

Annual cycle and inter-annual variability of gross primary production and ecosystem respiration in a floodprone river during a 15-year period

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SUMMARY

1. Temporal variation in ecosystem metabolism over a 15-year period (1986–2000) was evaluated in a seventh order channelised gravel bed river (mean annual discharge $48.7 \text{ m}^3 \text{ s}^{-1}$) of the Swiss Plateau. The river is subject to frequent disturbance by bed-moving spates. Daily integrals of gross primary production (GPP) and ecosystem respiration (ER) were calculated based on single-station diel oxygen curves.
2. Seasonal decomposition of the time series of monthly metabolism rates showed that approximately 50% of the variation of GPP and ER can be attributed to season. Annual GPP averaged $5.0 \pm 0.6 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ and showed no long-term trend.
3. Ecosystem respiration, averaging $6.2 \pm 1.4 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$, declined from 8.8 to $4.1 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ during the 15-year period. This significant trend paralleled a decline in nitrate and soluble reactive phosphorus concentrations, and the biochemical oxygen demand discharged by sewage treatment facilities upstream of the study reach. The ratio of GPP to ER (P/R) increased from 0.53 to about 1 as consequence of ER reduction.
4. Bed moving spates reduced GPP by 49% and ER by 19%. Postspate recovery of GPP was rapid between spring and autumn and slow during winter. Recovery of ER lacked any seasonal pattern. Annual patterns of daily GPP and to a minor extent of daily ER can be described as a sequence of recovery periods frequently truncated by spates.
5. The study showed that disturbance by frequent bed-moving spates resulted in major stochastic variation in GPP and ER but annual patterns were still characterised by a distinct seasonal cycle. It also became evident that stream metabolism is a suitable method to assess effects of gradual changes in water quality.

Keywords: disturbance, long-term trend, P/R, river metabolism, stability

Introduction

Light, temperature and flow are major factors controlling the metabolism of lotic ecosystems (Fisher *et al.*, 1982; Bott *et al.*, 1985; Uehlinger, König & Reichert, 2000). Light is the ultimate energy source for primary producers and temperature an important regulator of metabolic processes. Both factors are

subject to strong seasonal variation, especially at mid and high latitudes, and account for much of the temporal variability in primary production and ecosystem respiration (ER) when flow variability is moderate (Kelly, Thyssen & Moeslund, 1983; Servais, Debecker & Billen, 1984; Uehlinger, 1993). In many streams, however, flow variability is typically high. Flow may range from zero to channel-modifying floods, and flow patterns range from distinct seasonal cycles to random variation at different time scales (Poff & Ward, 1989; Molles & Dahm, 1990). Floods and spates severely affect ecosystem metabolism, particularly when moving bed sediments damage or

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eliminate auto- and heterotrophic biofilms (Fisher *et al.*, 1982; Uehlinger & Naegeli, 1998). Depending on season, metabolism rates may rapidly return to predisturbance levels, i.e. disturbance by spates and subsequent recovery can be a major source of variation apart from the seasonality in light and temperature (Uehlinger & Naegeli, 1998).

Annual differences in stream metabolism can be substantial, e.g. when inter-annual climate fluctuations translate into corresponding flood and flow patterns (Acuña *et al.*, 2004). However, there are no long-term records of river metabolism, from which information on inter-annual variation can be extracted. In contrast to records of physico-chemical parameters, most metabolism studies typically extend over periods <2 years and the temporal resolution of measurements is often less than the variation in environmental conditions (e.g. Webster & Meyer, 1997).

The River Thur is a seventh order gravel-bed river subject to frequent disturbance by bed-moving spates. Records of dissolved oxygen by the National Long-Term Surveillance of Swiss Rivers (NADUF, Jakob, Binderheim-Bankay & Davis, 2002) provided the opportunity to calculate metabolism rates over a 15-year period (1986–2000) at a high temporal resolution. These data made it possible to examine the relative importance of seasonal factors and the stochastic impact of spates on ecosystem metabolism at different time scales. Because concentrations of major nutrients decreased during the observation period (Jakob *et al.*, 2002), the time series of ecosystem metabolism was also examined for a corresponding trend.

Methods

Study site

The River Thur is a tributary of the upper Rhine. The headwaters are in the alpine region of north-eastern Switzerland (highest altitude in the catchment 2502 m a.s.l.). Major parts of the upper catchment are in the prealpine zone (foothills of the Alps), where altitudes range from 600 to 1800 m a.s.l. The catchment area above the gauging station near the mouth of the Thur (river km 10.1) is 1696 km². About 25% of the area is forested, 61% is fields, orchards and pastureland, and 8% is urban. The River Thur has been channelised between the lower end of the prealpine zone (river km

76) and its confluence with the Rhine (river km 0.0). Banks of the low-water channel are stabilised by stone rip-rap and at a few sites by short groynes. In the study reach, which extends from river km 10.1 upstream to river km 27.9 (mouth of the Murg River), altitude ranges from 357 to 386 m a.s.l. and slope is 0.17%. The average width of the wetted channel is 35 m at low flow (15 m³ s⁻¹). Between 1993 and 2000, the low water channel was opened (removal of the rip-rap) and the channel was fixed with groynes for about 2.5 km of the uppermost 8 km of the study reach. Bed sediments consist of gravel (mean b-diameter = 2.5 cm). Mean annual discharge at river km 10.1 was 48.5 m³ s⁻¹ from 1986 to 2000. The entire reach is open canopied with only minor valley shading.

Data source

Discharge, water temperature and dissolved oxygen were recorded by the Federal Office for Water and Geology in Berne (Switzerland) at river km 10.1. Intervals between oxygen and temperature measurements were ≤1 h. The instrumental setup of the oxygen and temperature measurements was described in detail by Uehlinger (2000). Global radiation (hourly integrals) and barometric pressure (hourly values) of a station 12 km north of the lower end of the study reach were obtained from the national weather service (MeteoSwiss, Zürich). The Swiss National River Survey Program (NADUF) provided data (bi-weekly) on nitrate, soluble reactive phosphorus (SRP) and dissolved organic carbon (DOC) of a station at river km 10.1. NADUF data are annually published in the Hydrological Year Books by the Federal Office for Water and Geology (e.g. FOWG, 2004). The Environmental Protection Agency of the Canton Thurgau (Amt für Umweltschutz) provided data on the annual discharge of biochemical oxygen demand (BOD₅) by five major sewage treatment plants upstream of the study reach. BOD₅ is a surrogate for organic matter that can be decomposed by micro-organisms.

Discharge and disturbance thresholds

In the study reach, sediment transport begins if flow exceeds 150 m³ s⁻¹ and disruption of the surface layer starts at flows above 350 m³ s⁻¹. These thresholds

were calculated using an empirical formula (Günter, 1971) and have been successfully used to establish a sediment balance for the River Thur (Schilling, Hunziker & Hunzinger, 1995).

