomes may rarely show light saturation effects because different types of autotroph communities develop and adapt to use the greater available light resource.

Nutrient concentration appeared to be a secondary determinant of GPP in our streams, as indicated by the inclusion of SRP concentration in the best-fit, multiple regression model. The streams in our study had relatively low SRP concentration (3–14 μg L^{-1}), potentially sufficient to limit primary production (Bothwell, 1989). A number of studies have demonstrated nutrient limitation of algal biomass accrual in oligotrophic streams (e.g. Elwood *et al*., 1981; Peterson *et al*., 1983; Grimm & Fisher, 1986; Hill & Knight, 1988; Rosemond, Mulholland & Elwood, 1993). The effect of SRP on GPP in our study was highly influenced by one stream (Sycamore Creek) with high values of GPP and SRP. When Sycamore Creek was removed from the multiple regression analysis, SRP no longer entered the model as a significant predictor. Because of the low number of streams in our study, the power of these tests is rather low and the importance of SRP as a predictor of GPP at broad spatial scales is unclear.

Respiration rate

Our results suggest that phosphorus concentrations and channel hydraulic conditions control the whole-stream rate of respiration over large geographic areas. The effect of nutrients on heterotrophic microbial processes in streams is relatively well documented and the rate of leaf decomposition increases with nutrient enrichment (Elwood *et al*., 1981; Meyer & Johnson, 1983; Suberkropp & Chauvet, 1995). The production and respiration rates of bacteria and fungi colonizing leaf detritus have also been shown to be

nutrient limited in some streams (Tank & Webster, 1998; Grattan & Suberkropp, 2001). Our study suggests that whole-ecosystem respiration rate in streams is also influenced by nutrients and that nutrient limitation may be an important large-scale control on heterotrophic metabolism in streams.

Channel hydraulic conditions, notably the extent of the hyporheic zone, have been shown to have strong effects on respiration rate in streams. Other studies in two of our streams, Sycamore Creek (Grimm & Fisher, 1984) and Gallina Creek, New Mexico (Fellows *et al*. 2001) have shown that ≥ 50% and about 85% of whole-ecosystem R, respectively, was the result of hyporheic respiration. Similarly, Naegeli & Uehlinger (1997) reported that hyporheic respiration contributed about 85% of the total ecosystem respiration rate in a gravel-bed river in Switzerland. In a comparative study of metabolism and phosphorus uptake in two small forested streams, with similar temperature, nutrient concentration and organic matter input but a 15-fold difference in the size of hyporheic zone, Mulholland *et al*. (1997) showed that the stream with the larger hyporheic zone had 2.5-fold higher R and P uptake rates. Our study indicates that the size of transient storage zones (as defined by A_s) was a secondary predictor of R, accounting for an additional 17% of the variation in R beyond that resulting from variation in SRP concentration. Although backwater zones along the margins of channels may have accounted for some of the transient storage zone areas determined in our streams, hyporheic sediments probably also accounted for a substantial portion of A_s, particularly in the streams with relatively large A_s. Presumably, the effect of A_s on R was the result of greater storage of organic matter and increased surface area for heterotrophic microbes in streams with larger A_s values. However, the correlation between benthic detritus standing crop and R in our study was not strong ($r = -0.41$, $P = 0.25$) and opposite in sign to that expected. In addition, Webster *et al*. (1995) reported that evidence for a positive effect of BOM storage on respiration rate in eastern U.S.A. streams is weak. Perhaps most techniques for measuring BOM standing crop (including ours) do not account for the deeper storage of material in streams with higher A_s.

The variation in R among our streams was not the result of variation in concurrent autochthonous production. The correlation between R and GPP was poor ($r^2 = 0.05$) and the fivefold variation in R was small compared with the 150-fold variation in GPP among streams. These results probably reflect the fact that stream respiration is fuelled by both autochthonous and allochthonous sources of organic matter contributed over extended periods of time.

