

# Multiple Scales of Temporal Variability in Ecosystem Metabolism Rates: Results from 2 Years of Continuous Monitoring in a Forested Headwater Stream

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## ABSTRACT

Headwater streams are key sites of nutrient and organic matter processing and retention, but little is known about temporal variability in gross primary production (GPP) and ecosystem respiration (ER) rates as a result of the short duration of most metabolism measurements in lotic ecosystems. We examined temporal variability and controls on ecosystem metabolism by measuring daily rates continuously for 2 years in Walker Branch, a first-order deciduous forest stream. Four important scales of temporal variability in ecosystem metabolism rates were identified: (1) seasonal, (2) day-to-day, (3) episodic (storm-related), and (4) inter-annual. Seasonal patterns were largely controlled by the leaf phenology and productivity of the deciduous riparian forest. Walker Branch was strongly net heterotrophic throughout the year with the exception of the open-canopy spring when GPP and ER rates were co-equal. Day-to-day variability in weather conditions influenced light reaching the streambed, resulting in high day-to-day variability in GPP particularly during spring (daily light levels explained 84% of the variance in daily GPP in April). Episodic storms depressed GPP

for several days in spring, but increased GPP in autumn by removing leaves shading the streambed. Storms depressed ER initially, but then stimulated ER to 2–3 times pre-storm levels for several days. Walker Branch was strongly net heterotrophic in both years of the study, with annual GPP being similar (488 and 519 g O<sub>2</sub> m<sup>-2</sup> y<sup>-1</sup> or 183 and 195 g C m<sup>-2</sup> y<sup>-1</sup>) but annual ER being higher in 2004 than 2005 (–1,645 vs. –1,292 g O<sub>2</sub> m<sup>-2</sup> y<sup>-1</sup> or –617 and –485 g C m<sup>-2</sup> y<sup>-1</sup>). Inter-annual variability in ecosystem metabolism (assessed by comparing 2004 and 2005 rates with previous measurements) was the result of the storm frequency and timing and the size of the spring macroalgal bloom. Changes in local climate can have substantial impacts on stream ecosystem metabolism rates and ultimately influence the carbon source and sink properties of these important ecosystems.

**Key words:** primary production; ecosystem respiration; seasonal patterns; inter-annual variability; storms; disturbance; light; periphyton; bryophytes; macroalgae; *Oedogonium*; leaf litter; reaeration.

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## INTRODUCTION

Headwater streams are important sites of nutrient and organic matter processing and retention, often altering their delivery to downstream ecosystems (Alexander and others 2000; Peterson and others 2001). Stream ecosystem metabolism constitutes the processes controlling nutrient cycling and organic matter processing and thus provides critical information defining the role of stream ecosystems in nutrient and organic matter dynamics across the landscape. The number of studies on whole-ecosystem metabolism rates in streams (for example, Mulholland and others 1997a; Young and Huryn 1999; Fellows and others 2001; Mulholland and others 2001; Hall and Tank 2003; Ortiz-Zayas and others 2005; Bott and others 2006) has increased in recent years as a result of recent refinements (Marzolf and others 1994; Young and Huryn 1998; Hall and Tank 2005) in open-system oxygen change methods to measure whole-ecosystem rates of gross primary production (GPP) and total ecosystem respiration (ER) in flowing waters (Odum 1956; Bott 1996).

Several abiotic and biotic factors have been shown to be important factors controlling ecosystem metabolism rates in stream ecosystems. Autotrophs require light energy for photosynthesis and nutrients for growth. As a result, GPP is often limited by either light availability (Steinman 1992; Hill and others 1995, 2001; Mulholland and others 2001), nutrients (Elwood and others 1981; Peterson and others 1985; Grimm and Fisher 1986; Hill and Knight 1988; Rosemond and others 1993; Flecker and others 2002), grazing pressure (Hill and others 1992; Rosemond and others 1993), or a combination of the three (Rosemond and others 2000). Both autotrophs and heterotrophs respire and require nutrients for growth with heterotrophs having an additional requirement of an external carbon source. ER rates should therefore be influenced by the availability of both organic matter (Petersen and Cummins 1974; Webster and Benfield 1986) and nutrients (Elwood and others 1981; Tank and Webster 1998; Grattan and Suberkropp 2001; Mulholland and others 2001) as well as being regulated by temperature (Bott and others 1985; Sinsabaugh 1997; Uehlinger and others 2000).

Unpredictable episodic disturbances, such as storms, also affect stream ecosystems. Previous studies have shown that stream periphyton communities can suffer drastic declines in biomass and compositional changes following storms (Grimm and Fisher 1989; Uehlinger 1991). Flash flooding can strongly affect primary production and respi-

ration rates (Fisher and others 1982). Bed-moving spates in large rivers in Switzerland (Uehlinger and Naegeli 1998; Uehlinger 2000, 2006) depressed both GPP and ER, but because GPP was disproportionately reduced, ecosystem metabolism was shifted towards heterotrophy. Currently, we lack a similar understanding of the response of GPP and ER to storms in headwater streams.

A major constraint on our understanding of controls on GPP and ER in stream ecosystems is the low frequency at which metabolism measurements are made. In most studies, metabolism estimates consist of either spot (one to a few days) or seasonal (one to a few days with intervals between measurements ranging from weeks to months) measurements. These infrequent measurements are usually made at baseflow and often target optimal conditions (for example, sunny days) during periods that are thought to be key times of the year. It is difficult to assess how representative these infrequent GPP and ER measurements are of temporal dynamics in stream ecosystem metabolism. In addition, other potentially important scales of temporal variability (for example, day-to-day, episodic, inter-annual) and their controls are undetectable from spot or limited seasonal measurements.

In recent years, continuous measurements of carbon fluxes have begun to be made in diverse ecosystems. For example, an extensive network of sites measuring net ecosystem exchange using eddy covariance approaches have been set up in terrestrial ecosystems across the globe (for example, Wofsy and others 1993; Running and others 1999; Baldocchi and others 2001). Continuous measurements of ecosystem metabolism have been made over several summer growing seasons in temperate lakes (Cole and others 2000, 2002, 2006). Similarly, continuous ecosystem metabolism measurements have been made over multiple years in several large Swiss Rivers (Uehlinger and Naegeli 1998; Uehlinger and others 2000; Uehlinger 2006). To date, no such measurements have been made in headwater streams. Continuous stream ecosystem metabolism measurements made over long time scales will provide greater confidence in observed temporal patterns by minimizing the effect of sampling errors that can potentially hinder spot measurements. In addition, continuous measurements of stream metabolism rates over annual cycles allow for an assessment of temporal scales of variation in carbon source and sink properties, factors that control metabolism, and the resistance and resilience of GPP and ER to storms. Understanding the factors that control ecosystem

metabolism rates at multiple temporal scales will allow for better predictions of how the role of headwater streams in nutrient and organic matter dynamics may change in response to changes in land use and climate regimes.

In this study, we examined temporal patterns and controls on ecosystem metabolism rates in a well-studied forested headwater stream, the West Fork of Walker Branch, in eastern Tennessee. We report 2 years of continuous daily ecosystem metabolism measurements made using an open-system, single station diel oxygen approach. Using this approach, we were able to identify and examine four important scales of temporal variability in GPP and ER rates in Walker Branch: (1) seasonal, (2) day-to-day, (3) episodic (storm-related), and (4) inter-annual.

## Study Site

This study was conducted in the West Fork of Walker Branch (hereafter referred to as Walker Branch), a first order, forested stream in the Ridge and Valley province of eastern Tennessee. It drains a 38.4 ha catchment on the U.S. Department of Energy's Oak Ridge National Environmental Research Park (35°58' N, 84°17' W). The catchment is underlain by siliceous dolomite that has weathered to develop deep soils abundant in chert (McMaster 1963). The Walker Branch watershed is a second-growth deciduous forest dominated by chestnut oak (*Quercus prinus*), tulip poplar (*Liriodendron tulipifera*), red maple (*Acer rubrum*), white oak (*Q. alba*), and American beech (*Fagus granifolia*) (Johnson and Van Hook 1989). The climate is typical of the humid Appalachian region of the southeastern United States, with a mean annual temperature of approximately 14.5°C and mean annual precipitation of approximately 135 cm (distributed relatively evenly throughout the year, Mulholland 2004).

Stream discharge (monitored at a 120° v-notch weir with 15-min stage recordings) is highly seasonal with higher baseflows and more frequent spates during winter and early spring when evapotranspiration rates are low (Mulholland 2004). Walker Branch can be classified as either a mesic (Poff and Ward 1989) or stable (Poff 1996) groundwater stream. Stream water chemistry is dominated by calcium, magnesium, and bicarbonate, and the pH is moderately basic (usually 8.0–8.3) (Mulholland 1992, 2004). The channel gradient is relatively gentle ( $\sim 0.035 \text{ m m}^{-1}$ ). The streambed in the study reach is composed of bed-

rock outcrops, gravel and cobble in a series of shallow (<10 cm deep) riffle-run sections.

Periphyton growth is light-limited for most of the year, but can be limited by both nitrogen and phosphorus during spring when light levels are highest (Rosemond and others 2000). Periphyton photosynthesis rates increase during the open-canopy spring period (Hill and others 2001), but biomass is maintained at low levels by intense grazing (Rosemond and others 2000; Hill and others 2001) primarily by the snail *Elimia clavaeformis*, which accounts for up to 95% of total invertebrate biomass (Newbold and others 1983). Bryophytes are common year-round with the leafy liverwort, *Porella pinnata*, being the most abundant. Despite their patchy distribution (5–20% of the streambed area), they accounted for 20–50% of Walker Branch primary production during 1990–1991 (Steinman and Boston 1993). Earlier studies have noted the occurrence of the macroscopic red alga *Batrachospermum* from late winter to spring but its abundance has not been quantified (Hill and others 2001). In recent years, the filamentous green algae *Oedogonium* has also been observed during the open-canopy spring period (Mulholland and others 2006).