Assessment of ecosystem metabolism

Metabolism rates were based on single-station diel O₂ curves (Odum, 1956). The net production rate of O₂ in mg O₂ m⁻² h⁻¹ was calculated as described in detail by Uehlinger & Naegeli (1998). The night-time method was used to estimate the reaeration coefficient K_s (Hornberger & Kelly, 1975). A total of 213 night-time oxygen curves were analysed. Temperature dependence of gas exchange was described according to Elmore & West (1961). To account for the influence of discharge, the following equation was used:

$$K_s(20^\circ) = aQ + b \quad (1)$$

K_s(20°) is the reaeration coefficient at 20 °C. The parameters $a = 0.00182 \text{ m}^{-3} \text{ s h}^{-1}$ and $b = 0.313 \text{ h}^{-1}$ were estimated using linear regression. Mean water depth as a function of discharge was obtained from runs of a numerical model of the lower Thur River (Schilling *et al.*, 1995). The model simulated open-channel flow between river km 10 and 30.

The influence of the upstream on downstream O₂ concentration decreases exponentially with length of the reach and can be neglected if $\frac{1}{K_s} \cdot \frac{1}{\tau} \geq 3$ (Chapra & DiTorro, 1991). τ is the travel time of water between the upstream and downstream station. As information on O₂ concentrations of the Murg River (mean annual discharge = 4.1 m³ s⁻¹) is lacking, and $\frac{1}{K_s} \cdot \frac{1}{\tau} = 2$ between river km 10.1 and 27.9, differences in O₂ between the Thur and Murg at river km 27.9 may affect the calculation of net oxygen production rates. Murg water is on average diluted 12-fold by the Thur River and reaeration reduces the upstream influence by 85% along the reach. If O₂ concentrations in the Murg River differ by 8 mg O₂ L⁻¹ from those in the Thur River, the effect on the O₂ signal at river km 10.1 will be ±0.1 mg O₂ L⁻¹, which is within the accuracy of the O₂ measurement.

Metabolic parameters

Calculation of ER and gross primary production (GPP) were based on net production rates of O₂. ER was calculated as the average net production rate of O₂

during the dark period extrapolated to 24 h. Respiration rates during the light period were calculated as the average respiration rates of the night before and after the day of interest; GPP was the sum of net production of O₂ during the light period and the average dark respiration rate multiplied by the length of the light period. Calculations of ER and GPP relied on the assumption that day respiration equals night respiration. The estimate of day respiration is subject to errors because the open system method is not suitable to separately measure autotrophic and heterotrophic respiration, to assess photorespiration or to provide information on the asynchrony between photosynthesis and associated metabolic costs (Bott, 1996). Uehlinger & Naegeli (1998) estimated that for these reasons in a open canopied sixth order reach of a nutrient rich tributary of the Thur River day respiration may have been over- or underestimated by 20%.

Resistance of GPP (R_{GPP}) and ER (R_{ER}) to bed-moving spates was calculated as:

$$R_X = 1 - \frac{X_{\text{before}} - X_{\text{after}}}{X_{\text{before}}} \quad (2)$$

where X_{before} is the last measurement of GPP or ER before a spate and X_{after} is the first measurement of GPP or ER after a spate. Recovery of GPP and ER during the first 2 weeks after a spate (short-term recovery) was described as a linear functions of the time since spate (Uehlinger, 2000); inter-spate periods shorter than 7 days were not considered. The slopes (m_{GPP} and m_{ER}) of these functions were used as a measure of resilience (Grimm & Fisher, 1989; Uehlinger, 2000).

Data analysis

Gaps in the time series of daily metabolism rates resulted from malfunction of the equipment. Moreover, during rapid flow increases the calculation of net production rates yielded suspicious results (Uehlinger, 2000), which were excluded from the data analysis. The period from January 1986 to December 2000 finally included 4212 values of daily GPP and ER rates. Gaps in the time series of daily rates were filled by linear interpolation prior to the calculation of monthly and yearly means.

The time series of monthly means of GPP, ER, P/R and physico-chemical parameters were decomposed as:

$$X_{ij} = T_{ij} + S_{ij} + R_{ij} \quad (3)$$

T_{ij} is the trend component, S_{ij} the seasonal component and R_{ij} the residual term; the subscripts i and j are year and month, respectively. Time series were decomposed by Seasonal and Trend decomposition using Loess (STL) implemented in DATAPLOT™ software (Statistical Engineering Division, National Institute of Standards and Technology, Gaithersburg, MD, U.S.A.). Loess (short for local regression) is a locally-weighted regression procedure used to fit curves to data sets, which are too complex to be described by parametric functions (Cleveland, 1993). The long-term trend is characterised by a loess line and the seasonal component by 12-month specific loess lines (for more details see Cleveland, 1993). Autocorrelation plots were used to check R_{ij} for randomness (Box & Jenkins, 1976). The sum of squares (SS) of T , S and R are approximately additive (exact additivity only exists if T , S and R are orthogonal), thereby providing an estimate of the relative contribution of each component to the variation in X_{ij} .

Stepwise multiple linear regression (SMLR) was used to explore the influence of factors such as light, temperature, flow and disturbance by spates on stream metabolism and related parameters. To assess the importance of these factors on ER and GPP, a backward elimination analysis was performed starting with the full linear model that considers all factors and iteratively eliminating the least important factor at each step. For each of the two modelled variables, $2^{p'-1}$ models were tested (p' is the number of parameters of the full model). The Schwarz Bayesian Criterion (Schwarz, 1978) was used to support the decision of factors considered to be significant. Uehlinger *et al.* (2000) gave a more detailed description of the SMLR procedure.

Water quality (annual mean) was characterised using the first axis of a principal component analysis (PC1) from annual BOD-load, and annual mean $\text{NO}_3\text{-N}$ and SRP concentrations.

Results

Flow and disturbance regime

Flow patterns of the lower Thur River were characterised by frequent flow peaks (Fig. 1a). Monthly discharge peaked in April (snow melt in the prealpine

zone) and was lowest in October. The seasonal component of flow only contributed 16% to the SS of monthly discharge. The annual number of spates with $Q_{\max} > 150 \text{ m}^3 \text{ s}^{-1}$ varied between 10 and 19 (average 14.9) from 1986 to 2000, and spates with $Q_{\max} > 350 \text{ m}^3 \text{ s}^{-1}$ occurred between two and eight times per year (average 3.7). Recurrence intervals of spates with $Q_{\max} > 150 \text{ m}^3 \text{ s}^{-1}$ varied between 2 and 124 days (median = 15 days). One-way ANOVA indicated a significant influence of season (month) on spates of this magnitude ($P < 0.05$) but *post hoc* comparison (Tukey's test) showed significant differences only between February and June. Autocorrelation analysis of the time series 'spates per month with $Q_{\max} > 150 \text{ m}^3 \text{ s}^{-1}$ ', suggested that such events were randomly distributed in time.

Light and water temperature

Daily integrals of global radiation (GLR) ranged from 110 to 8560 W m^{-2} , and daily mean water temperature from 0.06 to 24.2 °C (Fig. 1b,c). Weather-induced short-term variations in daily GLR were substantial but monthly values integrated these fluctuations; seasonal components of monthly GLR and temperatures dominated the respective time series (the seasonal components contributed >95% to the SS of GLR and temperature).

