Ecosystem metabolism and nutrient uptake of springs in the Swiss Alps

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Abstract

Open system metabolism, nutrient uptake as well as bacterial abundance, sediment organic matter content and hyporheic respiration were examined for sub-alpine spring brooks during summer 2004 in the Swiss Alps. Whole system metabolism was estimated by the dual-station diel oxygen method. Liv23b, PA1 and PP11 had average gross primary production (GPP) of 4.2, 2.4 and 4.3 g O_2 m^{-2} d^{-1}, respectively. Measurement for ecosystem respiration (ER) averaged 5.8, 3.6 and 6.7 g O_2 m^{-2} d^{-1} for Liv23b, PA1 and PP11, respectively. GoFuO had an average GPP of 65 g O_2 m^{-2} d^{-1} and an ER of 96 g O_2 m^{-2} d^{-1}. Mean phosphorus and nitrogen uptake length ranged from 5 to 46 m and 20 to 63 m, respectively. Assessment of uptake rates averaged from 0.3 to 3.1 µg m^{-2} h^{-1} and 57 to 178 µg m^{-2} h^{-1} for P and N, respectively. Sediment samples were stained with 4', 6-diamidino-2-phenylindole (DAPI)-solution and subsequent counting of bacteria. Counts of DAPI-stained cells per mL sediment ranged from 1.1 x 10^6 to 3.4 x 10^6.

Key words: open system metabolism, nutrient uptake, bacterial abundance, direct cell counting, DAPI, hyporheic respiraction

Introduction

Nutrient spiraling is an important functional process in stream ecosystems (Webster 1975, Webster et al. 1975). As materials cycle between biotic and abiotic compartments in stream ecosystems, they are subject to downstream transport. Forested spring brooks, such as the studied systems, often exhibit low concentrations of N and P, little upstream transport of nutrients by adult insects, low benthic invertebrate or fish abundances, and usually depend on allochthonous inputs of organic matter. Differentiation between hydrological and non-hydrological processes is critical towards understanding nutrient spiraling. Downstream transport processes physically deliver nutrients and other solutes to reactive sites. These transport processes can be conceptually distinguished from exchanges between various reactive sites. Exchanges between sites can include chemical transformations (i.e., changes in chemical species), changes in physical state such as phase changes, microbial oxidation and reduction, and invertebrate consumption of algae. In this study, we focus on nutrient uptake, which can be measured in situ using amendment experiments (STREAM SOLUTE WORKSHOP 1990).

Other important factors driving nutrient cycling are primary production and respiration, measures of ecosystem metabolism. Primary production represents the organic matter supply produced within the ecosystem, whereas respiration provides an indication of total consumption of organic matter supplied by sources both within (autochthonous) and outside (allochthonous) the ecosystem. Using these factors the trophic state can be determined. In a net-autotrophic system primary production dominates over respiration. If ecosystem respiration exceeds production, the system is net-heterotrophic.

The hyporheic zone is a crucial component of most stream ecosystems (Meyer and Edwards 1990). Bacteria are abundant and play an important role in sediments with implications for the stream through exchange of material at the boundary between the two zones. One

way to estimate the importance of the hyporheos for a stream is to assess bacterial abundance in benthic sediments and to relate this to its organic matter content (Bott and Kaplan 1985, Cole et al. 1988). Sediment respiration also reflects hyporheic processes by assessing oxygen demand. Previous studies (e.g. Logue et al. 2004) have shown that sediment respiration can be dependent on organic matter content or bacterial abundance.

In this study we aimed at gaining an insight into the variation in ecosystem metabolism in sub-alpine springs in the Swiss National Park. Furthermore, we wanted to assess the range in nutrient uptake of these systems and compare results with other stream ecosystems. Based on other studies (e.g. Robinson et al. 2002), we assume that nutrient uptake lengths will be short in comparison with other stream ecosystems.

Methods

Field work took place from mid-May until end of September 2004. Springs were measured for temperature, conductivity (LF323 conductivity meter, WTW, Weilheim, