Limnol. Oceanogr., 51(3), 2006, 1443–1453

Regulation of nutrient uptake in eutrophic lowland streams

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Abstract

We studied nutrient uptake in relation to water chemistry, stream hydrodynamics, and ecosystem metabolism in two eutrophic lowland streams located near Berlin, Germany. Ambient nutrient uptake rates ranged from 0.180 to 12.880 g NO_3-N m^{-2} d^{-1}, from 0.035 to 0.517 g NH_4-N m^{-2} d^{-1}, and from 0.017 to 0.750 g PO_4-P m^{-2} d^{-1}. Temporal and spatial variability in nutrient uptake rates within single streams were mainly controlled by concentrations of metabolic substrates (i.e., nutrients, dissolved organic carbon, and dissolved oxygen) and rates of ecosystem metabolism, highlighting the importance of assimilative nutrient uptake. According to stoichiometric accounts, dissimilative uptake of dissolved inorganic nitrogen was an important uptake mechanism. Thus, nutrient uptake was subject to controls similar to those reported from pristine study sites, indicating that basic patterns of nutrient retention are comparable in pristine and eutrophic streams. In contrast to pristine streams, eutrophic streams exhibited long nutrient uptake lengths (in the range of several kilometers), as elevated uptake rates could only partially compensate for high nutrient loads. Our results indicate that ecosystem nutrient uptake is unable to efficiently reduce nutrient exports from the investigated eutrophic lowland streams.

The intrinsic ability of stream ecosystems to store or even eliminate inorganic nutrients is termed nutrient retention. Nutrient retention is generally analyzed by applying the nutrient spiraling concept, which combines the evaluation of the antagonistic processes of nutrient cycling and transport in running waters (Webster and Patten 1979; Newbold et al. 1981; Stream Solute Workshop 1990). In pristine headwater streams, nutrient retention has been demonstrated to effectively reduce nutrient loads (e.g., Peterson et al. 2001). These results give rise to the assumption that nutrient retention could potentially counteract water quality problems originating from point and diffuse anthropogenic sources. However, excessive nutrient loads due to wastewater discharge can cause low load-specific nutrient retention efficiencies (Haggard et al. 2001; Martí et al. 2004).

Under pristine conditions, channel morphology, hydrologic interaction between surface and hyporheic water, and the geologic origin and grain size of streambed sediments (Munn and Meyer 1990; Valett et al. 1996; Gücker and Boëchat 2004), as well as biological productivity and ambient nutrient concentration (Martí and Sabater 1996; Dodds et al. 2002; Hall and Tank 2003), appear to be important determinants of nutrient retention. However, the functioning of nutrient retention is especially interesting in eutrophic streams, whose nutrient exports affect downstream rivers, lakes, and estuaries. Nevertheless, little is known about the rates, mechanisms, and controls of nutrient uptake in eutrophic streams.

In this study, we examined nutrient uptake in two eutrophic lowland streams. To assess ammonium, nitrate, and phosphate uptake rates and lengths in relation to a variety of potential controls, such as water chemistry, stream hydrodynamics, and ecosystem metabolism, we conducted seasonal short-term nutrient addition experiments in four eutrophic stream reaches. We aimed to test the following four hypotheses:

1) Nutrient uptake rates in eutrophic lowland streams are high.
2) The temporal and spatial variability in nutrient uptake depends on the variability in ecosystem metabolism and nutrient concentrations.
3) Nutrient uptake capacities in eutrophic lowland streams are overwhelmed by high nutrient loads.
4) Ecosystem inorganic nitrogen : phosphorus uptake ratios differ from Redfield ratios because of the importance of dissimilative nitrogen uptake (i.e., nitrification and denitrification).

Methods

Site descriptions—Both investigated lowland streams, the Erpe and the Demnitzer Mill Brook (DMB), are tributaries to the River Spree in and upstream of Berlin, Germany. To account for different stream sizes, we studied

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Acknowledgments
We thank B. Kiergaßner, R. Biskupek, B. Schütze, and E. Nöthen for their assistance in the field and in the laboratory. T. Hintze, M. Graupe, H. Winkler, E. Zwirnmann, T. Rossoll, and J. Exner are acknowledged for their help with chemical measurements and for technical assistance. J. Gelbrecht and H. Lengsfeld provided valuable background information on the study sites. We also thank I. G. Boëchat, H. Fischer, M. Schulz, H. M. Valett, R. Willmott, and two anonymous reviewers for valuable comments on earlier versions of the manuscript. This research was funded by the European Union through the STREAMES project (EVK1-CT-2000-00081), which was initiated and headed by F. Sabater and E. Martí. B.G. is currently supported by the German Academy of Natural Scientists Leopoldina with funds from the German Federal Ministry of Education and Research (BMBF-LPD 9901/8-135).

a third-order section of the Erpe at 52°29′14″N and 13°38′42″E and a first-order section of the DMB at 52°25′14″N and 14°14′7″E. Agriculture is the dominant land use in the catchments of both investigated streams. Hence, the streams receive considerable nutrients through diffuse source inputs. Additionally, point sources of nutrients, such as tile drainages, septic tank spillways, and private and municipal sewage plants, contribute substantially to the high nutrient concentrations in these drainage systems (Köhler et al. 2002).

All studied stream reaches are eutrophic. In 2002, nutrient concentrations ranged from 0.03 to 0.3 mg L^{-1} NH_4-N, 0.8 to 16.4 mg L^{-1} NO_3-N, and 0.01 to 0.27 mg L^{-1} soluble reactive phosphorus (SRP) and followed typical seasonal patterns (Köhler et al. 2002). Highest SRP concentrations occur in summer, and highest concentrations of dissolved inorganic nitrogen (DIN) occur in winter. Organic carbon concentrations in the stream water do not exhibit discernible seasonal patterns and ranged from 4.8 to 11.2 mg L^{-1} dissolved organic carbon (DOC) and from 0.4 to 4.9 mg L^{-1} particulate organic carbon (POC) in 2002.

Large sections of both streams were incised and straightened in the 1970s. Primary production in the Erpe is dominated by submerged macrophytes (*Potamogeton pectinatus* L. and *Sparganium emersum* Rehmann) growing from May to September. In the smaller stream, the DMB, benthic diatom blooms occur in the unshaded channel in spring, while dense stands of emergent macrophytes (mainly *Phalaris arundinacea* L., *Glyceria maxima* [Hartman] Holmberg, and *G. fluitans* [L.] Brown) shade the stream channel from early summer to fall. In both streams, submerged and emergent macrophytes are removed annually in the fall by local water management authorities. The streambeds consist of clogged and anaerobic fine-sandy sediments with high contents of organic carbon (5.9% ± 2.2% dry weight; mean ± standard deviation).

Sampling—The temporal variability in nutrient uptake and in its controls was investigated in five seasonal campaigns in 2002. To account for spatial variability in these structurally homogeneous, incised and straightened streams, we chose two stream reaches in each stream, one of which was only affected by diffuse agricultural nutrient inputs (hereafter referred to as Erpe-D and DMB-D) and the other of which was affected by additional point-source inputs of nutrients by wastewater treatment plants (Erpe-P and DMB-P). In each sampling campaign, nutrient uptake as well as stream hydrodynamics were studied using short-term nutrient and conservative tracer release experiments (Stream Solute Workshop 1990). Ecosystem metabolism was measured with the dissolved oxygen (DO) change technique (Odum 1956; Marzolf et al. 1994). Simultaneously, water samples were taken and analyzed for background nutrient, DOC, and POC concentrations. Additionally, stream water was sampled weekly for physicochemical analyses.