Water quality

Nitrate nitrogen, and to a minor extent SRP, displayed distinct seasonal variation (Fig. 1d,e). At the beginning of the study period, average annual concentrations of nitrate and SRP were 3.24 $\text{mg NO}_3\text{-N L}^{-1}$ and 0.187 mg SRP L^{-1} . Linear regression of the STL trend components of $\text{NO}_3\text{-N}$ and SRP on time were significant ($\text{NO}_3\text{-N}$: $R^2 = 0.69$, $P < 0.01$, SRP: $R^2 = 0.78$, $P < 0.001$); concentrations of $\text{NO}_3\text{-N}$ and SRP declined on the average by 0.05 and 0.007 $\text{mg L}^{-1} \text{ year}^{-1}$, respectively, between 1986 and 2000. In 2000, $\text{NO}_3\text{-N}$ and SRP averaged 2.19 and 0.047 mg L^{-1} , respectively. Total phosphorus and total nitrogen showed similar (significant) trends as SRP and nitrate. The discharge of biochemical oxygen demand (BOD_5) by major sewage treatment facilities upstream of the study reach significantly decreased during the observation method (Fig. 2). DOC concentrations averaged $3.0 \pm 0.7 \text{ mg C L}^{-1}$ and did not change with time.

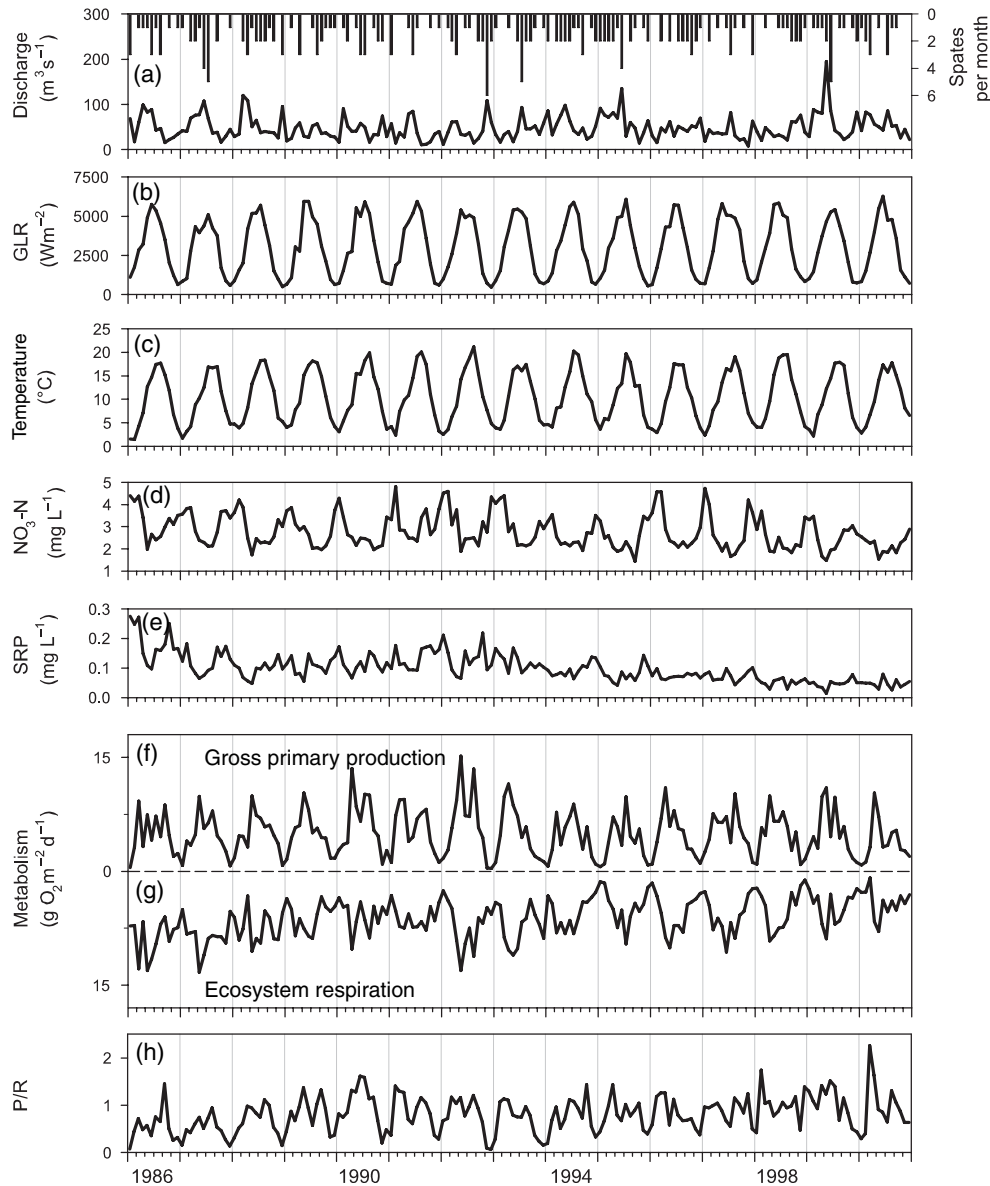


Fig. 1 (a) Number of spates with $Q_{\max} > 150 \text{ m}^3 \text{ s}^{-1}$ per month (bars) and monthly discharge (solid line). Monthly means of: (b) global radiation measured 12 km from the lower end of the study reach, (c) water temperature, (d) nitrate nitrogen, (e) soluble reactive phosphorus, (f) gross primary production, (g) ecosystem respiration) and (h) P/R.

Ecosystem metabolism

Mean seasonal metabolism patterns showed distinct seasonality (Fig. 3). Rates of GPP and ER reached annual maxima in May and subsequently declined to minimum values in December (ER) and January (GPP). The P/R ratio exhibited a weak bimodal pattern with an annual maximum in April and a local maximum in September; from November to January P/R were distinctly lower than during other times of the year.

Daily values. Gross primary production, and to a minor extent ER, exhibited substantial short-term variability that primarily reflected spate impact and subsequent recovery (Fig. 4). Flow peaks $>150 \text{ m}^3 \text{ s}^{-1}$ reduced GPP and ER on average by 49% and 19%, respectively. Smaller spates ($Q_{\max} < 150 \text{ m}^3 \text{ s}^{-1}$) occasionally coincided with reductions in GPP and ER (e.g. March 1991 and October 1994), suggesting that the disturbance threshold of $150 \text{ m}^3 \text{ s}^{-1}$ is conservative. In May 1992, both GPP and ER declined despite a relatively low and constant flow (Fig. 4); this

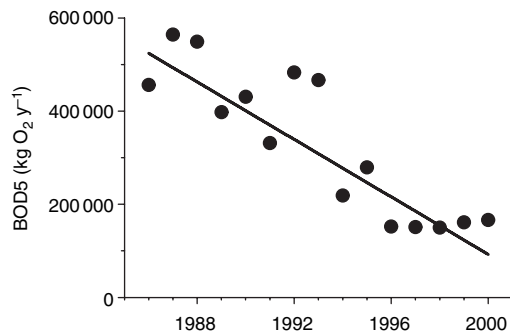


Fig. 2 Biological oxygen demand (BOD₅) annually discharged by the five major sewage treatment facilities located upstream of the study reach between 1986 and 2000.