## METHODS

### Dissolved O<sub>2</sub> and Temperature

Gross primary production (GPP) and ecosystem respiration (ER) rates were determined using an open-system, single station diel approach (Odum 1956; Bott 1996). Diel dissolved O<sub>2</sub> (DO) and temperature readings were collected using YSI Model 6920 sondes equipped with YSI model 6562 DO probes. DO and water temperature were continuously recorded at 15 minute intervals from 28 January 2004 to 1 February 2006. YSI sondes were deployed at the same well-mixed location as the downstream location ( $\sim 120 \text{ m}$  upstream from the weir) of the reach used in previous metabolism studies in Walker Branch (for example, Marzolf and others 1994; Mulholland and others 1997a, 2000, 2006; Hill and others 2001). We calibrated sondes in water-saturated air every 7–14 days. The calibration DO data were corrected for barometric pressure recorded during calibration and consecutive calibrations were used to detect instrument drift over deployment. When changing sondes, we overlapped deployment for at least 24 h to inter-calibrate between sondes. Percent saturation was determined from the measured DO concentration,

water temperature, and barometric pressure. Instantaneous barometric pressure readings were measured with a Vaisala Model PTB101B analog barometer and recorded every 15 min with a Campbell Scientific Model CR10WP datalogger at a streamside site located approximately 10 m upstream from the DO sonde. During periods when on-site barometric pressure readings were not available, we obtained readings from a NOAA monitoring site (unpublished data of Tilden Myers, NOAA) located in the Walker Branch watershed and applied an elevation-based correction (based on >8,000 comparisons between the two sites) to estimate the barometric pressure at our study reach.

### Relationships Between Stream Discharge and O<sub>2</sub> Reaeration Coefficient, Stream Width, and Depth

Reaeration coefficients ( $k_{O_2}$ ) were determined for a 62-m study reach immediately upstream from the sonde deployment site using simultaneous, continuous injections of propane gas (volatile tracer) and a concentrated NaCl solution (conservative tracer) as in Genereux and Hemond (1992). Background conductivity was recorded at the upstream and downstream ends of the study reach before the injection using a YSI Model 55 Conductivity Meter. During the injection, a concentrated solution of NaCl was introduced to surface water at a point of natural constriction located approximately 15 m above the upstream station of the study reach by a battery-powered fluid metering pump (Fluid Metering Inc., Syosset, New York) over a 1–2 h period. Simultaneously, propane gas was injected at a constant rate through a 30-cm × 6-cm aeration stone. Specific conductance was monitored at 30 s intervals at two stations downstream from the injection site. The injection continued until specific conductance had clearly reached plateau (specific conductance did not increase more than 0.1  $\mu\text{s cm}^{-1}$  over 5 min). The difference in time between the occurrence of the maximum rate of change in conductivity (that is, maximum slope) at the upstream and downstream stations was the average water travel time. Stream velocity was calculated as the reach length (62 m) divided by the water travel time.

Propane reaeration coefficients were determined from steady-state propane concentrations corrected for dilution using conductivity values. Six replicate water samples were collected for propane analysis at both the upstream and downstream stations. A 10-ml plastic syringe was rinsed once with stream

water to remove air bubbles, and refilled with 6 ml of water. The sample was then injected into a 7-ml pre-evacuated vacutainer. Air-equilibrated head-space gas from each vacutainer was analyzed on a Hewlett Packard Model 5890 Series II gas chromatograph equipped with an Agilent HP-PLOT AI203 column and a flame ionization detector. The propane reaeration coefficient was determined from the equation:  $k_{\text{propane}} = a_{\text{propane}} \times u$ , where  $a_{\text{propane}}$  is calculated as the difference in the natural log of upstream and downstream propane concentrations divided by the reach length and  $u$  is stream velocity ( $\text{m min}^{-1}$ ). The O<sub>2</sub> reaeration coefficient,  $k_{O_2}$ , was calculated from  $k_{\text{propane}}$  using the standard conversion  $k_{O_2} = k_{\text{propane}} \times 1.39$  (Rathbun and others 1978). Stream width was determined for each injection as the average of wetted-width measurements taken every 1 m along the study reach. Stream discharge rate at each station ( $Q_i$ ) was determined from the increase in streamwater specific conductance during the injection using the following equation:

$$Q_i = \frac{Q_{\text{pump}} \times \text{Cond}_{\text{inj}}}{(\text{Cond}_i - \text{Cond}_b)} \quad (1)$$

where  $Q_{\text{pump}}$  is the injection rate of the NaCl solution,  $\text{Cond}_{\text{inj}}$ ,  $\text{Cond}_i$ , and  $\text{Cond}_b$  represent the specific conductance of the injection solution, the specific conductance at station  $i$  during the injection, and the background specific conductance at station  $i$  prior to the injection, respectively. Mean depth ( $Z_{\text{mean}}$ , m) was calculated from  $Q$ , velocity ( $u$ ), and average stream width ( $w$ ) using the equation  $Z_{\text{mean}} = Q / (1,000 \times u \times w)$ .

We carried out a total of 31 NaCl/propane injections in Walker Branch during the period when leaves were not covering the stream surface (January through mid-September). The injections were performed when discharges (as measured at the weir) ranged from 5 to 57  $\text{l s}^{-1}$  (note: only 6 days had greater daily mean discharge during the study). During many years, the stream surface of Walker Branch becomes covered in leaves for a variable but often extended period during late autumn (extending until the first large storm). Reaeration coefficients are expected to be lower under these conditions than during non-leaf cover conditions under a similar discharge regime because leaves provide a direct diffusive barrier to air–water gas exchange and may also dampen surface turbulence thus slowing the gas exchange rate. To determine the magnitude of the effect that leaf cover has on  $k_{O_2}$ , we conducted 5 NaCl/propane



injections in November and December 2005 when leaves covered the stream surface (~75–80% percent areal coverage: B. J. Roberts, unpublished data).

The calculation of continuous volumetric rates of GPP and ER ( $\text{g O}_2 \text{ m}^{-3} \text{ day}^{-1}$ ) requires estimates of  $k_{\text{O}_2}$  for each 15 min interval we measure DO and temperature. We used the results from the dual injection experiments described above to develop a relationship between stream discharge and  $k_{\text{O}_2}$  in Walker Branch. We have also developed similar relationships between discharge and both stream depth and stream width enabling us to calculate continuous rates of GPP and ER in both areal units ( $\text{g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ ) and per unit of stream length ( $\text{g O}_2 \text{ m}^{-1} \text{ day}^{-1}$ ).

### Metabolism Rate Calculations

Daily gross primary production (GPP) and ecosystem respiration (ER) rates were calculated from the diel DO and temperature data as described by Houser and others (2005). This method is similar to the two-station method of Marzolf and others (1994), with the corrections presented in Young and Huryn (1998), except that the rate of change in DO concentration was calculated as the difference between consecutive 15-min readings instead of the difference between readings at upstream and downstream stations. Ecosystem metabolism rates were determined from the rate of change in DO concentration over 15-min intervals using the equation

$$\Delta_{\text{DO}} = \text{GPP} - \text{ER} + \text{E} \quad (2)$$

where  $\Delta_{\text{DO}}$  is the change in DO concentration ( $\text{g O}_2 \text{ m}^{-3}$ ), GPP is volumetric gross primary production ( $\text{g O}_2 \text{ m}^{-3}$ ), ER is volumetric ecosystem respiration ( $\text{g O}_2 \text{ m}^{-3}$ ), and E is net exchange of  $\text{O}_2$  with the atmosphere ( $\text{g O}_2 \text{ m}^{-3}$ ) between consecutive measurements. The net exchange of  $\text{O}_2$  with the atmosphere is the product of the  $\text{O}_2$  reaeration coefficient ( $k_{\text{O}_2}$ ) and the average DO deficit (DO concentration at 100% saturation minus the DO concentration in stream water) over the measurement interval.

The net metabolism flux for a given measurement interval is equal to  $\Delta_{\text{DO}} - \text{E}$ . During the night, GPP is zero, so the net metabolism flux is equal to ER. During the day, ER was determined by interpolating ER averaged over the hour before dawn and the first hour after dusk (as in Houser and others 2005). GPP for each daytime interval was the difference between the net metabolism flux and interpolated ER. Daily volumetric GPP and ER rates ( $\text{g O}_2 \text{ m}^{-3} \text{ day}^{-1}$ )

were calculated as the sum of the 15 min rates over each 24 h period (from 0000 h to 2400 h). These volumetric rates were converted to areal units ( $\text{g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ ) by multiplying by the mean water depth of the stream reach determined from discharge–mean depth relationships. We also calculated GPP and ER rates per meter of stream length ( $\text{g O}_2 \text{ m}^{-1} \text{ day}^{-1}$ ) by multiplying by average stream width determined from discharge–width relationships. Rates per meter stream length may be a more appropriate metric to account for the expansion of stream surface area during higher flow events. Daily net ecosystem production (NEP) rates ( $=\text{GPP}-\text{ER}$ ) were calculated as the sum of the 15 min net metabolism fluxes over each 24 h period.