Chemical analyses—Nitrate concentrations were determined by ion chromatography (CDD-6A, Shimadzu Deutschland) with electrochemical ion suppression (ERIS, Alltech Deutschland). We determined ammonium and SRP spectrophotometrically (Hach DR/2000) according to the German standard methods (Wasserchemische Gesellschaft 1992). DOC was quantified using a liquid chromatography–organic carbon detection system (DOC-Labor Huber), and total organic carbon (TOC) contents of seston were quantified with a thermal conductivity analyzer (Vario EL, Elementar).

Hydrodynamics—To investigate stream hydrodynamics as potential controls of nutrient uptake, short-term constant-rate conservative tracer addition experiments were conducted in each reach in each sampling campaign. To evenly distribute the injected tracer solution over the entire width of the advective channel, we used a branching hose system connected to a peristaltic pump. Known concentrations of NaCl (used as a conservative tracer in our experiments) were injected upstream of the studied stream reaches until a plateau concentration was observed at the end of the investigated reaches (Stream Solute Workshop 1990). Plateau concentrations resulted in increases in conductivity between 113 and 262 μS cm^{-1}, corresponding to the 0.11- to 0.32-fold measure of the background conductivity. Breakthrough curves of NaCl were recorded at intervals of 15 s at the start, in the middle, and also at the end of the investigated stream reaches using conductivity meters with data loggers (600XLM and 6920, Yellow Springs Instruments). Conductivity meters were calibrated with standard solutions and cross-calibrated with stream water directly before the experiments. Hydraulic parameters were estimated from the conservative tracer data by least-squares using OTIS-P, a one-dimensional advection–dispersion model that includes transient storage and lateral inflow (Runkel 1998). Transient solute storage, characterized by the transient storage zone size (A_S; i.e., the cross-sectional area of the storage zones), by the relative transient storage zone size (A_S/A; i.e., transient storage zone size divided by main channel cross-sectional area), and by the storage zone exchange coefficient (α; i.e., the fraction of water entering the storage zones per unit of time), describes the temporary detainment of solutes in zones of stagnant or slowly moving water (Harvey and Wagner 2000). Turnover times of water (T_W = [$1/\alpha$]; i.e., the residence time due to advection and longitudinal dispersion) and of storage (T_H = [$A_S/(\alpha A)$]; i.e., the residence time due to transient storage) were calculated from the model parameters. Hydraulic uptake lengths (S_H) were calculated as the product of T_W and average water velocities.

Ecosystem metabolism—To estimate whole-stream metabolism, which is another potential control of nutrient uptake, an open-system two-station diel oxygen mass balance technique was used (Marzolf et al. 1994). We measured DO concentrations at the start and end of each stream reach for 36 h using cross-calibrated DO meters with data loggers (600XLM and 6920, Yellow Springs Instruments).

To account for oxygen exchange between the stream water and the atmosphere, we estimated reaeration coefficients based on DO change rates and DO deficits at night. Here we used an adaptation of the single-station approach of Young and Huryn (1996), developed by E. Martí (pers. comm.). Briefly, we adopted the regression approach between DO change rates and DO deficit at night from Young and Huryn (1996), but we determined DO change rates as the difference between upstream and downstream DO concentrations corrected for average travel times. Normalized reaeration coefficients (K^{20}_{oxy}) obtained with the above-described method ranged from 18.1 to 73.8 d^{-1} and were in the range of data reported from other lowland streams (Thyssen and Erlandsen 1987) and other stream types (Melching and Flores 1999; Mulholland et al. 2001). To evaluate the reliability of our reaeration estimates, we conducted a short-term propane tracer experiment according to Marzolf et al. (1994), in parallel to a K^{20}_{oxy} estimation described above in the Erpe-D reach in May 2002. Reaeration measured by the "snap-shot" propane tracer method (K^{20}_{oxy}: 36.3) corresponded well with our estimate based on upstream/downstream DO differences (K^{20}_{oxy}: 34.6).

Community respiration (CR_{24}) and gross primary production (GPP) were calculated according to Marzolf et al. (1994), with the modification for air–water exchange of oxygen suggested by Young and Huryn (1998), and to obtain areal rates, we divided by the wetted bed surface area of the reach.

Nutrient uptake—To estimate nutrient uptake, we performed additions of combined ammonium and phosphate and combined nitrate and phosphate in parallel to conservative tracer injections (Stream Solute Workshop 1990). Single-nutrient addition experiments may cause methodological artifacts because they alter the DIN : SRP ratio. To avoid such artifacts, we conducted combined DIN and SRP injections and adjusted the DIN : SRP ratio of the injection solution to that of the stream water. Prior to each experiment and during the plateau phase, water samples were taken at eight equidistant stations along the stream reaches. In our experiments, experimental increases in ammonium, nitrate, and phosphate concentrations (I_C; i.e. experimental concentrations [C_{EXP}] divided by ambient concentrations [C_{AMB}]) ranged from 1.9 to 3.0. Using the conservative tracer results, we corrected concentrations of injected nutrients for dilution (Stream Solute Workshop 1990). However, dilution was small (i.e., <3.4%) and was detectable only in 7 out of the 20 samplings. Nutrient uptake length (S_W) was calculated as the negative inverse of the slope (k) of the regression between the natural logarithm of the dilution-corrected concentration of injected nutrients and the distance downstream, thus:

$$S_W = -\frac{1}{k} \quad (1)$$

Subsequently, areal nutrient uptake rates at ambient concentrations (U_{AMB}) were calculated as the product of discharge (Q) and C_{AMB} divided by the product of S_W and the width of the wet perimeter (w) of the stream reach (Stream Solute Workshop 1990):

$$U_{AMB} = \frac{Q \cdot C_{AMB}}{w \cdot S_W} \quad (2)$$

Uptake velocities (V_f) were calculated as the quotient of U_{AMB} and C_{AMB}:

$$V_f = \frac{U_{AMB}}{C_{AMB}} \quad (3)$$

Nutrient uptake length is a measure of a stream's load-specific nutrient uptake efficiency. According to the nutrient spiraling concept, uptake length is determined by the variability in specific nutrient load ([L/w]; i.e., nutrient load divided by stream width) and in areal nutrient uptake rate (U) (Stream Solute Workshop 1990). To evaluate nutrient dynamics in eutrophic streams, we visualized the $S_W - [L/w] - U$ continuum for our data set as well as for the data of Webster et al. (2003), from relatively pristine study sites, as a three-dimensional graph.

Molar ratios of ambient dissolved inorganic nitrogen (DIN; i.e., nitrate and ammonium) uptake rate (U_{DIN}) and phosphate uptake rate (U_{SRP}) were used to evaluate the importance of assimilative versus dissimilative DIN uptake processes. Molar $U_{DIN} : U_{SRP}$ ratios that are much higher than molar N : P ratios of aquatic organisms should indicate that biotic assimilation is not the dominant uptake process. Further, ratios between ambient nitrate uptake rate (U_{NO_3}) and DOC concentration (C_{DOC}) were calculated as a rough estimate of the availability of DOC to support denitrification.

To estimate the contribution of nitrification to ammonium uptake, we fitted a two-compartment model for ammonium and nitrate fluxes to the longitudinal nitrate concentration profile obtained during the ammonium addition experiments (Mulholland et al. 2000; Bernhardt et al. 2002). Ambient nitrification rates ($U^{NIT}_{NH_4}$) were expressed as fractions of ecosystem ammonium uptake (%) and as absolute rates (g NH_4-N m^{-2} d^{-1}). Further, ratios between $U^{NIT}_{NH_4}$ and DO concentration (C_{DO}) were calculated to compare the availability of DO to support nitrification in both streams.