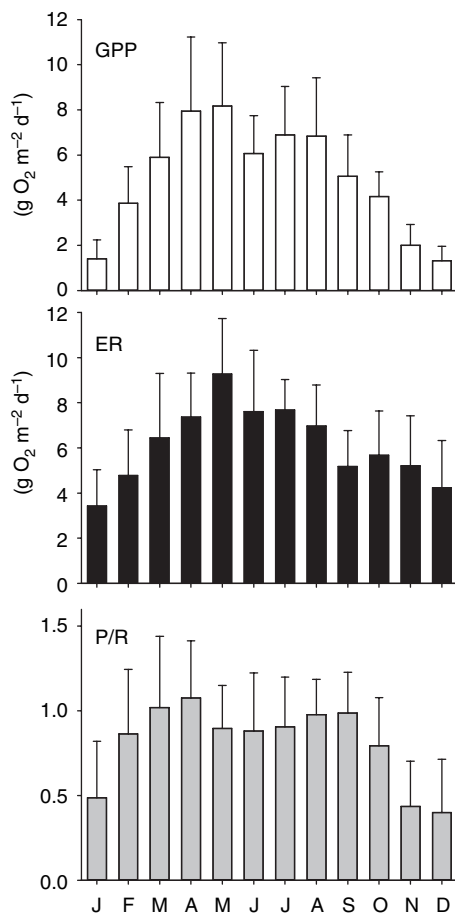


Fig. 3 Seasonal patterns of gross primary production (GPP), ecosystem respiration (ER), and P/R. Average monthly rates (1986–2000) + 1 SD.

phenomenon presumably reflects the sloughing of ageing biofilms and was observed approximately 10 times. Spates transiently reduced P/R because GPP was less resistant to spates than ER (mean R_{GPP} was

Table 1 Resistance and resilience of gross primary production (GPP): results of the stepwise multiple linear regression (backward procedure)

Independent variable	R^2
Resistance (R_{GPP})	
GPP_{bef} (–)	0.279
DS₁₅₀ (–)	0.429
<i>N</i> (–)	0.447
<i>Q</i> _{max} (–)	0.477
Resilience (m_{GPP})	
GLR (+)	0.425
<i>Q</i> (–)	0.430
<i>T</i> (–)	0.441

Bold indicates independent variables selected using the Schwarz Bayesian Criterion (Schwarz, 1978). Signs in parenthesis indicate whether the effect of independent variables on resistance or resilience is positive (+) or negative (–).

R_{GPP} , resistance of GPP (see eqn 2); m_{GPP} , slope of linear recovery trajectories of GPP; GPP_{bef}, gross primary production measured before a spate with peak flow >150 m³ s^{–1}; DS₁₅₀, days since the last spate with peak flow >150 m³ s^{–1}; Q_{max} , maximum discharge during a spate (>150 m³ s^{–1}); *N*, number of flow peaks (>150 m³ s^{–1}) during one flood event; GLR, average global radiation during the recovery period; *Q*, average discharge during the recovery period; *T*, average water temperature during the recovery period; R^2 , adjusted squared correlation coefficient.

significantly less than R_{ER} ; paired *t*-test: $P < 0.0001$, $n = 143$). GPP measured before a spate and time since the last spate with $Q_{max} > 150$ m³ s^{–1} explained 44% of the variation in R_{GPP} (Table 1). No relationship was found between R_{ER} and parameters such as ER measured before a spate or time since the last spate. Slopes of postspate recovery trajectories of GPP (m_{GPP}) and ER (m_{ER}) were significantly different (paired *t*-test: $P < 0.0001$, $n = 118$). Recovery of GPP varied significantly with season (ANOVA, $P < 0.05$), and global radiation explained 45% of the variation in m_{GPP} (Table 2, Fig. 5). Recovery of ER tended to be higher from April to June but differences between months were not significant and no significant relationship was found between m_{ER} and factors such as temperature or discharge.

Monthly values (Fig. 1g,f). STL decomposition of monthly mean GPP, ER and P/R revealed trends in seasonal components (Fig. 6). The amplitude of GPP declined during the first 7 years and subsequently increased again. ER changed from a trimodal to a bimodal pattern, and PR shifted from bimodality towards unimodality. Amplitudes in ER and PR

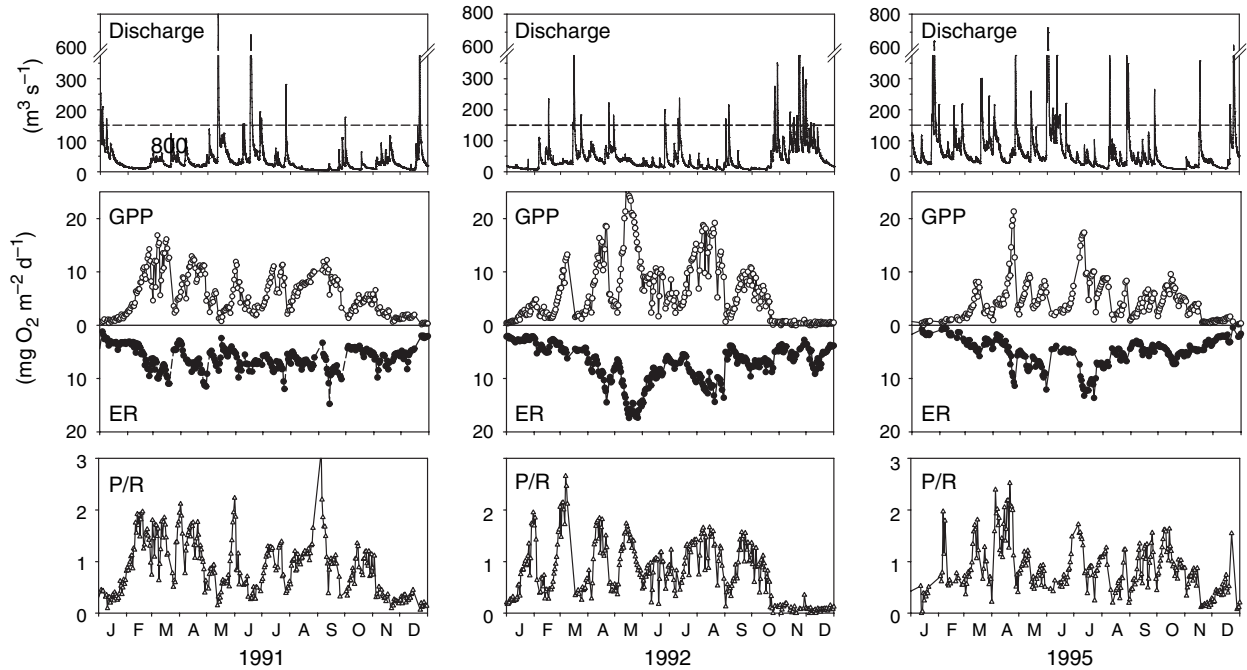


Fig. 4 Discharge, gross primary production (GPP), ecosystem metabolism (ER), and P/R ratio in 1991, 1992, and 1995. The dashed line in the upper panels indicates the disturbance threshold of $150 \text{ m}^3 \text{ s}^{-1}$. The number of spates with $Q_{\text{max}} > 150 \text{ m}^3 \text{ s}^{-1}$ was 10 in 1991, and 19 in 1992 and 1995.