We were surprised by the lack of evidence for an effect of water temperature on R in our study. In part, this may have been the result of the relatively small range in temperature (12–25 °C) compared with the 10–30-fold range in nutrient concentration and size of transient storage zones among streams (Table 1). Several other studies have suggested a modest effect of water temperature on respiration rate in streams. Bott *et al*. (1985) found that temperature was the best single predictor of R in a study of streams in four different biomes in the U.S.A., explaining 33% of the variation in R for all streams. Unlike our study, however, Bott *et al*. (1985) made measurements during all seasons in each stream, which may have increased the likelihood of showing an effect of temperature. Sinsabaugh (1997) found that mean annual temperature explained 38% of the variation in mean annual respiration rate in a comparative study of 22 streams. In an intensive study of metabolism in a Swiss river over an annual period, Uehlinger *et al*. (2000) found that R was significantly related to water temperature, although temperature explained only 22% of the variation in R. In our study, the effect of temperature on R may have been obscured by effects of differences in organic matter supply and nutrient concentration.

Net ecosystem production and P : R ratio

Respiration dominated whole-stream metabolism in most of our streams. Only Sycamore Creek, with high light (PAR of 50 mol m^{-2} day^{-1}), had a positive NEP (P : R ratio > 1). Even in South Kings Creek, with PAR of 38 mol m^{-2} day^{-1}, R exceeded GPP on the date we measured metabolism (P : R of 0.75), although earlier in the spring NEP may have been positive. We observed that the large biomass of periphyton appeared to be undergoing partial senescence when the metabolism measurements were made in this stream. The highly negative NEP values and very low P : R ratios for most of our streams emphasize the importance of allochthonous sources of carbon in fuelling heterotrophic metabolism. This

is not surprising because six of the eight streams (all those with low P : R ratios) were in forests with closed or semi-closed canopies. Even when light supply in the forested streams was moderately high, as for Walker Branch (12.6 mol m^{-2} day^{-1}) and Eagle Creek, Michigan (18 mol m^{-2} day^{-1}), NEP and P : R ratios were quite low, presumably because of respiration associated with large allochthonous organic matter inputs.

Our multiple regression results suggested that NEP was controlled primarily by factors influencing production (PAR), probably because rates of GPP varied considerably more than rates of R among our streams. Others have also shown the positive influence of light on NEP. Bott *et al*. (1985) reported that NEP increased with stream size as the canopy opened and light increased. They reported that light was the strongest predictor of NEP, although it accounted for only about 14% of the variation in NEP. Young & Huryn (1999) reported that NEP was positively correlated with incident light which, in turn, was related to land use. In their intensive, 2-year study of metabolism in a sixth order prealpine Swiss river, Uehlinger & Naegeli (1998) showed that hydrologic fluctuations strongly influenced the balance between GPP and R. Bed-moving spates resulted in a sharp decline in P : R ratio because they had greater negative effects on GPP than on R. Although we selected baseflow periods to perform our measurements, variation in the length of time since large storms among our streams may have added additional variation in rates of metabolism in our study.

The generality of our results is somewhat limited because of the low number of streams in the study and because measurements were made on only one date in each stream. As a consequence, the statistical power of tests for the effect of various factors on rates of metabolism was generally low. In each stream our results are a snapshot in time, representative of a period of relatively high metabolism for most of the streams. However, there have been few studies that have examined stream metabolism across large geographic areas using the same method. Our study included streams in climates ranging from tropical to cool temperate and from humid to arid. Further, our measurements are of metabolism of entire stream ecosystems as we used the open-system, two-station diurnal oxygen change method. Thus, our findings provide a large-scale and synthetic picture of the factors that control metabolism in streams, but they must await further test across a larger number of streams and seasons.

In conclusion, we show that inter-biome variation in the whole-ecosystem rate of GPP, respiration and NEP in streams is related primarily to differences in the availability of light and phosphorus. Variation in the rate of ecosystem respiration also appears to be related to differences in channel hydraulic characteristics, such as the size of the transient storage zone. While the effect of light on primary production in streams is relatively well documented, our results suggest that nutrient limitation and channel hydraulics may also be important in the control of stream ecosystem metabolism across large geographic areas.

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