Evaluation of the nutrient addition approach—The nutrient addition technique has been demonstrated to overestimate ambient uptake rates (Dodds et al. 2002) and uptake lengths (Mulholland et al. 2002), depending on the increase in concentration. Therefore, we tried to keep experimental increases in nutrient concentration (I_C) low. To evaluate the degree of overestimation in our study, we conducted a series of several separate short-term ammonium and nitrate addition experiments with increasingly higher nutrient concentrations from 14 to 16 August and 19 to 23 August in the DMB-D reach. Subsequently, uptake lengths (S_W) and uptake rates at experimental concentrations (U_{EXP}), as well as uptake rates at ambient concentrations (U_{AMB}), were calculated for each short-term addition, as described previously. For each series of experiments, we

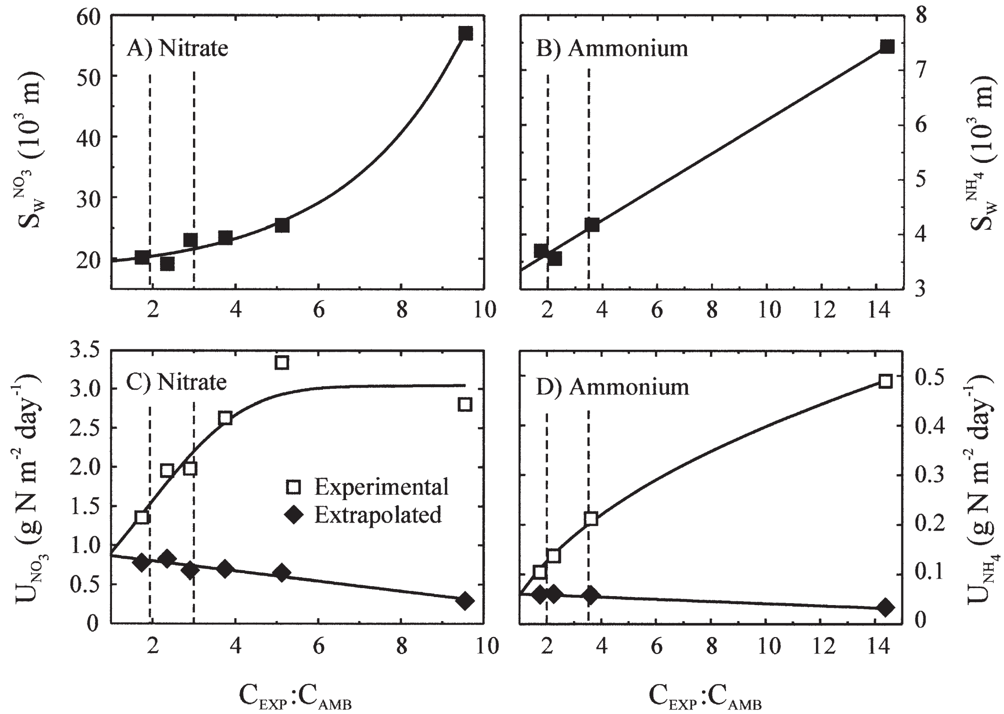

Fig. 1. (A, C) Short-term nitrate and (B, D) ammonium addition experiments with increasingly higher concentrations were performed to evaluate the reliability of the nutrient addition approach. Nutrient uptake lengths (filled squares), uptake rates at experimental concentration (open squares), and extrapolated ambient uptake rates (filled diamonds) are depicted as a function of concentration increase. C_{EXP} = experimental nutrient concentration; C_{AMB} = ambient nutrient concentration. Y-axis intercept points represent values of ambient uptake parameters corrected for methodological artifacts of the nutrient addition technique (P_{EXTRA}). Dotted lines indicate minimum and maximum increases in concentration (I_C) applied in the seasonal sampling campaigns. Y-axis values of intercept points between dotted lines and concentration kinetics of nutrient spiraling parameters (P_{SIM}) were used to estimate degrees of over- and underestimation of ambient parameters due to the nutrient addition technique.

extrapolated the relationship between S_W and I_C and between U and I_C back to the ambient nutrient concentration (ordinate intercept points in Fig. 1). Extrapolated values of S_W and U at ambient concentrations (P_{EXTRA}) should be a reliable measure of ambient nutrient uptake parameters (Dodds et al. 2002; Mulholland et al. 2002).

Subsequently, we introduced the minimum and maximum I_C values from all nutrient additions performed during the five seasonal sampling campaigns in all stream reaches (dotted lines in Fig. 1) into the regression equations between uptake parameters and I_C obtained from the above-described evaluation experiments. We thus simulated uptake parameters (P_{SIM}) that mimic the variability of over- or underestimation of ambient uptake in our data from the seasonal sampling campaigns. The percentage difference between the extrapolated uptake parameters at ambient concentrations (P_{EXTRA}) and the simulated uptake parameters accounting for I_C (P_{SIM}) was taken as an accuracy measure for our nutrient uptake results.

According to this calculation, the nitrate and ammonium uptake lengths measured with the experimental concentration increases (I_C) applied in our study overestimate ambient uptake lengths by 3.7% to 10.6% and 8.9% to 22.4%, respectively (Fig. 1A,B). The nitrate and ammonium uptake rates at ambient concentrations (U_{AMB}) reported here should underestimate ambient rates by 6.5% to 14.9% and 3.3% to 8.3%, respectively (Fig. 1C,D). Thus, the nutrient addition approach applied in our study caused moderate overestimation of ambient uptake lengths and moderate underestimation of ambient uptake rates for ammonium and nitrate. Interestingly, uptake rates were not saturated by the high experimental concentrations applied in our study (uptake rates at experimental concentration in Fig. 1C,D). Consequently, the high ambient nutrient concentrations did not saturate uptake rates as well. Hence, a basic assumption for the application of the nutrient addition method was fulfilled (Stream Solute Workshop 1990).

Statistical analyses—Data were first tested for normality and homogeneity of variances using Shapiro–Wilk, Bartlett, and Cochran tests. Spearman rank correlations were calculated to reveal relationships between metabolic variables and temperature and between ratios of DIN and SRP uptake rate and ratios of DIN and SRP concentration in the respective stream reaches.

Relationships between nutrient uptake and its potential determinants (i.e., the hydrochemical, morphometric, hydrodynamic, and metabolic variables measured) were explored by applying uni- and bivariate nonlinear regression analyses. Distributions of residuals and Durbin–Watson coefficients indicated that simple linear and multiple linear regression models did not adequately fit the data, even after logarithmic, square-root, or inverse transformation of variables. Bivariate nonlinear regression

Table 1. Hydrologic and hydrodynamic characteristics of the lowland stream reaches. Data are median values (ranges) from five sampling campaigns in 2002.