Table 2 (A) Correlations between selected seasonal components of global radiation (GLR), water temperature (T), ecosystem respiration (ER), gross primary production (GPP) and P/R. $n = 180$ data pairs. (B) Correlations between the residual components (R) of the time series of monthly spates (R_N), maximum monthly discharge ($R_{Q_{\text{max}}}$), ecosystem respiration (R_{ER}), gross primary production (R_{GPP}) and P/R ($R_{\text{P/R}}$). $n = 180$ data pairs.

	GLR	T	ER	GPP
(A)				
T	0.857*			
ER	0.798*	0.0639*		
GPP	0.821*	0.610*	0.813*	
P/R	0.707*	0.526*	0.543*	0.856*
	R_N	$R_{Q_{\text{max}}}$	R_{ER}	R_{GPP}
(B)				
$R_{Q_{\text{max}}}$		0.466*		
R_{ER}	-0.377*	-0.262*		
R_{GPP}	-0.437*	-0.317*	0.603*	
$R_{\text{P/R}}$	-0.230*	-0.245*	n.s.	n.s.

*Significant ($P < 0.01$).
n.s., not significant ($P > 0.05$).

were relatively constant. Seasonal components contributed between 46% and 54% to the SS of GPP, ER and P/R. Correlations between seasonal components

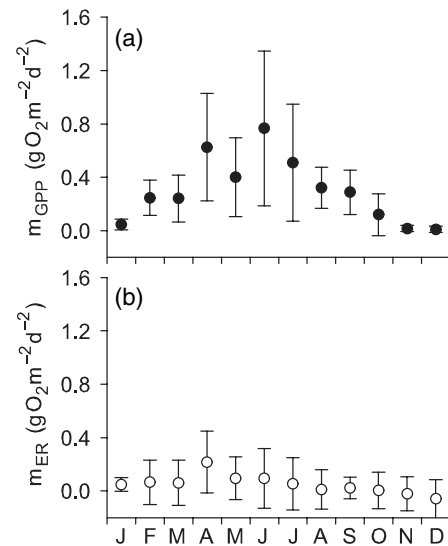


Fig. 5 Resilience of gross primary production (GPP) (a) and ecosystem respiration (ER) (b) during the annual cycle. m_{GPP} and m_{ER} are the slopes of linear functions describing GPP and ER as function of time since a spate with peak flow $>150 \text{ m}^3 \text{ s}^{-1}$.

of solar radiation, temperature and metabolism parameters were highly significant (Table 2). Autocorrelation analysis indicated random residual

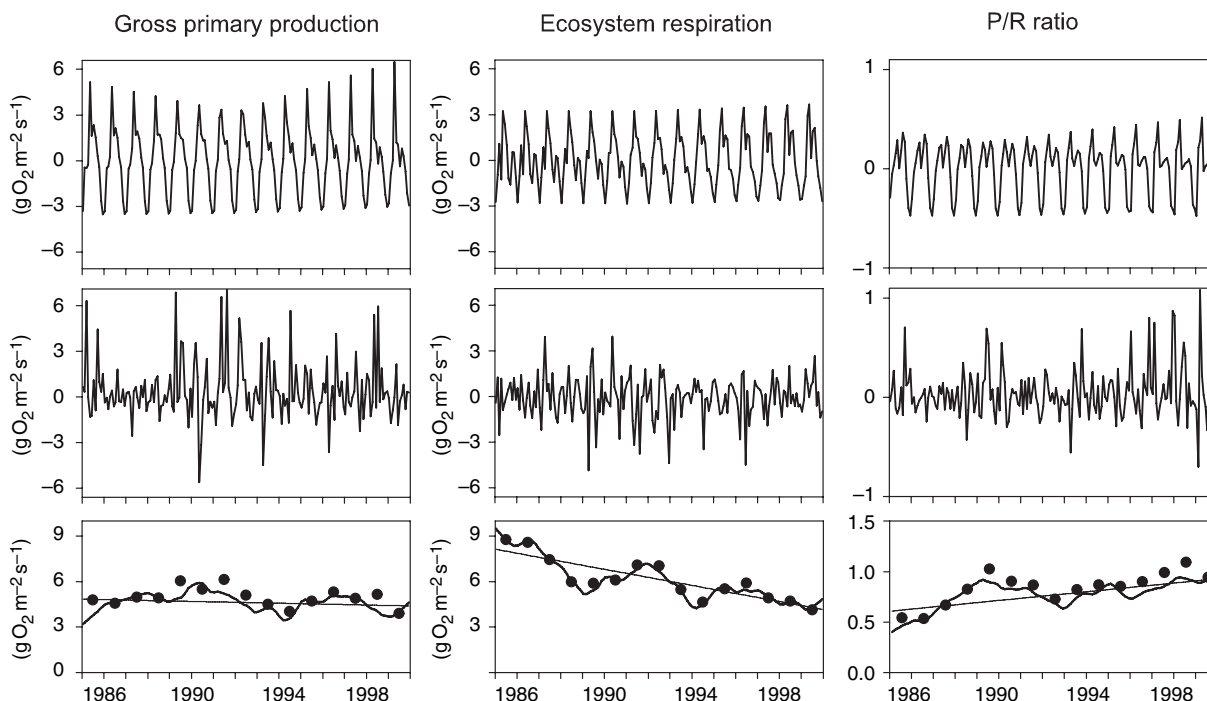


Fig. 6 Seasonal decomposition of gross primary production, ecosystem respiration and P/R performed with the STL procedure. Upper panels: seasonal component. Central panel: residual component. Lower panel: trend component. Straight lines = linear functions fitted to long-term trend. Seasonal and residual components are plotted as departures from the long-term mean. Filled circles are annual means.

components, except for ER showing a weak 9-month cycle. Residual components of ER, GPP and P/R, which added 28%, 39% and 44% to the SS of the each respective time series, were negatively correlated with residual components of disturbance related factors (Table 2). Linear regression of STL trend components of ER and P/R on time were significant (ER: $R^2 = 0.72$, $P < 0.01$, P/R: $R^2 = 0.47$, $P < 0.001$) and suggested an average annual decline of ER of $0.27 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ and an average annual increase of P/R of 0.022. SMLR resulted in a 3-parameter model for GPP (Table 3). This model explained 58% of the variation in monthly rates by global radiation and spates ($Q_{\text{max}} > 150 \text{ m}^3 \text{ s}^{-1}$) per month. The two-parameter model, with global radiation as the only independent variable, accounted for 49% of the variation in GPP. The SMLR procedure suggested a three-parameter model for ER with GPP and time since the beginning of the observation period as independent variables explaining 62% of the variation in ER. GPP accounted for 47% of the variation in ER. The rationale to use GPP as predictor of ER was that autotrophic communities may expend a

substantial fraction of GPP in respiration (e.g. Whittaker & Likens, 1973; Duarte & Cebrián, 1996).

Annual rates. Average annual rates of GPP and ER varied between 3.9 and $6.1 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$ and 4.1 and $8.8 \text{ g O}_2 \text{ m}^{-2} \text{ day}^{-1}$, respectively (Fig. 6). Annual P/R ratios increased from 0.53 in 1986 to about 1 in 2000. Coefficients of variation of metabolic parameters ranged from 13% (GPP) to 23% (ER) (Table 4). SMLR was used to evaluate the possible influence of temperature, discharge, global radiation, number of spates and water quality on annual metabolism rates but no significant relationship was found between these parameters and GPP. A two-parameter model with water quality (first principal component of annual $\text{NO}_3\text{-N}$, SRP and BOD_5) as independent variable explained 83% of the variation in ER.