### Comparison of Daily Versus Less Frequent Metabolism Measurements

We examined the potential inaccuracies of making less frequent spot measurements of ecosystem metabolism by calculating annual GPP and ER rates from quarterly and monthly measurements and comparing those rates to the daily rates calculated as described above. Because it is unlikely that measurements would be made completely at random within each quarter or month, we assumed that measurements would be made at consistent time intervals. For example, monthly measurements were assumed to be made on the same day of the month in each month (for example, 1 January, 1 February, and so on). Similarly, quarterly measurements were assumed to be made on same day of each quarter (for example, 1 January, 1 April, 1 July, 1 October). We then calculated annual GPP and ER rates for each of the possible monthly ( $n = 28$ ) and quarterly ( $n = 88$ ) sampling possibilities for both 2004 and 2005 and compared those rates to the annual fluxes calculated from daily measurements.

### Light

Photosynthetically active radiation (PAR) was monitored with a quantum sensor (LiCor 190SA) and data logger (LiCor 1000) at stream level [quantum sensor attached to a fallen tree that spanned Walker Branch within the study reach ~1 m above the stream surface (Hill and others (2001))]. Instantaneous PAR was measured by the quantum sensor every 5 s, averaged, and recorded by the datalogger every 15 min. Daily PAR was determined by integrating the 15 min readings for each day. PAR data above the forest canopy were obtained from the Walker Branch Throughfall Displacement Experiment (TDE) Data Archive (<http://www.tde.ornl.gov/tdedata.html>).

## Nutrients

Streamwater samples were collected for chemical analyses weekly at a station 60 m upstream from the weir (~60 m below the study reach) as described in Mulholland (2004). Water samples were collected in well-rinsed polyethylene bottles between 0900 and 1200 on Tuesdays, immediately returned to the laboratory, and filtered (0.4- $\mu\text{m}$  pore size Nucleopore polycarbonate filters) within 3 h of collection. Filtered water was kept frozen until chemical analyses could be performed. Concentrations of soluble reactive phosphorus (SRP) were determined by the ascorbic acid–molybdenum blue method (APHA 1992) using a 10-cm spectrophotometer cell to achieve low detection limits. Concentrations of nitrite ( $\text{NO}_2^-$ ) + nitrate ( $\text{NO}_3^-$ ) were determined by Cu–Cd reduction followed by azo dye colorimetry (APHA 1992) and ammonium ( $\text{NH}_4^+$ ) by phenate colorimetry (APHA 1992), both using an autoanalyzer (Bran Lubbe Model AA3). Dissolved inorganic nitrogen (DIN) concentration is the sum of  $\text{NO}_2^- + \text{NO}_3^-$  and  $\text{NH}_4^+$ .

## Periphyton Chlorophyll *a* Analysis

Walker Branch periphyton was sampled monthly for chlorophyll *a* analysis. Three composite samples were taken each month at three sites along a 30 m stretch of Walker Branch that included the downstream end of the metabolism reach. Each sample comprised four separate brushings of bedrock periphyton. The brushings were made by pressing a 2.1-cm diameter Plexiglas tube fitted with a rubber ring onto the bedrock, removing most of the water within the tube (the top end of the 10-cm-long tube extended above the water surface) with a basting syringe, and dislodging the enclosed epilithic periphyton by inserting a cylindrical wire brush within the tube and rotating it against the rock. The resulting mixture of periphyton and water was removed from the tube with the basting syringe and deposited into a glass jar. The four brushings from each site were placed in the same jar; all three jars were returned to the laboratory, where aliquots were filtered onto Whatman GF/F glass fiber (0.7  $\mu\text{m}$  nominal cut-off) filters. Filters were kept in a  $-85^\circ\text{C}$  freezer until analysis. The filters were then placed in glass tubes with 10 ml of 90% ethanol, sonicated with a probe sonicator for 30 s at 50 W, and allowed to extract overnight in the dark at  $4^\circ\text{C}$ . The tubes were centrifuged the next day and, after centrifugation, aliquots of the clarified extract were

analyzed spectrophotometrically for chlorophyll *a* concentration (Sartory and Grobbelaar 1984).

## Bryophyte and Macroalgae Abundance

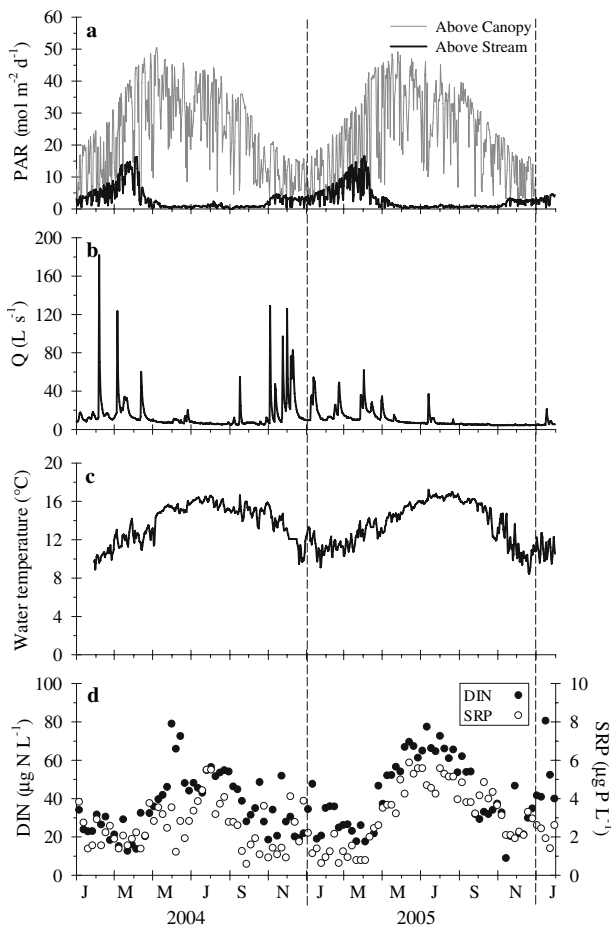
We measured the abundance of bryophyte and macroalgae species during repeated surveys consisting of transects across the stream at 1-m intervals over the study reach (total of 60 transects per survey). Presence or absence of bryophytes (the liverwort *Porella pinnata* and moss *Amblystegium riparium*) and macroalgae (the filamentous green alga, *Oedogonium* sp., the macrothallus phase of the red alga *Batrachospermum* sp., and the yellow-green alga *Vaucheria* sp.) species were determined at 0.1-m intervals along each transect and percent coverage of each species was calculated for each survey. Surveys were conducted at least once per month beginning in May 2004 through the end of the study (January 2006).

## RESULTS

### Physical and Chemical Parameters

Photosynthetically active radiation (PAR) above the forest canopy displayed a distinct seasonal pattern with PAR increasing gradually from January to May because of seasonal increase in sun angle and day length, declining slightly in mid-summer as cloud cover increased, and then declining to a December minimum (Figure 1A). Solar radiation reaching the stream surface also increased from January through the first week in April in each year (Figure 1A). Leaf emergence in early April caused a rapid decline in daily integrated PAR reaching the stream surface from 17 mol photons  $\text{m}^{-2} \text{day}^{-1}$  during the first week to less than 1 mol photons  $\text{m}^{-2} \text{day}^{-1}$  by the end of April in both 2004 and 2005 (Figure 1A). Stream PAR remained very low until leaf fall, which peaked in early November (Figure 1A).

Daily discharge was seasonal in Walker Branch with highest baseflows during winter and spring and lowest flows occurring prior to leaf fall (September and October) (Figure 1B). Low baseflows in summer and early autumn were the result of high rates of evapotranspiration during the forest-growing season. A total of 5 storms resulted in daily mean discharges of 100  $\text{l s}^{-1}$  or more during 2004, but no spates of this magnitude occurred in 2005. The occurrence of large storms in 2004 led to a greater mean annual discharge in the first year of the study (15.7  $\text{L s}^{-1}$ ) than in the second (9.4  $\text{L s}^{-1}$ ) (Table 1).



**Figure 1.** **A** Daily photosynthetically active radiation (PAR, mol photons  $\text{m}^{-2} \text{day}^{-1}$ ) above the forest canopy and above the stream, **B** daily mean discharge ( $Q$ ,  $\text{l s}^{-1}$ ), **C** daily mean water temperature ( $^{\circ}\text{C}$ ) and **D** weekly dissolved inorganic nitrogen (DIN;  $\mu\text{g N l}^{-1}$ ) and soluble reactive phosphorus (SRP;  $\mu\text{g P l}^{-1}$ ) concentrations from January 2004 through January 2006 in Walker Branch.

Mean daily water temperature exhibited a consistent seasonal pattern with lowest temperatures occurring in winter and highest temperatures occurring in summer of each year (Figure 1C). The annual range of water temperature was only approximately  $7^{\circ}\text{C}$  ( $9\text{--}16^{\circ}\text{C}$ ) because of the importance of discharge from perennial springs, and the mean annual values were similar in 2004 and 2005 (Table 1).

Concentrations of dissolved inorganic nitrogen (DIN) and soluble reactive phosphorus (SRP) were highest during the summer and lowest during the spring and autumn (Figure 1D) as has been seen in previous years in Walker Branch (Mulholland and Hill 1997; Mulholland 2004). DIN was almost all in the form of  $\text{NO}_3^-$  in Walker Branch as  $\text{NH}_4^+$  con-

centrations were low (typically  $< 5 \mu\text{g N l}^{-1}$ ) and did not vary seasonally.

### Relationships Between Stream Discharge and Stream Width, Depth, and $k_{\text{O}_2}$

Mean wetted width ( $w$ , Figure 2A) and depth ( $Z_{\text{mean}}$ , Figure 2B) increased as stream discharge (measured at the weir) increased in Walker Branch. Discharge explained 85 and 74% of the variance in stream width and depth, respectively. Because  $Z_{\text{mean}}$  can be accurately predicted for every 15-min period using records of stream discharge ( $Q_{\text{weir}}$ ) and the linear regression

$$Z_{\text{mean}} = 0.0006 \times Q_{\text{weir}} + 0.05, \quad (3)$$

we were able to accurately convert measured volumetric metabolism rates to areal rates. Similarly, the linear regression

$$w = 0.0139 \times Q_{\text{weir}} + 1.95 \quad (4)$$

was used to calculate  $w$  for each sampling interval and convert areal metabolism rates to units of per length of stream.