	Stream water depth, d (m)	Discharge, Q (m^3 s^{-1})	Velocity, v (m s^{-1})	Dispersion, D (m^2 s^{-1})	Cross-section area, A (m^2)	Cross-section area of storage zone, A_S (m^2)	$A_S : A$	Storage exchange coefficient, α (10^{-4} s^{-1})	Turnover time of water, T_W (min)	Turnover time of storage, T_H (min)	Hydraulic uptake length, S_H (m)
DMB-D	0.27 (0.22–0.30)	0.023 (0.013–0.040)	0.091 (0.080–0.133)	0.178 (0.144–0.202)	0.26 (0.16–0.30)	0.009 (0.005–0.012)	0.037 (0.016–0.076)	1.30 (1.23–1.32)	128 (126–135)	4.8 (2.0–9.7)	699 (613–1,013)
DMB-P	0.25 (0.20–0.31)	0.022 (0.012–0.042)	0.089 (0.081–0.132)	0.183 (0.130–0.197)	0.25 (0.15–0.32)	0.008 (0.005–0.011)	0.036 (0.016–0.074)	1.29 (1.28–1.39)	129 (120–131)	4.7 (1.9–9.6)	680 (624–973)
Erpe-D	0.46 (0.44–0.48)	0.164 (0.130–0.195)	0.150 (0.130–0.164)	0.198 (0.085–0.253)	1.30 (1.02–1.40)	0.095 (0.073–0.123)	0.072 (0.054–0.120)	5.40 (4.10–6.80)	31 (25–41)	2.3 (1.8–2.9)	283 (192–366)
Erpe-P	0.77 (0.72–0.79)	0.511 (0.468–0.607)	0.177 (0.161 – 0.200)	0.718 (0.527–1.142)	2.97 (2.88–3.04)	0.704 (0.649–0.848)	0.244 (0.214–0.286)	8.00 (7.47–8.90)	21 (19–22)	5.3 (4.4–5.7)	230 (193–254)

analyses were checked for multicollinearity and variance inflation.

To evaluate controls of seasonal nutrient uptake dynamics on different spatial scales, regression analyses were conducted using data on three different levels of aggregation using (1) seasonal data from single stream reaches, (2) pooled data from reaches of the same stream, and (3) pooled data from all stream reaches. Similar results derived from regression analyses performed at different levels of aggregation would indicate that the same independent variables that explain seasonal nutrient uptake dynamics can also explain spatial variability of nutrient uptake rates (i.e., variability in uptake rates between different reaches of the same stream or between different lowland streams)

Results

Hydrodynamics—Discharge, current velocity, and stream water depth remained quite stable during the sampling period, but differences were observed between the studied streams. Discharge and water depth in the third-order Erpe study reaches were greater than in the first-order DMB reaches, with median values measuring 7 to 22 and 1.7 to 3.1 times greater. Median discharge, current velocity, and stream depth in DMB reaches were very similar. Also, variation in discharge, current velocity, and stream depth was comparable in both DMB reaches. In contrast, median discharge and water depth in the Erpe-P reach were 3.1 and 1.7 times greater, respectively, than in the Erpe-D reach. Flow and water depth variation were higher in the Erpe-D reach as well (ranges: 0.139 vs. 0.065 m^3 s^{-1} and 7 vs. 4 cm, respectively). However, current velocities were only slightly higher in the Erpe-D reach (Table 1). Interestingly, absolute and normalized transient storage zone sizes were relatively high in the Erpe-P reach compared to the DMB reaches and the Erpe-D reach (Table 1). Concomitantly, the Erpe-P reach was the only stream reach under study exhibiting small side-pools.

Ecosystem metabolism—Community respiration dominated the ecosystem metabolism of the investigated stream reaches, so that GPP : CR_{24} ratios were generally less than one and values of net ecosystem production (NEP) less than zero (Table 2). In only 1 out of 20 measurements did GPP : CR_{24} ratios and NEP slightly exceed values of one and zero, respectively. Rates of GPP and CR_{24} exhibited a pronounced seasonal variability and ranged from <0.1 and 3.9 g O_2 m^{-2} d^{-1}, respectively, in winter to 58.9 and 69.5 g O_2 m^{-2} d^{-1} in spring.

In both studied reaches of the Erpe, rates of GPP and CR_{24} were positively correlated with temperature (Spearman rank correlations, $r > 0.90$, $p < 0.05$, $n = 5$). In the DMB, no positive relationships between ecosystem metabolism and temperature were observed because of the presence of emergent macrophytes, which did not contribute to instream DO production but shaded the stream channel in summer, when temperatures were high. Accordingly, rates of instream GPP tended to be inversely related to the biomass of emergent macrophytes (Gücker, et al.

Table 2. Ecosystem metabolism of the lowland stream reaches. Data are median values (ranges) from five sampling campaigns in 2002.

	Gross primary production, GPP (g DO m^{-2} d^{-1})	Community respiration, CR_{24} (g DO m^{-2} d^{-1})	GPP : CR_{24}	Net ecosystem production, NEP (g DO m^{-2} d^{-1})
DMB-D	3.74 (0.05–18.01)	24.3 (3.9–33.8)	0.11 (0.01–0.74)	−13.1 (−30.1 to −3.8)
DMB-P	2.60 (0.02–58.92)	35.1 (4.4–52.4)	0.07 (<0.01–1.12)	−16.6 (−35.5 to 6.5)
Erpe-D	8.47 (0.07–32.13)	12.4 (6.1–33.1)	0.50 (0.01–1.00)	−6.0 (−16.7 to −0.1)
Erpe-P	27.53 (0.05–46.55)	59.2 (17.6–69.5)	0.40 (<0.01–0.79)	−21.5 (−42.0 to −12.7)

2006) in the DMB-D and the DMB-P reach when data from the December sampling campaign (with low metabolic rates due to low temperature) were excluded from the analyses (Spearman rank correlations, $r < -0.89$, $p = 0.051$ and 0.106, $n = 4$). In the DMB, the highest rates of GPP occurred during the diatom bloom in the unshaded channel in spring.

Nutrient uptake—Ambient nutrient uptake rates exhibited a high temporal variability and ranged from 0.035 to 0.517 g NH_4-N m^{-2} d^{-1}, from 0.180 to 12.880 g NO_3-N m^{-2} d^{-1}, and from 0.017 to 0.750 g SRP m^{-2} d^{-1} (Table 3; Fig. 2, for ammonium and nitrate). In winter (i.e., the December sampling campaign), uptake rates were lower than in other seasons. However, uptake rates did not show a systematic seasonal pattern from early spring to fall. In the Erpe-P reach, nitrate and phosphate uptake rates were higher than in the other stream reaches (Table 3). Vertical uptake velocities (V_f) ranged from 3.9×10^{-3} to 6.0×10^{-2} mm s^{-1} for ammonium, from 2.1×10^{-4} to 2.8×10^{-2} mm s^{-1} for nitrate, and from 4.2×10^{-3} to 6.9×10^{-2} mm s^{-1} for phosphate. As was the case with uptake rates, uptake lengths showed a high temporal variability and ranged from 1,310 to 30,657 m for ammonium, from 4,601 to 167,763 m for nitrate, and from 960 to 9,358 m for phosphate (Table 3; Fig. 2, for ammonium and nitrate). Moreover, uptake lengths were higher in winter than in other seasons. The Erpe-P reach exhibited higher uptake lengths of ammonium and phosphate, but lower uptake lengths of nitrate than the other stream reaches (Table 3).

Estimated ambient nitrification rates ($U_{NH_4}^{NIT}$) ranged from 0.008 to 0.238 g NH_4-N m^{-2} d^{-1} (Table 3). In the Erpe, 63% (36 to 89; median and range) of the ammonium uptake during the addition experiments was due to nitrification. In the DMB, significantly less of the ammonium taken up was nitrified (paired t-test, $p < 0.01$, $n = 10$). Here only 29% (7 to 61) of the ecosystem ammonium uptake was due to nitrification. According to

Table 3. Ecosystem nutrient uptake of the investigated lowland stream reaches. Data from five sampling campaigns in 2002.

	Sampling campaign	Ammonium uptake rate, U_{NH_4} (g N m^{-2} d^{-1})	Nitrification rate, $U_{NH_4}^{NIT}$ (% U_{NH_4})	Ammonium uptake length, $S_W^{NH_4}$ (m)	Nitrate uptake rate, U_{NO_3} (g N m^{-2} d^{-1})	Nitrate uptake length, $S_W^{NO_3}$ (m)	Phosphate uptake rate, U_{PO_4} (g P m^{-2} d^{-1})	Phosphate uptake length, $S_W^{PO_4}$ (m)
DMB-D	Spring	0.109	7	1,777	2.11	17,977	0.081	960
	Early summer	0.061	16	3,404	0.69	23,081	0.070	2,142
	Late summer	0.188	34	1,310	0.38	10,304	0.071	2,074
	Fall	0.160	23	1,928	0.36	28,860	0.030	7,087
	Winter	0.035	62	8,421	0.29	167,763	0.017	8,932
DMB-P	Spring	0.085	9	2,486	1.98	20,946	0.077	1,551
	Early summer	0.066	22	3,641	0.83	19,082	0.072	2,107
	Late summer	0.097	41	2,885	0.18	27,534	0.041	4,180
	Fall	0.117	36	3,077	0.24	47,834	0.046	4,783
	Winter	0.050	57	6,643	0.47	121,902	0.024	8,100
Erpe-D	Spring	0.214	55	4,720	1.83	25,552	0.037	2,322
	Early summer	0.282	54	1,367	1.31	8,444	0.152	974
	Late summer	0.174	36	1,586	0.39	11,529	0.185	1,436
	Fall	0.059	79	2,094	0.19	18,569	0.086	1,637
	Winter	0.112	73	4,914	0.41	38,184	0.017	4,670
Erpe-P	Spring	0.307	64	7,665	11.38	8,595	0.262	4,821
	Early summer	0.383	62	2,162	12.88	4,601	0.750	3,645
	Late summer	0.517	44	2,028	7.96	6,977	0.578	4,502
	Fall	0.240	76	5,609	5.00	13,534	0.398	5,369
	Winter	0.076	89	30,657	5.01	25,695	0.178	9,359

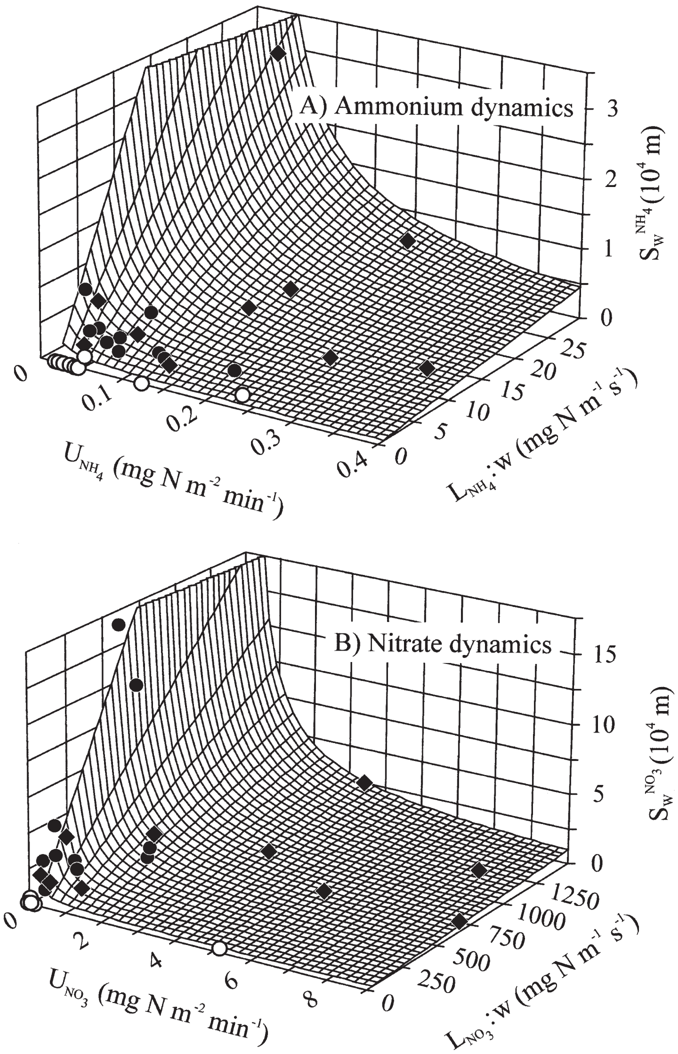

Fig. 2. Patterns of (A) ammonium and (B) nitrate uptake and transport in the eutrophic lowland streams (DMB: filled circles; Erpe: diamonds) compared to the data reported by Webster et al. (2003) from more pristine streams (open circles). Note that we report data from two streams, each studied in two stream reaches on five dates, whereas Webster et al. (2003) reported data from 11 streams without replication.

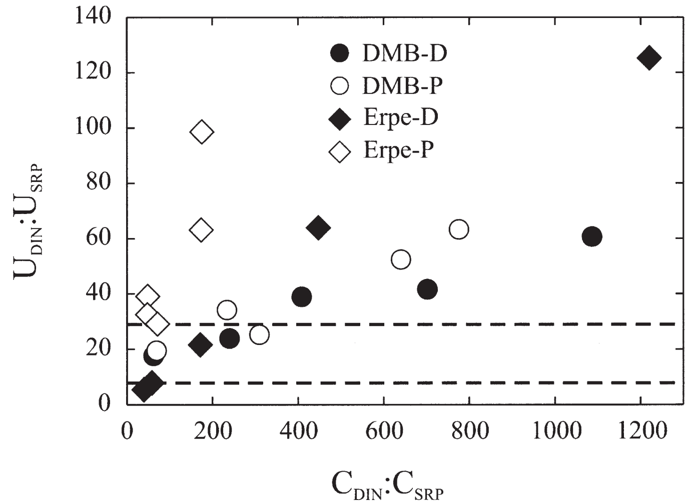

Fig. 3. Stoichiometric evaluation of DIN uptake in the eutrophic lowland streams. $U_{DIN} : U_{SRP}$ ratios higher than the range of N : P ratios reported for freshwater organisms indicate that dissimilative nitrogen uptake occurs. Dashed lines indicate the N : P range reported for freshwater organisms.

paired Wilcoxon tests ($p < 0.05$, $n = 10$), $U_{NH_4}^{NIT} : C_{DO}$ as well as $U_{NO_3} : C_{DOC}$ ratios in the Erpe were significantly higher than the respective ratios in the DMB.

Relationships between nutrient uptake and its potential determinants—Significant relationships between molar $U_{DIN} : U_{SRP}$ ratios and molar $C_{DIN} : C_{SRP}$ ratios (Fig. 3) were revealed in the DMB ($r = 0.93$, $p < 0.01$, $n = 10$) and in the Erpe ($r = 0.78$, $p < 0.01$, $n = 10$), as well as for pooled data from both streams ($r = 0.68$, $p < 0.01$, $n = 20$). Molar ratios between DIN and SRP concentrations ($C_{DIN} : C_{SRP}$) and between DIN and SRP uptake rates ($U_{DIN} : U_{SRP}$) were 173 (41 to 1,220; median and range) and 37 (5 to 125), respectively (Fig. 3).

We found several significant ($p < 0.05$) and marginally significant ($p < 0.1$) nonlinear relationships between environmental variables and ambient phosphate, nitrate, and ammonium uptake rates (U_{AMB}) when conducting regression analyses for the seasonal data of single stream reaches. Similar (i.e., the same independent variables and similar regression models) but more significant relationships emerged when data from both reaches of the respective stream were pooled (Table 4), indicating that the same independent variables can also explain spatial variability of nutrient uptake rates within the same stream. No significant relationships were detected after pooling data from both streams, indicating that the controls of nutrient uptake differ between the studied streams.

In the DMB, ambient nutrient uptake rates were positively related to ambient nutrient concentrations and metabolic rates (Table 4, Eqs. 1–5). Also, phosphate uptake rates in the Erpe were positively related to ambient phosphate concentrations and metabolic rates (Table 4, Eqs. 6, 7). However, variability in nitrate and ammonium uptake rates in the Erpe was explained by different independent variables (Table 4, Eqs. 9, 10). Here, rates of nitrate uptake were best explained by concentrations of DOC. Ammonium uptake rates were most closely related to ambient ammonium and DO concentrations. Interestingly, no significant relationships between uptake rates and stream hydrodynamics were found in either stream ($p > 0.1$), although there was considerable temporal and spatial variability in stream hydrodynamics.

Discussion

Nutrient uptake—Areal nutrient uptake rates measured in our study were generally high compared with values presented in previous studies (e.g., Doyle et al. 2003; Webster et al. 2003). In contrast, mass transfer coefficients (i.e., uptake rates normalized for concentration) were generally low, indicating that from the intersite perspective, nutrient uptake rate in the studied eutrophic streams was

Table 4. Significant nonlinear relationships between nutrient uptake and its potential determinants.†

	Regression model	df adj. r^2	df	F
DMB	$U_{\mathrm{PO_4}}=0.052\ C_{PO_4}^{0.18}\ GPP^{0.18}$ (1)	0.81***	8	38.3
	$U_{\mathrm{PO_4}}=-3.55+3.6\ GPP^{0.0014}$ (2)	0.61*	9	8.7
	$U_{\mathrm{NO_3}}=0.14+0.0013\ C_{NO_3}^{2.5}-20.6\ CR_{24}^{-2.0}$ (3)	0.97***	8	175.3
	$\ln(U_{\mathrm{NO_3}})=-2.2+0.16\ C_{NO_3}-1.6\ e^{-GPP}$ (4)	0.96***	8	160.1
	$U_{\mathrm{NH_4}}=0.034+0.41\ C_{NH_4}^{3.0}+0.022\ GPP^{0.50}$ (5)	0.74*	8	16.8
Erpe	$U_{\mathrm{PO_4}}=0.059+3.6\ C_{PO_4}^{2.0}+0.0027\ e^{CR_{24}(17CR_{24})^{-1.0}}$ (6)	0.90***	8	49.7
	$U_{\mathrm{PO_4}}=0.073-1.8\ C_{PO_4}\ \ln(C_{PO_4})^{-1.0}-0.083\ e^{-GPP}$ (7)	0.89***	8	42.8
	$U_{\mathrm{PO_4}}=0.013^{\ C_{PO_4}\ 0.063^{-1.0}}$ (8)	0.66**	9	22.4
	$U_{\mathrm{NO_3}}^{0.50}=0.080\ DOC^{2.5}$ (9)	0.97***	9	322.6
	$U_{\mathrm{NH_4}}=-1.4+0.0063\ CR_{24}+0.62\ \ln(DO)$ (10)	0.46*	8	6.5

† C, nutrient concentration (mg L^{-1}); CR_{24}, community respiration (g DO m^{-2} d^{-1}); DO, dissolved oxygen (mg L^{-1}); DOC, dissolved organic carbon (mg L^{-1}); GPP, gross primary production (g DO m^{-2} d^{-1}); NH_4, ammonium (NH_4-N); NO_3, nitrate (NO_3-N); PO_4, phosphate (SRP); U, uptake rate (mg m^{-2} min^{-1}).
* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

low in relation to nutrient supply. Concomitantly, uptake lengths in the studied streams were in the range of kilometers. According to nutrient spiraling theory (Stream Solute Workshop 1990), long uptake lengths indicate that uptake processes cannot efficiently compensate for nutrient loads. In this sense, uptake lengths in the kilometer range (e.g., after wastewater discharge) indicate an overload of the system (Haggard et al. 2001; Martí et al. 2004). In our study, ammonium uptake lengths were much shorter than nitrate uptake lengths. For energetic reasons, ammonium is the preferentially assimilated nitrogen compound (Ward and Wetzel 1980). Moreover, intense nitrification due to well-oxygenated stream water contributed significantly to ecosystem ammonium uptake and consequently also to the relatively short ammonium uptake lengths.

Uptake processes—The molar $U_{\mathrm{DIN}} : U_{\mathrm{SRP}}$ ratio of 37 (5 to 125; median and range) indicates that DIN uptake was at least partially decoupled from biotic assimilation (Fig. 3), as molar N : P ratios of aquatic organisms should vary between 7 and 30 (Sommer 1994; Chrzanowski and Kyle 1996). Further, molar $U_{\mathrm{DIN}} : U_{\mathrm{SRP}}$ ratios correlated with molar $C_{\mathrm{DIN}} : C_{\mathrm{SRP}}$ ratios, despite the fact that phosphorus was the stoichiometrically least-abundant inorganic nutrient in the studied streams (Fig. 3). Hence, dissimilative nitrogen uptake processes likely contributed heavily to DIN uptake and made the community's relative nitrogen demand (i.e., $U_{\mathrm{DIN}} : U_{\mathrm{SRP}}$ ratios) fairly different from Redfield ratios, even at low $C_{\mathrm{DIN}} : C_{\mathrm{SRP}}$ ratios (Fig. 3, lower left part). As nitrate uptake dominated total DIN uptake (Table 3), denitrification should account for much of the dissimilative DIN uptake in the investigated streams.

It is worth noting that $U_{\mathrm{DIN}} : U_{\mathrm{SRP}}$ ratios in the investigated eutrophic streams were much lower than $C_{\mathrm{DIN}} : C_{\mathrm{SRP}}$ ratios but were still much higher than Redfield ratios (Fig. 3). Hence, nutrient concentration ratios may neither be indicative of the relative rates of nutrient cycling nor be of nutrient limitation in these eutrophic streams. Consequently, nutrient concentration ratios should be interpreted with caution not only for pristine but also for eutrophic streams (Dodds 2003).

Our nutrient addition experiments could not separate biotic uptake processes from abiotic adsorption to the stream sediments, which might be another important uptake mechanism. However, a clear separation between abiotic and biotic processes might generally be problematic, as both processes may interact (i.e., that biological uptake can occur after initial abiotic adsorption to the sediments; Peterson et al. 2001). Adsorption has been demonstrated to be an important uptake mechanism for phosphate and ammonium in oligotrophic streams (Mulholland et al. 1990; Triska et al. 1994). In the nearby mesotrophic River Spree, whose sediments exhibit a geochemical composition similar to the ones observed in our streams, phosphate sorption processes of sediments were found to be negligible (Schulz and Herzog 2004), indicating that adsorption sites for nutrients may already be occupied in streams with constantly high nutrient concentrations. For ammonium, nitrification rates of up to 89% of ecosystem ammonium uptake illustrate that abiotic sorption may not be the dominating process.

Relationships between nutrient uptake and its potential determinants—In these lowland streams, nutrient uptake rates were related to concentrations of metabolic substrates (i.e., nutrients, DOC, and DO) and to rates of ecosystem metabolism. No relationships between nutrient uptake rates and hydrodynamic variables were observed. Hydrodynamic variables were in the range of data reported in the literature (e.g., Runkel 2002; Webster et al. 2003) but exhibited typical traits of deep, soft-bottom lowland streams, such as high values of longitudinal dispersion and relatively small values of Manning's roughness coefficients (Sukhodolov et al. 1997; Wilcock et al. 1999). Also, the low values of normalized transient storage sizes ($A_S : A$) compared to reported values (Runkel 2002) are not surprising, as the fine-sandy organic sediments present in the studied streams should not exhibit extended hyporheic zones (Morrice et al. 1997). We hypothesize that variability in hydrodynamics was too small in these incised and straightened streams, so that hydrodynamics did not exert control on uptake rates. Such relationships were also absent in an interbiome comparison of ammonium uptake in 11 hydrodynamically relatively similar streams, in which the assimilative nitrogen demand of the stream biota was assumed to control DIN uptake (Webster et al. 2003). Thus, relationships between nutrient uptake and stream hydrodynamics are more likely to be found in regional comparisons of morphologically contrasting stream reaches (Gücker and Boëchat 2004).