Discussion

Results showed that annual metabolism patterns in the lower Thur River reflected both the impact of spates randomly distributed in time and the

Table 3 Gross primary production (GPP) and ecosystem respiration (ER): results of stepwise multiple linear regression analyses (backward procedure)

X	R ²
<i>Monthly rates (n = 180)</i>	
GPP	
GLR (+)	0.490
N (-)	0.582
Q _{max} (-)	0.588
NO ₃ (+)	0.692
SRP (+)	0.594
T (-)	0.594
ER	
GPP (+)	0.470
Time (-)	0.621
T (+)	0.628
Q (+)	0.634
N (-)	0.645
SRP (+)	0.645

Bold indicates independent variables selected using the Schwarz Bayesian Criterion (Schwarz, 1978). Signs in parenthesis indicate whether the effect of independent variables on GPP or ER is positive (+) or negative (-).

X, independent variables; GLR, global radiation (W m²); Q, monthly discharge (m³ s⁻¹); Q_{max}, monthly peak flow (m³ s⁻¹); T, water temperature (°C); Time, time (days) since 1 January 1986; SRP, soluble reactive phosphorus (µg L⁻¹); N, number of spates per month with peak flow >150 m³ s⁻¹; R², adjusted squared correlation coefficient.

predictable influence of the annual solar cycle. The study also showed a significant reduction in annual mean ER rates during the 15-year period that paralleled a gradual change in water quality. This change shifted ecosystem metabolism towards autotrophy because annual GPP was relatively stable in time.

Seasonal and stochastic variation

Bed moving spates and subsequent recovery were a source of variation in ecosystem metabolism in the lower Thur River. Spates reduced GPP and to a minor extent ER. This difference in resistance, which transi-

ently shifted ecosystem metabolism towards heterotrophy, may be explained by the partial separation of both processes in space (Naegeli & Uehlinger, 1997; Uehlinger & Naegeli, 1998). Autotrophic communities are restricted to the surface of the river bed and suffer more from the abrasive impact of suspended and moving bed sediments than substrata-contained microbial communities in the hyporheic zone. Reduction of GPP by spates was negatively related to the magnitude of prespate GPP, presumably reflecting increasing susceptibility of autotrophic biofilms to high flow with increasing biofilm density (Biggs & Close, 1989; Uehlinger, Bühler & Reichert, 1996). Spate-induced loss of autotrophs may substantially contribute to the reduction in ER because benthic algae respire 20–30% of GPP (Meyer, 1989; Duarte & Cebrián, 1996) and release dissolved organic matter that fuels respiration (Kaplan & Bott, 1982). During high flow, increased transport of particulate organic matter (including detached algae) to the hyporheic zone may enhance respiration and partly mitigate the reduction of heterotrophic activity (Jones, Fisher & Grimm, 1995; Naegeli *et al.*, 1995).

Bed moving spates reset ecosystem metabolism, especially GPP, which becomes relatively independent from the prespate state. Postspate recovery in metabolism rates determines the extent to which spate impacts endure in time. Slopes of GPP recovery trajectories exhibited distinct seasonal variation. From April to July, GPP reached prespate rates within 15–25 days (except when subsequent spates interrupted the recovery phase). Such fast recovery may be explained by favourable light conditions in combination with high concentrations of major nutrients. Low GPP rates between November and January reflected the impact of winter spates in combination with slow postspate recovery. Recovery of ER was low compared with GPP, particularly between April and July, and lacked significant seasonality. Differences in

Table 4 Variation in annual values of temperature (T), global radiation (GLR), discharge (Q), number of spates (N), gross primary production (GPP), ecosystem respiration (ER) and P/R. ER* = linear detrended ER[†], P/R* = GPP/ER*

	T (°C)	GLR (W m ²)	Q (m ³ s ⁻¹)	N (year ⁻¹)	GPP (g O ₂ m ⁻² day ⁻¹)	ER (g O ₂ m ⁻² day ⁻¹)	ER* (g O ₂ m ⁻² day ⁻¹)	P/R	P/R*
Mean	10.5	3025	48.4	15	5.0	6.2	4.3	0.8	1.2
SD	0.5	102	9.6	3	0.6	1.4	0.7	0.2	0.3
CV (%)	5	3	20	21	13	23	17	19	23

[†]The trend component T_i was determined by linear regression of ER_i on time (years) and ER* was calculated as ER*_i = ER_i - T_i.

postspate recovery in GPP and ER presumably reflect the different energy base of auto- and heterotrophic communities (Uehlinger & Naegeli, 1998) and account for the rapid shift from heterotrophy to autotrophy following bed moving spates, particularly from March to October. In nutrient-limited systems, spate impacts (e.g. reduced primary production) may be sustained for longer periods than in the Thur River because recovery of benthic primary producers depends on nutrient availability (Lohmann, Jones & Perkins, 1992; Valett *et al.*, 1994).

In the Thur River, time series of daily GPP, and to a minor extent also of ER, can be described as sequence of recovery periods frequently truncated by spates, i.e. variability of ecosystem metabolism is characterised by a distinct seasonal cycle (Fig. 3) to which substantial but short-term stochastic (aseasonal) variations are superimposed. This pattern seems to be typical for stream and rivers in the northern foothills of the Alps, where flashy flow regimes (*sensu* Poff & Ward, 1989) prevail (Uehlinger & Naegeli, 1998).

Annual patterns such as shown in Fig. 4 characterise ecosystem function in systems where short inter-disturbance periods prevent the expression of biotic interactions (e.g. disturbance controlled systems *sensu* Fisher & Grimm, 1991). A few observations indicate that variation due to biotic processes can also occur in the Thur River. The rapid decline in GPP and ER during moderate flow could be a consequence of biofilm ageing, which is paralleled by an increased susceptibility to the impact of bottom shear stress and, as consequence, enhanced algal sloughing. Nevertheless, such events play a minor role as sources of variability compared with the impact from spates.

Seasonal decomposition and regression analysis of mean monthly metabolism rates indicated that annual patterns are more influenced by the seasonal annual cycle than by frequent disturbance. Spates had a distinct impact on metabolism but were quite short episodes (average duration of periods with $Q_{\max} > 150 \text{ m}^3 \text{ s}^{-1} = 0.8 \text{ days}$) compared with relatively benign inter-spate periods (average duration = 24 days) in which metabolism recovers within the constraints imposed by season (primarily light and temperature).

Inter-annual variation

During the 15-year observation period, annual patterns of daily and monthly metabolism rates were

relatively uniform (Figs 1 & 4). Among the factors expected to control ecosystem metabolism, temperature and solar radiation showed minor variation among years (Fig. 1b,c, Table 4) and concentrations of major nutrients were above the level considered to be limiting, even at the end of the observation period. Inter-annual variation in GPP, and to a minor extent also in ER and P/R, was moderate (Table 4). Regression analysis provided no evidence that flow was a major source of variation in annual metabolism rates. Flow patterns were characterised by frequent and unpredictable bed-moving spates, but the number of such events varied moderately between years (Table 4). Because these events were of short duration and postspate recovery fast, their effect on ecosystem metabolism was transient. Substantial inter-annual variation in ecosystem metabolism can be expected when discharge patterns largely differ between years, for example, as consequence of variation in atmosphere–ocean coupling such as the El Niño Southern Oscillation (Molles & Dahm, 1990; Young & Huryn, 1996).