$\text{O}_2$  reaeration coefficient ( $k_{\text{O}_2}$ ) during non-leaf cover periods of the year increased with increased stream discharge (Figure 2C) according to the equation

$$k_{\text{O}_2} = 0.0009 \times Q_{\text{weir}} + 0.08 \quad (5)$$

Differences in  $Q_{\text{weir}}$  explained 91% of the variation in  $k_{\text{O}_2}$  in Walker Branch, allowing us to accurately determine the net exchange of  $\text{O}_2$  with the atmosphere from  $Q_{\text{weir}}$  and the average DO deficit for a given measurement interval.

Mean ( $\pm\text{SD}$ )  $k_{\text{O}_2}$  during leaf cover conditions (generally in November and December) was  $0.052 \pm 0.002 \text{ min}^{-1}$  at mean ( $\pm\text{SD}$ ) discharge of  $4.4 \pm 0.1 \text{ l s}^{-1}$  (Figure 2C). During non-leaf cover periods,  $k_{\text{O}_2}$  was  $0.081 \text{ min}^{-1}$  at the same discharge, indicating that leaf cover reduced  $k_{\text{O}_2}$  by 46% in Walker Branch. To account for leaf cover in our metabolism calculations, we applied the leaf cover  $k_{\text{O}_2}$  value in the autumn beginning when integrated daily PAR (measured 1 m above the stream) increased to above  $2 \text{ mol photons m}^{-2} \text{ day}^{-1}$  (indicating that a significant proportion of leaves had fallen from the riparian trees). This  $k_{\text{O}_2}$  value was used until a stormflow event occurred (defined as maximum instantaneous  $Q > 50 \text{ l s}^{-1}$ ). This threshold was based on personal observations of the size of storm needed to remove a large proportion of leaves from the stream surface in the study reach.

**Table 1.** Annual Rates of Gross Primary Production (GPP), Ecosystem Respiration (ER), and Net Ecosystem Production (NEP) both per Unit Area ( $\text{g O}_2 \text{ m}^{-2} \text{ y}^{-1}$ ) and per Unit Distance ( $\text{g O}_2 \text{ m}^{-1} \text{ y}^{-1}$ ) for 2004 and 2005. Annual means (annual ranges) for daily mean discharge and water temperature are also presented.

	2004		2005	
	$\text{g O}_2 \text{ m}^{-2} \text{ y}^{-1}$	$\text{g O}_2 \text{ m}^{-2} \text{ y}^{-1}$	$\text{g O}_2 \text{ m}^{-2} \text{ y}^{-1}$	$\text{g O}_2 \text{ m}^{-2} \text{ y}^{-1}$
Annual totals				
GPP	488 (183)	1,078 (404)	519 (195)	1,128 (423)
ER	-1,645 (-617)	-3,655 (-1371)	-1,292 (-485)	-2,723 (-1,021)
NEP	-1,156 (-434)	-2,577 (-966)	-773 (-290)	-1,596 (-598)
Annual means				
Discharge ( $\text{l s}^{-1}$ )	15.7 (4.9–181.7)		9.4 (4.3–61.8)	
Water temperature ( $^{\circ}\text{C}$ )	13.7 (9.1–16.6)		13.6 (8.4–17.2)	

Annual rates expressed in carbon currency ( $\text{g C}$ ) were calculated using a photosynthetic quotient of 1.0 and are presented in parentheses. Each annual period began on 1 February and included all dates through 31 January of the following calendar year.

We examined the impact that overestimating  $k_{\text{O}_2}$  during leaf cover periods has on metabolism rate calculations by comparing daily GPP and ER rates calculated using  $k_{\text{O}_2}$  determined from the non-leaf cover regression with  $Q_{\text{weir}}$  and the  $k_{\text{O}_2}$  directly calculated during leaf cover in November 2005. The mean daily rates of GPP, ER and NEP for November 2005 were +0.58, -3.46, and -2.88  $\text{g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ , respectively using the leaf-cover  $k_{\text{O}_2}$  compared with +0.90, -5.30, -4.40  $\text{g O}_2 \text{ m}^{-2} \text{ day}^{-1}$  using the  $k_{\text{O}_2}$  calculated from the regression with  $Q_{\text{weir}}$ . Thus, not accounting for the effect of leaf cover on  $k_{\text{O}_2}$  would have resulted in an overestimate of each rate by 53%, highlighting the importance of considering the influence that leaf cover when estimating  $k_{\text{O}_2}$  for deciduous forest streams.

### Dissolved $\text{O}_2$ Patterns and Calculation of GPP, ER, and NEP rates

Dissolved  $\text{O}_2$  (DO) concentrations showed a distinct diel pattern with DO values peaking during mid-day (a typical early spring day with above stream  $\text{PAR} = 13 \text{ mol photons m}^{-2} \text{ day}^{-1}$  is displayed in Figure 3A). Although this pattern was strongest during the open-canopy spring period (Figure 3A), it was also observed (to a lesser extent) during the summer low light availability period. During a typical high PAR spring day, DO was less than 100% saturation at night but was supersaturated for an extended period during the day (Figure 3B). This pattern corresponded to a positive DO deficit at night (net exchange of  $\text{O}_2$  was from the atmosphere into the water) that became a negative DO deficit (net exchange of  $\text{O}_2$  was from the water to the atmosphere) within the first couple of hours after sunrise (Figure 3C). Calculated rates of GPP

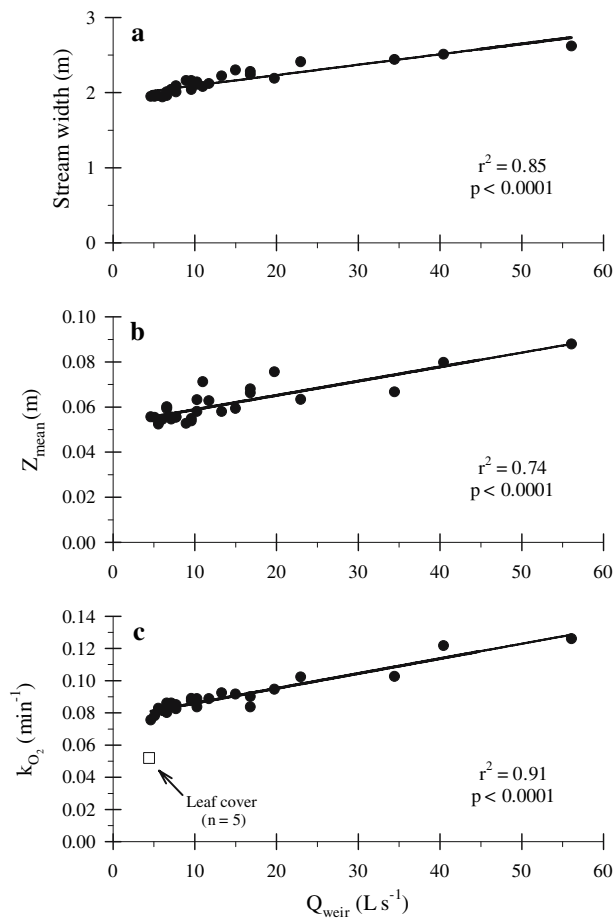
(vertical lines) and ER (horizontal lines) are shown in Figure 3D. Daily rates of GPP, ER, and NEP on the day illustrated in Figure 3 (10 March 2005) were +6.48, -5.50, and +0.98  $\text{g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ , respectively.

### Temporal Patterns in Ecosystem-Scale Rates of GPP, ER, and NEP

Distinct seasonal patterns in daily rates of GPP and ER were observed in Walker Branch during the 2 year study with daily GPP and ER rates ranging between +0.01 and +10.80  $\text{g O}_2 \text{ m}^{-2} \text{ day}^{-1}$  and -0.99 and -16.01  $\text{g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ , respectively (Figure 4A). Daily ER rates were high in spring and autumn and lowest in summer of each year. Daily GPP rates were highest during the open-canopy spring period, peaked in late March–early April, and declined sharply as light availability declined during canopy closure (Figure 1A). Daily GPP remained low throughout the closed-canopy summer period and exhibited a slight increase after the canopy re-opened in early November. Walker Branch was strongly net heterotrophic ( $\text{NEP} < 0$ ) throughout most of the year, except during spring when daily rates of GPP and ER were often similar (Figure 4B). In 2004, daily rates of GPP exceeded ER ( $\text{NEP} > 0$ ) on only 5 dates (3 in March and 2 in April), but in 2005 Walker Branch was net autotrophic on a total of 28 dates (3 in February, 13 in March and 10 in April). March of 2005 was the only month in the study during which the mean daily NEP rate was positive (Figure 4B).

The annual rate of GPP in 2004 was slightly lower than in 2005, when calculated either in areal units or per meter of stream length (Table 1). Annual rates of ER exhibited the opposite pattern, with 2004 rates being more negative than 2005





**Figure 2.** Relationships between **A** stream width, **B** mean depth ( $Z_{\text{mean}}$ ), and **C** reaeration coefficient ( $k_{\text{O}_2}$ ) with discharge measured at the weir ( $Q_{\text{weir}}$ ) derived from NaCl/propane injections in Walker Branch ( $n = 31$  for all regressions). *Open square* in panel **C** indicates the mean ( $\pm$ SD)  $k_{\text{O}_2}$  and  $Q_{\text{weir}}$  values for 5 injections during the leaf cover period of November–December 2005.

rates (Table 1). In both years, Walker Branch was highly net heterotrophic ( $\text{NEP} \ll 0$ ) with NEP being less negative in 2004 than in 2005 (Table 1).

In addition to seasonal variability, we observed high day-to-day variability in both GPP and ER, particularly during periods when rates were generally high (Figure 4A). PAR reaching the stream also exhibited high day-to-day variability at these times (Figure 1A). Large changes in daily rates of both GPP and ER also appeared to coincide with the occurrence of high discharge events (storms with maximum instantaneous  $Q \geq 100 \text{ l s}^{-1}$  are indicated by arrows in Figure 4A).

### Autotrophic Biomass

Periphyton biomass did not exhibit a seasonal pattern during the study, with mean ( $\pm$ SD) chl *a*

values of  $6.5 \pm 3.1 \mu\text{g chl } a \text{ cm}^{-2}$ . Similarly, there was no distinct seasonal pattern observed in percent areal coverage of either bryophyte species. Abundance of the moss *Amblystegium riparium* remained relatively constant throughout the study, with percent areal coverage ranging between 5.1 and 7.8% (mean  $\pm$  SD =  $6.2 \pm 0.6\%$ ) (Figure 5). The liverwort *Porella pinnata* increased in abundance throughout the course of the study with percent areal coverage increasing from 4.2% in May 2004 to 18.0% by January 2006 (Figure 5). In contrast to periphyton and bryophytes, macroalgal biomass was highly seasonal. Macroalgae first appeared in January, peaked in percent coverage in March and declined quickly as the canopy closed in April (Figure 5). During the peak of the 2005 spring bloom, macroalgae covered 10.7% of the streambed surface area with the filamentous green alga, *Oedogonium* sp. being responsible for more than 90% of the coverage. The macrothallus phase of the red alga *Batrachospermum* sp. and the yellow-green alga *Vaucheria* sp. accounted for the remainder of the macroalgae coverage during the bloom.

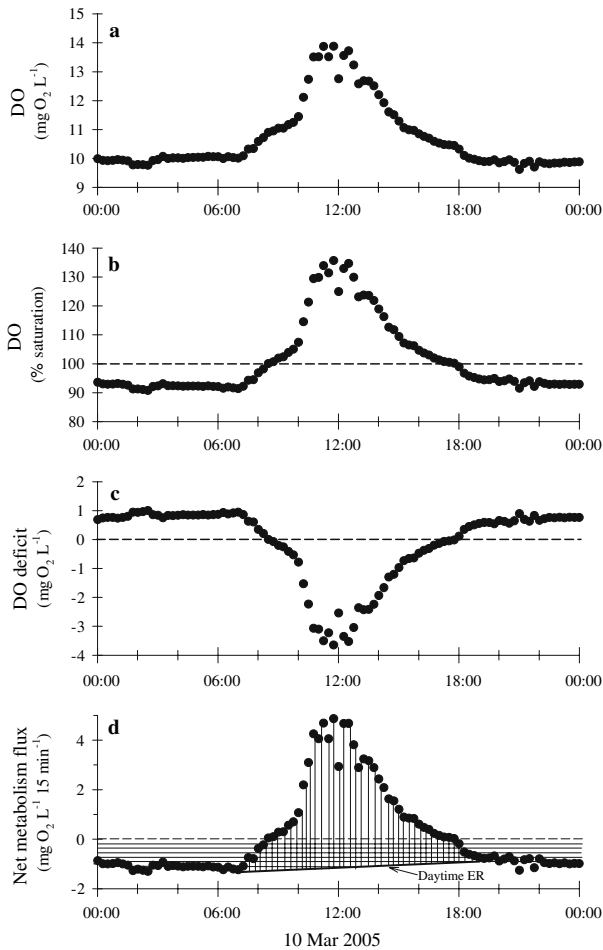
### PAR and GPP Relationship

Whole system rates of GPP were positively correlated with PAR over the entire study, with PAR explaining over 70% of the variance in daily GPP rates ( $r^2 = 0.71$ ,  $P < 0.0001$ ,  $n = 731$ ). Part of this correlation was due to increases in algal biomass (for example, *Oedogonium* bloom) in high light periods. Additionally, during the period of peak autotrophic biomass in early spring, GPP was also positively correlated with PAR, with PAR explaining 84% of variance in daily GPP rates for April 2004 and 2005 (Figure 6) illustrating the stimulating effect of light on biomass specific rates of GPP.

### Storm Effects on GPP and ER

To examine the potential effects of storms on GPP and ER we compared responses to similar-sized (daily mean  $Q = 123$  and  $129 \text{ l s}^{-1}$ ) storms in spring and autumn 2004. The spring 2004 storm occurred on 4 March, during the open canopy period after GPP began to increase, and the autumn storm occurred on 4 November and was the first of 4 consecutive large storms ( $Q > 100 \text{ l s}^{-1}$ ) over a 5-week period (Figure 4).

GPP and ER were both suppressed immediately following the large spring storm; however, the ensuing recovery patterns for GPP (Figure 7A) and ER (Figure 7C) were very different. GPP was suppressed to a greater extent and for longer duration, taking several days to return to pre-disturbance



**Figure 3.** Diel profiles of **A** dissolved  $O_2$  (DO) concentration, **B** percent saturation of DO, **C** DO deficit, and **D** net metabolism flux showing the area representing gross primary production (GPP, vertical lines) and ecosystem respiration (ER, horizontal lines). The dashed lines indicate 100% saturation in panel **B**, DO deficit of zero in panel **C**, and net metabolism flux of zero in panel **D**. The solid line in panel **D** indicates the interpolated values of daytime ER. Data are from 10 March 2005.

rates. ER rates exhibited a sharp decline on the day discharge increased, partly as a result of the near complete reduction in autotrophic activity. However, after the initial decline, ER rates increased to levels exceeding those prior to the storm for several days, resulting in a temporary decoupling of GPP and ER. Photosynthetic efficiency (GPP/PAR) followed a similar pattern to GPP, exhibiting a multi-day suppression following the storm (Figure 7B).

During autumn, GPP increased after the storm, probably as a result of increased light availability associated with export of leaves previously covering the stream surface (Figure 7D). This stimulation in GPP persisted for several days until the

stream surface was once again covered by leaves falling into the stream. GPP/PAR showed a similar pattern to GPP in response to the autumn storm (Figure 7E). During autumn, ER rates exhibited a similar, but perhaps dampened, response compared with the spring storm response (Figure 7F).

### Daily Versus Less Frequent Metabolism Measurements

Quarterly estimates of GPP resulted in annual rates of 111.8–1115.2 and 93.9–1084.6  $g O_2 m^{-2} y^{-1}$  compared to rates based on daily measurements of 488.5 and 519.3  $g O_2 m^{-2} y^{-1}$  in 2004 and 2005, respectively (Table 2). Thus, quarterly measurements would result in estimates of annual rates that varied over an order of magnitude, ranging between 23 and 228% of actual rates (based on daily measurements) in 2004 and between 18 and 208% in 2005. Quarterly estimates provided slightly improved estimates of ER rates with rates ranging between 68 and 150% of actual rates in 2004 and between 67 and 138% in 2005. Inaccuracies in NEP estimates based on quarterly estimates were intermediate, with rates ranging between 44 and 200% of actual rates in 2004 and between 23 and 186% in 2005.

Making monthly measurements of ecosystem metabolism improved estimates of annual fluxes of GPP, ER, and NEP (Table 2). However, annual GPP estimates from monthly measurements still varied by a factor of two, ranging between 65 and 127% of actual rates in 2004 and between 69 and 142% in 2005. ER estimates were between 86 and 135% of actual rates in 2004 and between 82 and 117% in 2005 with inaccuracies in annual NEP flux estimates again being intermediate between inaccuracies in GPP and ER estimates (Table 2).

## DISCUSSION

### Seasonal Variation in Metabolism Rates

Seasonal GPP and ER patterns in Walker Branch were highly influenced by the deciduous vegetation of the riparian forest. During the closed-canopy period (May–October), light (PAR) reaching the streambed was low and daily rates of GPP and ER were both at their annual minima. Autumn leaf fall began in September and resulted in an increase in ER, largely because of increased organic matter inputs fueling heterotrophic microbial respiration. GPP rates remained low through October. By early November, the canopy opened enough to allow an increase in light reaching the stream surface resulting in observable increases in GPP but rates

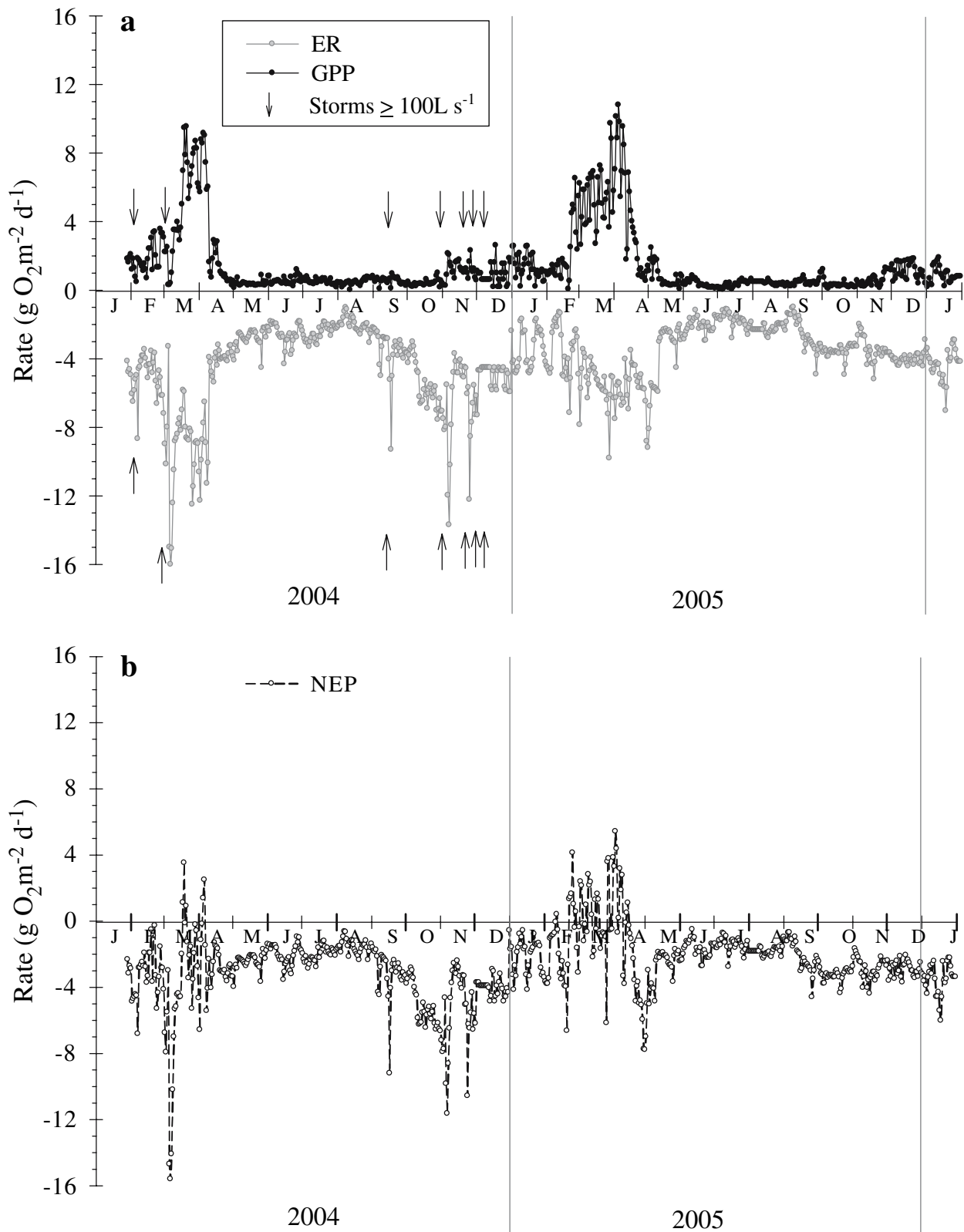
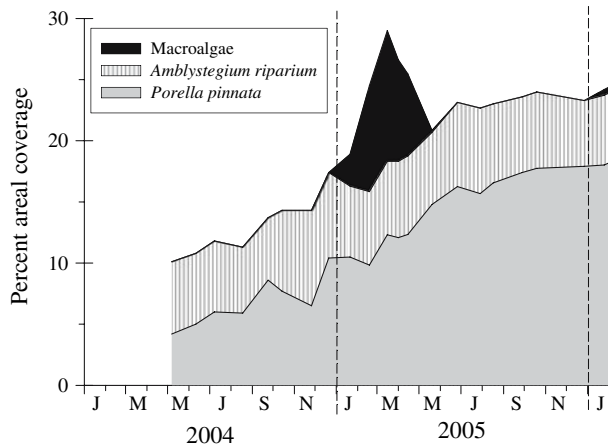


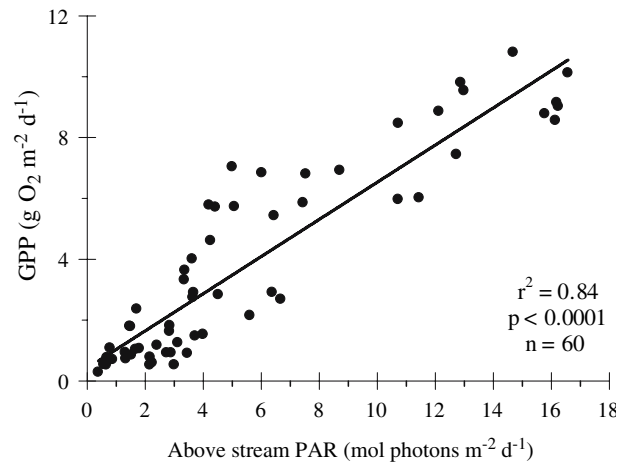
Figure 4. Daily rates of **A** gross primary production (GPP: positive values, *black line*) and ecosystem respiration (ER: negative values, *gray line*) and **B** net ecosystem production (NEP: positive and negative values, *hatched line*) measured in Walker Branch from 28 January 2004 through 31 January 2006. *Vertical lines* separate years. *Arrows* indicate storms during which maximum instantaneous discharge was greater than or equal to  $100\text{ l s}^{-1}$ .



**Figure 5.** Percent areal coverage of the liverwort *Porella pinnata*, moss *Amblystegium riparium*, and macroalgae (mostly the green alga *Oedogonium* sp.) based on frequent ( $\geq 1$  per month) surveys of the study reach in Walker Branch from May 2004 through January 2006. Vertical lines separate years.

remained relatively low as light availability was constrained by daylength and sun angle. Light reaching the stream surface increased throughout the winter and early spring, reaching an annual peak during the first week of April. Daily rates of GPP and ER both increased with the increase in daily integrated light. Leaf emergence in early April caused a rapid decline in light reaching the stream as well as rates of GPP and ER. High GPP during March and April suggest that high ER at this time was largely the result of autotrophic activity (either directly as autotrophic respiration or indirectly by providing labile organic matter for heterotrophic consumption).

We examined seasonal dynamics of the primary components of the autotrophic community in Walker Branch (periphyton, bryophytes, and macroalgae) in an attempt to determine the cause of the spring GPP peak. Previous studies have demonstrated that periphyton production per unit biomass increases with light in Walker Branch (Steinman 1992; Rosemond and others 2000; Hill and others 2001). However, as has been seen in previous studies (Rosemond 1994), periphyton biomass did not exhibit a seasonal pattern during our study due to high densities of snail herbivores ( $\sim 1,500 \text{ m}^{-2}$ , Hill and others unpublished data). Although *Porella* abundance increased steadily over time and was approximately 4 times more abundant at the end of the study, the increase was not seasonal so was not likely responsible for the spring GPP peak. The appearance, peak, and decline in macroalgal abundance (especially *Oedogonium*,

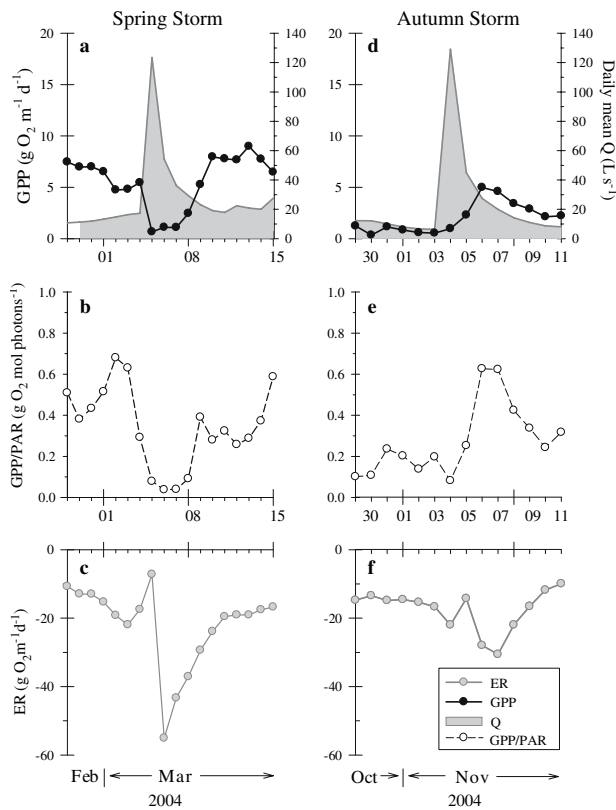


**Figure 6.** Relationships between daily gross primary production (GPP) rate and daily integrated photosynthetically active radiation (PAR) flux measured 1m above the stream surface during the period of peak autotrophic biomass (April 2004 and 2005,  $n = 60$ ). Solid line is the statistically significant ( $P < 0.0001$ ) linear regression ( $\text{GPP} = 0.61 \times (\text{PAR}) + 0.43$ ).

Figure 5) correlated well with GPP (Figure 4A) in 2005. *Oedogonium* is reported to have higher chlorophyll-specific carbon fixation rates under high light conditions than periphyton (either *Stigeoclonium* or diatoms) (Steinman and others 1992). The seasonally high biomass of *Oedogonium* and other macroalgae combined with high production rates was likely responsible for much of the large increase in area-specific rates of GPP observed in Walker Branch during spring.

Light explained 71% of the variance in daily GPP rate over the entire study and 84% of the variance at the time of peak autotrophic biomass (April, Figure 6), indicating that light is the dominant control on GPP in Walker Branch [as has also been seen in several multi-stream comparisons (for example, Bott and others 1985; Young and Huryn 1999; Mulholland and others 2001)]. Although previous studies have shown a saturating effect of light on instantaneous GPP in Walker Branch (Hill and others 2001; Mulholland and others 2001), we did not observe light saturation of daily GPP either when examining the entire dataset or the April period (Figure 6). Although GPP-PAR relationships developed from chamber studies of stream periphyton have frequently displayed light-saturation (Hill and others 1995; Hill and Dimick 2002), open-system studies have usually shown no evidence of saturation at high irradiances (Duffer and Dorris 1966; Hornberger and others 1976; Uehlinger and others 2000; Mulholland and others 2001). The lack of light saturation of daily GPP in Walker





**Figure 7.** Daily rates of gross primary production (*GPP*, **A**, **D**), photosynthetic efficiency (*GPP/PAR*, **B**, **E**), and ecosystem respiration (*ER*, **C**, **F**) before and after large spring (**A**, **B**, **C**) and autumn (**D**, **E**, **F**) storms in 2004. Daily *Q* is indicated as the shaded area in panels **A** and **B** for the spring and autumn storms, respectively.

Branch may be the result of both community changes (that is, development of an opportunistic autotroph—macroalgae) during the high light period and changes in daily-integrated PAR values reflecting changes in both daylength and instantaneous PAR.

Inorganic nutrient availability can often limit stream primary production when light is abundant (Peterson and others 1985; Grimm and Fisher 1986; Hill and Knight 1988; Flecker and others 2002) as well as *ER* (Elwood and others 1981; Tank and Webster 1998; Grattan and Suberkropp 2001; Mulholland and others 2001). In the current study, DIN and SRP concentrations (Figure 1D) were lowest during the spring and autumn when metabolism rates (Figure 4) were greatest. In addition, analyses of long-term NO<sub>3</sub><sup>-</sup> and SRP data (Mulholland and Hill 1997; Mulholland 2004) indicated that in-stream nutrient retention was greatest in spring and autumn. DIN and SRP concentrations increased (Figure 1D) as daily light

(Figure 1A) and *GPP* (Figure 4A) decreased during leaf emergence in both years of the study, a pattern also observed by Hill and others (2001) in 1992 and 1993. These results suggest that seasonal variation in rates of metabolism control seasonal patterns in nutrient concentrations as well as the potential for seasonal nutrient limitation (Mulholland and Rosemond 1992; Rosemond and others 2000).

Temperature is an important regulator of metabolic processes, and as temperature increases respiration is also expected to increase [as seen in Bott and others (1985), Sinsabaugh (1997) and Uehlinger and others (2000)]. However, water temperature explained less than 14% of variability in daily *ER* with the lowest rates occurring at the warmest temperatures. This is because the warmest temperatures occurred during summer, when organic matter availability was at its lowest (in contrast to high organic matter availability via *GPP* in spring and leaf litter inputs in autumn). Allochthonous organic matter inputs from leaf fall began in September, peaked in early November, and were coincident with high *ER* rates observed in autumn (Figure 4A). In contrast, when allochthonous carbon inputs were low (February–August), 55% of the variation in daily *ER* was explained by *GPP* [ $ER = -1.34 \times \ln(GPP) - 3.94$  ( $P < 0.001$ )]. These findings suggest that although metabolic reactions of individual organisms likely increase with temperature, the availability of substrate is a stronger driver when scaling to the entire ecosystem.

### Day-to-Day Variation In Metabolism Rates

Day-to-day variation in *GPP* and *ER* was quite large, particularly during the spring when rates were high (Figure 4A). Much of this variation in *GPP* in spring was related to variation in light (Figure 6) due to weather conditions. Because daily *GPP* explained 55% of the variation in daily *ER* during February–August, light variability also appeared to induce day-to-day variation in *ER*, explaining 49% of the variation in *ER* for the period [ $ER = -1.31 \times \ln(PAR) - 3.06$  ( $P < 0.0001$ )]. This is particularly surprising for a stream that was strongly net heterotrophic over the period (Figure 4B). The high day-to-day variation during periods that account for a significant portion of annual *GPP* and *ER* indicates a potential weakness of approaches that attempt to quantify annual metabolism rates with infrequent (for example, 1–2 days per season) measurements.

**Table 2.** Annual Rates of Gross Primary Production (GPP), Ecosystem Respiration (ER), and Net Ecosystem Production (NEP) based on Daily, Quarterly, and Monthly Measurements for 2004 and 2005

	2004		Ratio (estimate/ actual rate)		2005		Ratio (estimate/ actual rate)	
	Annual rate (g O <sub>2</sub> m <sup>-2</sup> y <sup>-1</sup> )				Annual rate (g O <sub>2</sub> m <sup>-2</sup> y <sup>-1</sup> )			
Based on daily measurements								
GPP	488				519			
ER	-1,645				-1,292			
NEP	-1,156				-773			
Based on quarterly measurements								
	Min	Max	Min	Max	Min	Max	Min	Max
GPP	112	1115	0.23	2.28	94	1,085	0.18	2.08
ER	-1,125	-2,460	0.68	1.5	-863	-1,786	0.67	1.38
NEP	-507	-2,315	0.44	2	-181	-1,442	0.23	1.86
Based on monthly measurements								
	Min	Max	Min	Max	Min	Max	Min	Max
GPP	316	621	0.65	1.27	359	740	0.69	1.42
ER	-1,418	-2,227	0.86	1.35	-1,059	-1,451	0.82	1.17
NEP	-865	-1,757	0.75	1.52	-511	-1,036	0.66	1.34

The minimum (min) and maximum (max) annual rates based on quarterly and monthly measurements were determined from all sampling combinations based on sampling the same day in each quarter (first day of quarter (1 January, 1 April, 1 July, and 1 October), second day of quarter (2 January, 2 April, 2 July, and 2 October), and so on) and in each month, respectively. The minimum and maximum ratios of annual rate based on either quarterly or monthly measurements compared to the actual rate derived from daily measurements are also presented.

## Episodic (storm-related) Variation in Metabolism Rates

Much of our knowledge of stream ecosystems is based on studying streams during baseflow conditions. In most streams, however, flow variability can be high and the effects of spates (for example, scour and deposition) may influence metabolism rates for some time afterward. Only one large storm ( $Q > 100 \text{ L s}^{-1}$ ) in this study occurred during the spring, open-canopy period (Figure 4A). The resistance (capacity to minimize the response to a disturbance) of both GPP and ER was low for the spring storm (Figure 7A, C). GPP was more strongly affected by the storm than ER, with rates being reduced by a factor of 10 on the day of peak discharge relative to the average pre-storm rate. The sharp decline in ER on the day of peak discharge is likely a result of declines in both autotrophic and heterotrophic R. Autotrophic R declined as result of near complete reduction in GPP. However, even if autotrophic R was equal to GPP prior to the storm (autotrophic R is more likely 20–50% of GPP), the reduction in autotrophic R would only have accounted for approximately 60% of the  $10 \text{ g O}_2 \text{ m}^{-1} \text{ day}^{-1}$  decrease in ER observed. Heterotrophic respiration must also have initially decreased in response to the storm.

The resilience (ability to recover rapidly after disturbance) of GPP to the spring storm event was much less than that of ER. Although light returned to pre-storm levels on the day after the storm, the recovery of GPP to pre-storm levels took 5 days and represented a growth rate of  $0.55 \text{ day}^{-1}$  (based on linear regression of  $\ln \text{ GPP}$  vs. time in days since disturbance). The sharp decline in GPP/PAR beginning on the day of the storm and persisting for several days (Figure 7B) suggests that the post-storm GPP drop was due to a sharp reduction in the photosynthetic capacity of autotrophs, likely due to biomass reduction from scour. ER recovered rapidly after an initial decline, with daily ER exceeding pre-storm levels by a factor of 3 on the day after peak discharge. Daily ER rates slowly declined back to pre-storm levels over the next 5 days. This short-term stimulation of ER may have been a result of the input and deposition of labile organic matter from the catchment during the storm.

On 4 November 2004, Walker Branch experienced its first large storm ( $Q > 100 \text{ l s}^{-1}$ ) after leaf fall. In contrast to spring, there was a multi-day increase in GPP following the storm, probably as a result of higher flows washing away a significant portion of leaves covering the stream bottom and thus allowing for increases in light reaching benthic autotrophs. This GPP pulse only persisted for a few

days as leaves continued to fall into the stream, reducing light availability to stream autotrophs.

The ER response to the autumn storm was qualitatively similar to the spring storm, with ER decreasing initially followed by a stimulation that persisted for several days. The initial decline in ER following the storm was much smaller than observed in the spring and probably was the result of a decrease in heterotrophic R alone because GPP was minimal prior to the storm (~10 times lower than prior to the March storm). Daily ER increased to twice pre-storm levels on 7 November before declining over the next 4 days to a stable rate. Although particulate organic matter availability in Walker Branch was already high from leaf litter inputs, the post-storm peak in ER may be the result of additional input of labile POC and increased DOC concentrations associated with stormflows (Mulholland and others 1990). Qualitatively similar responses were observed for the other 4 storms in November and December 2004 (note ER spikes after storms in Figure 4A), but it was difficult to quantitatively evaluate the responses to the individual storms because of the short time intervals between storms.

Few studies have examined the effect of storms on stream metabolism. In large Swiss rivers (mean discharge > 1,000 times that of Walker Branch in each case), bed-moving spates depressed both GPP and ER (Uehlinger and Naegeli 1998; Uehlinger 2000, 2006). The effects of storms on GPP and ER in Walker Branch in spring were similar to the Swiss Rivers in that GPP and ER were both depressed but with GPP being more strongly affected. However, although GPP followed a similar recovery trajectory in Walker Branch as in the Swiss rivers, the post-storm stimulation of ER observed in Walker Branch was absent in the Swiss rivers. In addition, the distinct seasonal differences in the effect of storms on metabolism we observed in Walker Branch were not observed in the Swiss rivers. The different responses to storms may be a result of the large size difference between the systems. Although the first-order Walker Branch is intimately connected to its surrounding catchment and riparian vegetation (in terms of regulating PAR, organic matter inputs, and extent to which leaves cover the stream bed), the larger Swiss rivers are probably less influenced by their immediate surroundings.

Stable groundwater streams like Walker Branch are common in the eastern United States (Poff 1996) and may be particularly vulnerable to disturbance from temporally unpredictable storm events (Poff and Ward 1989). Future climate

change scenarios that predict greater temporal variability in hydrologic regimes (Mulholland and others 1997b) suggest that episodic storms may play an increasing role in determining the metabolic balance of many forested headwater streams in the future.

### Inter-annual variation in metabolism rates

The spring peak in GPP in 2005 was considerably larger than in 2004 (Figure 4A) with GPP being approximately 13% greater in March and approximately 47% greater in April 2005 than in the corresponding months of 2004. The March 2004 storm (Figure 7) may have set back the development of the spring macroalgal bloom. This is consistent with visual observations that the *Oedogonium* bloom was more extensive in 2005 than in 2004 (Roberts and Hill personal observations). In addition, *Porella* abundance during March and April of 2005 was approximately 3 times greater than in May 2004 (Figure 5). However, the lack of storms in autumn 2005 led to a more extensive and persistent leaf cover which reduced light reaching the autotrophic community, resulting in GPP during November–January being approximately 25% lower in 2005 than in 2004. The net result of these factors was that annual GPP rates were similar in the two years.

In contrast to GPP, ER exhibited substantial inter-annual variability with ER in 2004 being approximately 27% higher than in 2005 (Table 1). This difference was largely the result of the higher frequency of storms in 2004 and the post-storm stimulation of ER rates that persisted for several days following each storm. ER on the 30 days associated with storms in 2004 totaled approximately 300 g O<sub>2</sub> m<sup>-2</sup> or 19% of the annual ER flux and accounted for approximately 85% of the difference between the annual ER rates for 2004 and 2005. Thus, climate variability appears to be an important driver of inter-annual variability in metabolism in Walker Branch, with wetter years (higher frequency of storms) resulting in greater annual ER and consequently making the ecosystem more net heterotrophic. This is similar to the findings from a New Zealand grassland river where the portion of the river that was net autotrophic was greater during low-discharge periods than during high-discharge periods (Young and Huryn 1996). These findings suggest that deciduous forest streams (stable groundwater streams in particular) may become increasingly heterotrophic in the future if precipitation increases or storms become more intense.

We attempted a more comprehensive analysis of inter-annual variability in ecosystem metabolism rates in Walker Branch by comparing the GPP results from the current study with previous measurements made in our study reach. Whole-stream rates of GPP were determined using the two-station, open system method (Marzolf and others 1994) and the corrected measure of the  $O_2$  air-water exchange flux (Young and Huryn 1998) on a total of 33 dates between 1992 and 2001 (Marzolf and others 1994, 1998; Mulholland and others 1997a, 2000, 2006; Hill and others 2001). Consistent with results from this study (Figure 8, line shows 2005 data), GPP rates measured during March and early April were higher than those measured at other times of the year (Figure 8, symbols). However, these results also provide evidence of large inter-annual variation in GPP (and presumably ER) because GPP during clear days in early April were much lower in earlier studies than those observed in 2004 and 2005. Although the relationship between daily GPP and light availability observed in 2001 (Mulholland and others 2006) was similar to the pattern observed in 2004 and 2005, the magnitude of seasonal GPP was substantially lower in the earlier studies with GPP on clear days of 2001 being comparable to GPP on low light days in 2005 (Figure 8).

All of the ecosystem metabolism measurements between 1992 and 2001 were made using the two-station approach whereas the measurements in the current study were made using a single-station approach. To test whether the higher spring GPP rates measured during the current study were an artifact of differences in methodologies, we also measured metabolism rates using the two-station approach on several dates during 2004 and 2005. GPP rates calculated using the two methods were compared on 12 days under baseflow conditions during spring 2005 (12–23 March) with mean daily GPP being 5.5 and 4.8  $g\ O_2\ m^{-2}\ day^{-1}$  for the one- and two-station methods, respectively. The average daily difference in GPP between the two methods was approximately 12%. Thus, it appears that the higher rates observed in 2004 and 2005 were not simply an artifact of the method being employed but reflected large inter-annual variability in ecosystem metabolism rates in Walker Branch.

The main difference between the spring, open canopy period during the current study (2004–2005) and previous studies (1992–2001) appears to be the size of the macroalgal bloom. Although the presence of macroalgae, namely *Batrachospermum*, was noted in the spring of 1992 and 1993 (Hill and others 2001), it was not considered a major component of

the autotrophic community. Further, when Mulholland and others (2000) characterized the major biomass and N storage compartments in Walker Branch in spring 1997, *Oedogonium* was not included. The presence of a large, spring filamentous algae bloom was first noted when metabolism measurements were conducted in April 2001 (Mulholland and others 2006). The *Oedogonium* blooms observed during the current study were the largest observed in Walker Branch to date (personal observations). Although further studies are needed to determine the controls on the size of the *Oedogonium* bloom, it is clear that differences in spring bloom size contribute greatly to the observed inter-annual variability in peak GPP rates in Walker Branch.

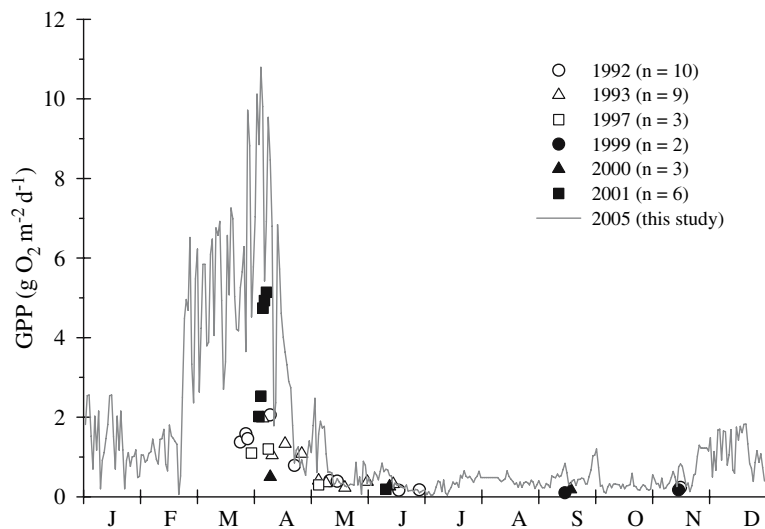
### Comparison of Walker Branch Metabolism Rates to Other Streams and Rivers

Annual GPP rates in Walker Branch were 2–4 times lower than those seen in sixth and seventh-order Swiss Rivers (Uehlinger 2000, 2006). Interestingly, annual ER rates in Walker Branch were comparable to those observed in the River Necker in 1993 (Uehlinger and Naegeli 1998) and the larger (seventh-order) River Thur in 2000 (Uehlinger 2006). Although the data presented in the current study represent the first annual GPP, ER, and NEP fluxes based on continuous daily measurements in a forested, headwater stream ecosystem, other studies have attempted to calculate annual fluxes based on less frequent measurements. Walker Branch metabolism rates fall within the range of rates observed in 13 forested stream reaches in the eastern United States physiographic province, where GPP, ER, and NEP ranged between +107 and +989  $g\ O_2\ m^{-2}\ y^{-1}$ , -701 and -1,855  $g\ O_2\ m^{-2}\ y^{-1}$ , and -1,440 and -285  $g\ O_2\ m^{-2}\ y^{-1}$ , respectively (Bott and others 2006). Similarly, Walker Branch annual rates fall between those reported for two forested tributary streams of the Taieri River in New Zealand (Young and Huryn 1999). The annual rates reported here also fall within the rates observed in three tributaries of the tropical forest stream Rio Mameyes in Puerto Rico, where GPP ranged between +69 and +634  $g\ O_2\ m^{-2}\ y^{-1}$  and ER ranged between -767 and -1,660  $g\ O_2\ m^{-2}\ y^{-1}$  (Ortiz-Zayas and others 2005).

### Daily Versus Less Frequent Metabolism Measurements

The results of our comparison of daily versus quarterly and month metabolism measurements





**Figure 8.** Daily rates of gross primary production (*GPP*) measured during 2005 (this study: *gray line*) and in previous studies in Walker Branch (*symbols*). All pre-2004 values were determined using the two-station approach detailed in Marzolf and others (1994) with the air–water exchange term modified as in Young and Huryn (1998). The data are from Marzolf and others (1994, 1998), Mulholland and others (1997, 2000, 2006), and Hill and others (2001).

indicated that infrequent measurements can result in highly erroneous estimates of annual carbon fluxes for a given stream. Annual estimates can be improved by increasing the sampling frequency from quarterly to monthly measurements, but still result in annual estimates that vary by up to a factor of 2 (Table 2). This exercise also demonstrated that annual *GPP* rates were more greatly affected by infrequent sampling than were *ER* rates in Walker Branch. This is likely the case in many stream ecosystems where much of annual *GPP* occurs during a shorter time period than does *ER*.

The continuous whole-ecosystem approach for measuring stream ecosystem metabolism rates provided us with a much more complete picture of ecosystem metabolism in Walker Branch. The results from this study highlight several important advantages of this approach. Continuous metabolism measurements over long time scales provide greater confidence in observed temporal patterns by minimizing the effect of sampling errors that can potentially hinder spot measurements. In addition, continuous measurements over time allowed us to identify four important levels of temporal variability in *GPP* and *ER* (day-to-day, episodic, seasonal, and inter-annual). Much of the important temporal dynamics associated with these scales of variability would have been missed with lower frequency measurements, which could have resulted in poor estimates of *GPP* and *ER* fluxes for this system (as was seen through annual estimates based on quarterly and monthly measurements).

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