In contrast, most of the seasonal and spatial variability in nutrient uptake rates within single lowland streams was explained by both concentrations of metabolic substrates and rates of ecosystem metabolism (Table 3). Rates of GPP and CR_{24} were generally high compared with the range of data that has been reported for pristine streams (Lamberti and Steinmann 1997; Mulholland et al. 2001; Webster et al. 2003). Maximum rates of GPP and CR_{24} in the Erpe-P reach were among the highest in the literature. In fact, eutrophic lowland streams have previously been demonstrated to exhibit extremely high rates of GPP and CR_{24} (Körner 1997), indicating a high assimilative demand for inorganic nutrients.

In the DMB, temporal and spatial variability in the uptake rates of all inorganic nutrients was best predicted by both nutrient concentrations and metabolic rates. Relationships between nutrient uptake rate and nutrient concentration can generally be expected in pristine streams, in which uptake rates are not saturated and variation in nutrient concentrations occurs (Dodds et al. 2002; Mulholland et al. 2002). Also, relationships between nutrient uptake rate and ecosystem metabolism have previously been found in pristine streams (Mulholland et al. 2000; Hall and Tank 2003). Here we provide evidence that these relationships are also valid for incised and straightened, eutrophic streams.

In the Erpe, additional metabolic substrates (i.e., DO and DOC) were important for ammonium and nitrate uptake, respectively. A potential explanation for these differences is the supply of metabolic substrates for nitrification and denitrification, as indicated by ratios of ammonium uptake rate due to nitrification and DO concentration ($U_{NH_4}^{NIT} : C_{DO}$) and ratios of nitrate uptake and DOC concentration ($U_{NO_3} : C_{DOC}$), respectively. In the Erpe, $U_{NH_4}^{NIT} : C_{DO}$ and $U_{NO_3} : C_{DOC}$ ratios were significantly higher than the respective ratios in the DMB, indicating a poorer supply of these metabolic substrates for nitrification and denitrification in the Erpe. This indicates that a poorer supply of DO and DOC to nitrification and denitrification in the Erpe caused a significant dependency of DIN uptake rates on these metabolic substrates.

Nutrient uptake efficiency of eutrophic streams—In contrast to areal nutrient uptake rate (U), uptake length (S_W) is a measure of the load-specific nutrient uptake efficiency of streams. Variability in U and specific nutrient load (L/w) determines S_W (Stream Solute Workshop 1990). In our data set, considerable independent variability in both L/w and U occurred, so that variation in S_W could not be attributed to a single parameter (Fig. 2). However, compared with more pristine streams, the relative importance of variability in L/w in determining S_W was greater (Fig. 2).

Specific nutrient load (L/w) is nutrient concentration (C) multiplied by specific discharge (Q/w). In our data set, C varies by factors of 27 for SRP, 21 for NO_3-N, and 10 for NH_4-N, whereas Q/w varies by a factor of 13. Therefore, variability in C seems to be more important in determining S_W of SRP and NO_3-N than variability in Q/w.

Moreover, a comparison between our data set from human-altered, eutrophic streams and the data reported by Webster et al. (2003) for more pristine study sites reveals that, from the intersite perspective, high ammonium (Fig. 2A) and nitrate (Fig. 2B) uptake lengths in our study were caused by high DIN loads. Resulting increases in uptake rates could only to a minor degree compensate for these high DIN loads.

Research on lotic ecosystem functioning has concentrated on relatively pristine streams. In studies of human-altered streams, ecosystem processes such as nutrient spiraling and productivity have been widely ignored (Paul and Meyer 2001). Recently, Royer et al. (2004) and Inwood et al. (2005) examined sedimentary denitrification, which is one of the key processes affecting ecosystem nitrogen uptake in pristine streams, in eutrophic streams. Interestingly, the authors concluded that this process was unable to significantly reduce nitrate export from the investigated eutrophic headwater streams. Here we presented a comprehensive analysis of nutrient uptake in two incised and straightened, eutrophic lowland streams and evaluated the regulation of nutrient uptake efficiency in such streams.

Nutrient uptake rates were related to both concentrations of metabolic substrates and rates of ecosystem metabolism, highlighting the importance of assimilative nutrient uptake. Furthermore, dissimilative DIN uptake was an important uptake mechanism. Hence, nutrient uptake in these eutrophic streams was subjected to similar controls as in more pristine streams, indicating that the qualitative nature of nutrient retention is comparable in pristine and eutrophic stream ecosystems. From the intersite perspective, absolute uptake rates were high, whereas concentration-specific uptake rates (i.e., V_f) were low. Thus, uptake rates could only to a very limited degree compensate for high nutrient loads, resulting in long nutrient uptake lengths.

Our findings are in contrast to results from relatively pristine streams, in which efficient nutrient retention has been evidenced (Peterson et al. 2001), and thus our findings call into question whether this functional property of stream ecosystems is similarly effective in human-altered, eutrophic streams. Nutrient uptake is clearly incapable of efficiently retaining nutrients in the eutrophic lowland streams under study. Consequently, water quality problems cannot be efficiently mitigated by merely relying on natural nutrient retention. Nutrient retention in streams may only be effective when excessive nutrient loading is reduced by efficient wastewater treatment at point sources or by measures to diminish diffuse sources.

References

BERNHARDT, E. S., R. O. HALL, AND G. E. LIKENS. 2002. Whole-system estimates of nitrification and nitrate uptake in streams of the Hubbard Brook experimental forest. Ecosystems **5:** 410–430.

CHRZANOWSKI, T. H., AND M. KYLE. 1996. Ratios of carbon, nitrogen and phosphorus in *Pseudomonas fluorescens* as a model for bacterial element ratios and nutrient regeneration. Aquat. Microb. Ecol. **10:** 115–122.

CLARKE, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. Aust. J. Ecol. **18:** 117–143.

———, AND R. H. GREEN. 1988. Statistical design and analysis for a 'biological effects' study. Mar. Ecol. Prog. Ser. **46:** 213–226.

———, AND R. M. WARWICK. 2001. Change in marine communities: An approach to statistical analysis and interpretation. Plymouth Marine Laboratory.

DODDS, W. K., AND OTHERS. 2002. N uptake as a function of concentration in streams. J. N. Am. Benthol. Soc. **21:** 206–220.

DOYLE, M. W., E. H. STANLEY, AND J. M. HARBOR. 2003. Hydrogeomorphic controls on phosphorus retention in streams. Water Resour. Res. **39:** 1147.

GÜCKER, B., AND I. G. BOËCHAT. 2004. Stream morphology controls ammonium retention in tropical headwaters. Ecology **85:** 2818–2877.

———, M. BRAUNS, AND M. T. PUSCH. 2006. Effects of wastewater treatment plant discharge on ecosystem structure and function of lowland streams. J. N. Am. Benthol. Soc. **25:** 313–329.

HAGGARD, B. E., D. E. STORM, AND E. H. STANLEY. 2001. Effect of a point source input on stream nutrient retention. J. Am. Water Resour. Assoc. **37:** 1291–1299.