Long-term trends

From 1986 to 2000, annual GPP exhibited no directional change. In contrast, annual ER declined by approximately 50% during this period. This marked reduction in ER shifted ecosystem metabolism from heterotrophy (P/R approximately 0.5) towards autotrophy (P/R approximately 1) within a relatively short time period. Among factors considered to influence metabolism, concentrations of N and P decreased during the same period, $\text{NO}_3\text{-N}$ by 32% and SRP by 75%. This reduction reflected the continuous improvements of wastewater treatment facilities in the Thur catchment, including the ban of phosphate in detergents since 1986 and improved fertilisation techniques in agriculture (Jakob *et al.*, 2002). The transition from nutrient saturation to nutrient limitation ranges from 0.6 to $15 \mu\text{g SRP L}^{-1}$ for inorganic phosphorus and from 50 to $60 \mu\text{g L}^{-1}$ for inorganic nitrogen compounds (Grimm & Fisher, 1986; Bothwell, 1989; Newbold, 1992). However, in 2000 corresponding concentrations in the Thur River were still about three (SRP) to 30 ($\text{NO}_3\text{-N}$) times higher than the upper range of these limits, and may explain the lack of any apparent response of GPP to reduced nutrient availability. The decline in ER

could, to some extent, also reflect the decline in nutrient concentrations because nutrient availability influences decomposition of organic matter and microbial respiration (Suberkropp & Chauvet, 1995; Diez *et al.*, 2002; Stelzer, Heffernan & Likens, 2003). However, nutrient concentrations were still relatively high at the end of the observation period. Riparian vegetation, as a source of allochthonous organic matter, did not change substantially during the observation period, and a change in autotrophic respiration or respiration fuelled by algal exudates or decaying primary producers is less probable because GPP remained relatively constant. The reduction in ER probably resulted from enhanced removal of organic matter in wastewater treatment facilities discharging treated sewage into the Thur River. Wastewater treatment plants located upstream of the study reach reduced their annual BOD₅ discharge from 523 000 to 159 000 kg O₂ within the observation period. It is likely that the decline in ER reflect these changes in water quality but the reduction of the oxygen consumption in the study reach during the same period exceeds the reduction of the BOD load about threefold. This inconsistency may be in part attributed to the fact that BOD is an indirect measure for organic matter released by wastewater plants. The River Glatt, a small river (annual mean discharge 8.4 m³ s⁻¹) draining a densely populated area in the Swiss Plateau, is an other example, where declining ER has been explained by the improved performance of sewage treatment facilities (Uehlinger *et al.*, 2000).

Ecosystem stability

In the Thur River, bed moving spates are frequent (pulse) disturbances having a major impact on ecosystem metabolism although recovery is fast during most of the year. This pattern concurs with many studies showing low resistance and high resilience of communities and processes influenced by bed-moving spates (Fisher *et al.*, 1982; Grimm & Fisher, 1989; Matthaei, Uehlinger & Frutiger, 1997; Uehlinger & Naegeli, 1998). However, many disturbance studies spanned relatively short time periods (<1 year) or focused on one or two events only, and this limits conclusions on ecosystem stability and dynamics over periods of several years. The 15-year metabolism record showed that annual patterns of

ecosystem metabolism exhibited substantial stochastic (short-term) variation because of randomly occurring bed moving spates. These patterns showed a relatively high year-to-year constancy indicating the ability of the system to cope with spates such as the extreme event in May 1999 with peak flow 1127 m³ s⁻¹ and discharge >350 m³ s⁻¹ (flow threshold for disruption of the river bed surface layer) over 3.2 days. This constancy may result from the elimination of natural alluvial dynamics. The channelisation of the river prevented natural channel modifications even during extreme events such as the May 1999 flood (recurrence interval approximately 80 years). Before channelisation, a flood of this magnitude would have resulted in major changes because of channel avulsion, reshaping or redirecting meanders and changes in organic matter storage (Cummins *et al.*, 1983). Major modifications in river physical structures are expected to result in more persistent changes in ecosystem metabolism. The trend in ER reflects the release from a press disturbance (reversal of pollution and river eutrophication). The tight correlation between water quality and metabolism indicates that the system also is highly resilient to this disturbance.

Conclusions

Gross primary production and ER respond differently to disturbance by bed-moving spates. The different response presumably reflects the spatial separation of both processes and differences in the energy sources driving each process, including post-spate recovery. Annual patterns exhibiting distinct seasonal variation with stochastic variations superimposed were relatively uniform during the 15-year period. This stable behaviour reflects minor inter-annual climatic variation and, in particular, a disturbance regime characterised by frequent spates randomly distributed in time. Analysis of the metabolism record also implies that characterisation of ecosystem metabolism in a system with a flashy flow regime requires a relatively high temporal resolution. This study emphasises the suitability of river metabolism as a method to assess effects of gradual changes in water quality at the ecosystem level, and illustrates the high value of long-term oxygen (metabolism) records for characterising variability and stability of lotic ecosystems.

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References

- Acuña V., Giorgi A., Muñoz I., Uehlinger U. & Sabater S. (2004) Flow extremes and benthic organic matter shape the metabolism of a headwater Mediterranean stream. *Freshwater Biology*, **49**, 960–971.
- Biggs B.J. & Close M.E. (1989) Periphyton biomass dynamics in gravel bed rivers: the relative effects of flows and nutrients. *Freshwater Biology*, **22**, 209–231.
- Bothwell M.L. (1989) Phosphorus-limited growth dynamics of lotic periphytic diatom communities: areal biomass and cellular growth rate responses. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 1293–1301.
- Bott T.L. (1996) Primary Productivity and Community Respiration. In: *Methods in Stream Ecology* (Eds F.R. Hauer & G.A. Lamberti), pp. 533–556. Academic Press, San Diego.
- Bott T.L., Brock J.T., Dunn C.S., Naiman R.J., Ovink R.W. & Petersen R.C. (1985) Benthic community metabolism in 4 temperate stream systems: an inter-biome comparison and evaluation of the river continuum concept. *Hydrobiologia*, **123**, 3–46.
- Box G.E.P. & Jenkins G.M. (1976) *Time Series Analysis: Forecasting and Control*. Holdenday, Oakland, CA, USA.
- Chapra S.C. & DiTorro D.M. (1991) Delta method for estimating primary production, respiration and reaeration in streams. *Journal of Environmental Engineering*, **117**, 640–655.
- Cleveland W.S. (1993) *Visualizing Data*. Hobart Press, Summit, NJ, USA.
- Cummins K.W., Sedell J.R., Swanson F.J., Minshall G.W., Fisher S.G., Cushing C.E., Petersen R.C. & Vannote R.L. (1983) Organic matter budgets for stream ecosystems: problems in their evaluation. In *Stream Ecology. Application and Testing of General Ecological Theory* (Eds J.R. Barnes & G.W. Minshall), pp. 299–353. Plenum Press, New York.
- Diez J., Elosegui A., Chauvet E. & Pozo J. (2002) Breakdown of wood in the Agüera stream. *Freshwater Biology*, **47**, 2005–2215.
- Duarte C.M. & Cebrián J. (1996) The fate of marine autotrophic production. *Limnology and Oceanography*, **41**, 1758–1766.
- Elmore H.L. & West W.F. (1961) Effect of water temperature on stream reaeration. *Journal of the Sanitary Engineering Division of the American Society of Civil Engineers*, **87**, 59–71.
- Fisher S.G. & Grimm N.B. (1991) Stream and disturbance: are cross-ecosystem comparison useful. In: *Comparative Analysis of Ecosystems. Patterns, Mechanisms, and Theories* (Eds J. Cole, G. Lovett & S. Findlay), pp. 196–221. Springer, New York.
- Fisher S.G., Gray L.J., Grimm N.B. & Busch D.E. (1982) Temporal succession in a desert stream ecosystem following flash flooding. *Ecological Monographs*, **52**, 93–110.
- FOWG. (2004) *Hydrologisches Jahrbuch 2003*. Federal Office for Water and Geology, Berne, Switzerland.
- Grimm N.B. & Fisher S.G. (1986) Nitrogen limitation in a Sonoran Desert (Arizona, USA) stream. *Journal of the North American Benthological Society*, **5**, 2–15.
- Grimm N.B. & Fisher S.G. (1989) Stability of periphyton and macroinvertebrates to disturbance by flash floods in a desert stream. *Journal of the North American Benthological Society*, **8**, 293–297.
- Günter A. (1971) *Die kritische mittlere Sohlenschubspannung bei Geschiebemischungen unter Berücksichtigung der Deckschichtbildung und der turbulenzbedingten Sohlenschubspannungsschwankungen*. Mitteilung VAW. Mitteilungen VAW 3. Laboratory of Hydraulics, Hydrology and Glaciology, Swiss Federal Institute of Technology, Zürich.
- Hornberger G.M. & Kelly M.G. (1975) Atmospheric reaeration in a river using productivity analysis. *Journal of the Environmental Engineering Division – ASCE*, **101**, 729–739.
- Jakob A., Binderheim-Bankay E. & Davis J.S. (2002) National long-term surveillance of Swiss rivers. *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie*, **28**, 1101–1106.
- Jones, J.B. Jr, Fisher S.G. & Grimm N.B. (1995) Vertical hydrologic exchange and ecosystem metabolism in a Sonoran Desert stream. *Ecology*, **76**, 942–952.
- Kaplan L.A. & Bott T.L. (1982) Diel fluctuations of DOC generated by algae in a piedmont stream. *Limnology and Oceanography*, **27**, 1091–1100.
- Kelly M.G., Thyssen T. & Moeslund B. (1983) Light and the annual variation of oxygen- and carbon based

- measurements of productivity in a macrophyte-dominated river. *Limnology and Oceanography*, **28**, 503–515.
- Lohmann K., Jones J.R. & Perkins, B.D. (1992) Effects of nutrients enrichment and flood frequency on periphyton biomass in Northern Ozark streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 1198–1205.
- Matthaei C.D., Uehlinger U. & Frutiger A. (1997) Response of benthic invertebrates to natural versus experimental disturbance in a Swiss prealpine river. *Freshwater Biology*, **37**, 61–77.
- Meyer J.L. (1989) Can P/R ratio be used to assess the food base of stream ecosystems? A comment on Rosenfeld and Mackay (1987). *Oikos*, **54**, 119–121.
- Molles M.C. & Dahm C.N. (1990) A perspective on El Niño and La Niña global implications for stream ecology. *Journal of the North American Benthological Society*, **9**, 68–76.
- Naegeli M.W. & Uehlinger U. (1997) Contribution of the hyporheic zone to ecosystem metabolism in a prealpine gravel-bed river. *Journal of the North American Benthological Society*, **16**, 794–804.
- Naegeli M.W., Hartmann U., Meyer E.I. & Uehlinger U. (1995) POM-dynamics and community respiration in the sediments of a floodprone prealpine river (Necker, Switzerland). *Archiv für Hydrobiologie*, **133**, 339–347.
- Newbold D.J. (1992) Cycles and spirals of nutrients. In: *The Rivers Handbook. Hydrological and Ecological Principles* (Eds P. Calow & G.E. Petts), pp. 379–408. Blackwell, London.
- Odum H.T. (1956) Primary production in flowing waters. *Limnology and Oceanography*, **1**, 102–117.
- Poff L.N. & Ward J.V. (1989) Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 1805–1818.
- Schilling M., Hunziker R. & Hunzinger L. (1995) The effect of river training works on the sediment balance. In: *Proceedings of the International Congress Interpraevent* (Eds F. Zollinger & G. Fiebiger), pp. 209–220. Internationale Forschungsgesellschaft, Interpraevent Klagenfurt, Klagenfurt, Austria.
- Schwarz G. (1978) Estimating the dimension of a model. *Annals of Statistics*, **6**, 461–464.
- Servais P., Debecker E. & Billen G. (1984) Annual cycle of gross primary production and respiration in the Viroin River (Belgium). *Hydrobiologia*, **111**, 57–64.
- Stelzer R.S., Heffernan J. & Likens G.E. (2003) The influence of dissolved nutrients and particulate organic matter quality on microbial respiration and biomass in a forest stream. *Freshwater Biology*, **48**, 1925–1937.
- Suberkropp K. & Chauvet E. (1995) Regulation of leaf break down by fungi in streams: influences of water chemistry. *Ecology*, **76**, 1433–1445.
- Uehlinger U. (1993) Primary production and respiration in the outlet of an eutrophic lake (River Glatt, Switzerland). *Archiv für Hydrobiologie*, **128**, 39–55.
- Uehlinger U. (2000) Resistance and resilience of ecosystem metabolism in a flood-prone river system. *Freshwater Biology*, **45**, 319–332.
- Uehlinger U. & Naegeli M.W. (1998) Ecosystem metabolism, disturbance, and stability in a prealpine gravel bed river. *Journal of the North American Benthological Society*, **17**, 165–178.
- Uehlinger U., Bühner H. & Reichert P. (1996) Periphyton dynamics in a floodprone prealpine river: Evaluation of significant processes by modelling. *Freshwater Biology*, **36**, 249–263.
- Uehlinger U., König C. & Reichert P. (2000) Variability of photosynthesis-irradiance curves and ecosystem respiration in a small river. *Freshwater Biology*, **44**, 493–507.
- Valet H.M., Fisher S.G., Grimm N.B. & Camill P. (1994) Vertical hydrologic exchange and ecological stability of a desert stream ecosystem. *Ecology*, **75**, 548–560.
- Webster J.R. & Meyer J.L. (1997) Organic matter budgets for streams. *Journal of the North American Benthological Society*, **16**, 3–161.
- Whittaker R.H. & Likens G.E. (1973) Carbon in the biota. In: *Carbon and the Biosphere. Brookhaven Symposium in Biology* (Eds G.M. Woodwell & E.V. Pecan), pp. 281–302. Brookhaven National Laboratory, Upton, New York.
- Young R.G. & Huryn A.D. (1996) Interannual variation in discharge controls ecosystem metabolism along a grassland river continuum. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 2199–2211.

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