HALL, R. O., AND J. L. TANK. 2003. Ecosystem metabolism controls nitrogen uptake in streams in Grand Teton National Park, Wyoming. Limnol. Oceanogr. **48:** 1120–1128.

HARVEY, J. W., AND B. J. WAGNER. 2000. Quantifying hydrologic interactions between streams and their subsurface hyporheic zones, p. 3–44. *In* J. B. Jones and P. J. Mulholland [eds.], Streams and ground waters. Academic Press.

INWOOD, S. E., J. L. TANK, AND M. J. BERNOT. 2005. Patterns of denitrification associated with land use in 9 midwestern headwater streams. J. N. Am. Benthol. Soc. **24:** 227–245.

KÖHLER, J., J. GELBRECHT, AND M. PUSCH. 2002. Die Spree—Zustand, Probleme, Entwicklungsmöglichkeiten. E. Schweizerbart'sche Verlagsbuchhandlung.

KÖRNER, S. 1997. Nutrient and oxygen balance of a highly polluted treated sewage channel with special regard to the submerged macrophytes. Acta Hydrochim. Hydrobiol. **25:** 34–40.

LAMBERTI, G. A., AND A. D. STEINMAN. 1997. A comparison of primary production in stream ecosystems. J. N. Am. Benthol. Soc. **16:** 95–104.

MARTÍ, E., J. AUMATELL, L. GODE, M. POCH, AND F. SABATER. 2004. Nutrient retention efficiency in streams receiving inputs from wastewater treatment plants. J. Environ. Qual. **33:** 285–293.

———, AND F. SABATER. 1996. High variability in temporal and spatial nutrient retention in Mediterranean streams. Ecology **77:** 854–869.

MARZOLF, E. R., P. J. MULHOLLAND, AND A. D. STEINMAN. 1994. Improvements to the diurnal upstream-downstream dissolved oxygen change technique for determining whole-stream metabolism in small streams. Can. J. Fish. Aquat. Sci. **51:** 1591–1599.

MELCHING, C. S., AND H. E. FLORES. 1999. Reaeration equations derived from U.S. Geological Survey database. J. Environ. Eng. ASCE **125:** 407–414.

MORRICE, J. A., H. M. VALETT, C. N. DAHM, AND M. E. CAMPANA. 1997. Alluvial characteristics, groundwater-surface water exchange and hydrological retention in headwater streams. Hydrol. Process. **11:** 253–267.

MULHOLLAND, P. J., A. D. STEINMAN, AND J. W. ELWOOD. 1990. Measurement of phosphorus uptake length in streams Comparison of radiotracer and stable PO_4 releases. Can. J. Fish. Aquat. Sci. **47:** 2351–2357.

———, J. L. TANK, D. M. SANZONE, W. M. WOLLHEIM, B. J. PETERSON, J. R. WEBSTER, AND J. L. MEYER. 2000. Nitrogen cycling in a forest stream determined by a ^{15}N tracer addition. Ecol. Monogr. **70:** 471–493.

———, AND OTHERS. 2001. Inter-biome comparison of factors controlling stream metabolism. Freshw. Biol. **46:** 1503–1517.

———, AND OTHERS. 2002. Can uptake length in streams be determined by nutrient addition experiments? Results from an interbiome comparison study. J. N. Am. Benthol. Soc. **21:** 544–560.

MUNN, N. L., AND J. L. MEYER. 1990. Habitat-specific solute retention in two small streams: An intersite comparison. Ecology **71:** 2069–2082.

NEWBOLD, J. D., J. W. ELWOOD, R. V. O'NEILL, AND A. L. SHELDON. 1981. Measuring nutrient spiralling in streams. Can. J. Fish. Aquat. Sci. **38:** 860–863.

ODUM, H. T. 1956. Primary production in flowing waters. Limnol. Oceanogr. **1:** 102–117.

PAUL, M. J., AND J. L. MEYER. 2001. Streams in the urban landscape. Annu. Rev. Ecol. Syst. **32:** 333–365.

PETERSON, B. J., AND OTHERS. 2001. Control of nitrogen export from watersheds by headwater streams. Science **292:** 86–90.

ROYER, T. V., J. L. TANK, AND M. B. DAVID. 2004. Transport and fate of nitrate in headwater agricultural streams in Illinois. J. Environ. Qual. **33:** 1296–1304.

RUNKEL, R. L. 1998. One dimensional transport with inflow and storage (OTIS): A solute transport model for streams and rivers. United States Geological Survey Water-Resources Investigation Report 98-4018.

———. 2002. A new metric for determining the importance of transient storage. J. N. Am. Benthol. Soc. **21:** 529–543.

SCHULZ, M., AND C. HERZOG. 2004. The influence of sorption processes on the phosphorus mass balance in a eutrophic German lowland river. Water Air Soil Pollut. **155:** 251–301.

SOMMER, U. 1994. Planktologie. Springer.

STREAM SOLUTE WORKSHOP. 1990. Concepts and methods for assessing solute dynamics in stream ecosystems. J. N. Am. Benthol. Soc. **9:** 95–119.

SUKHODOLOV, A. N., V. I. NIKORA, P. M. ROWINSKI, AND W. CZERNUSZENKO. 1997. A case study of longitudinal dispersion in small lowland rivers. Water Environ. Res. **69:** 1246–1253.

THYSSEN, N., AND M. ERLANDSEN. 1987. Reaeration of oxygen in shallow, macrophyte rich streams: II. Relationship between the reaeration rate coefficient and hydraulic properties. Int. Rev. Hydrobiol. **72:** 575–597.

TRISKA, F. J., A. P. JACKMAN, J. H. DUFF, AND R. J. AVANZINO. 1994. Ammonium sorption to channel and riparian sediments—a transient storage pool for dissolved inorganic nitrogen. Biogeochemistry **26:** 67–83.

VALETT, H. M., J. A. MORRICE, C. N. DAHM, AND M. E. CAMPANA. 1996. Parent lithology, surface-groundwater exchange, and nitrate retention in headwater streams. Limnol. Oceanogr. **41:** 333–345.

WARD, A. K., AND R. G. WETZEL. 1980. Interactions of light and nitrogen source among planktonic blue-green algae. Arch. Hydrobiol. **90:** 1–25.

WASSERCHEMISCHE GESELLSCHAFT. 1992. Deutsche Einheitsverfahren zur Wasser-, Abwasser- und Schlammuntersuchung. Wiley VCH.

WEBSTER, J. R., AND B. C. PATTEN. 1979. Effects of watershed perturbation on stream potassium and calcium dynamics. Ecol. Monogr. **49:** 51–72.

———, AND OTHERS. 2003. Factors affecting ammonium uptake in streams—an inter-biome perspective. Freshw. Biol. **48:** 1329–1352.

WILCOCK, R. J., P. D. CHAMPION, J. W. NAGELS, AND G. F. CROKER. 1999. The influence of aquatic macrophytes on the hydraulic and physico-chemical properties of a New Zealand lowland stream. Hydrobiologia **416:** 203–214.

YOUNG, R. G., AND A. D. HURYN. 1996. Interannual variation in discharge controls ecosystem metabolism along a grassland river continuum. Can. J. Fish. Aquat. Sci. **53:** 2199–2211.

———, AND ———. 1998. Comment: Improvements to the diurnal upstream-downstream dissolved oxygen change technique for determining whole-stream metabolism in small streams. Can. J. Fish. Aquat. Sci. **55:** 1784–1785.

Received: 8 March 2005
Accepted: 14 November 2005
Amended: 8 December 2005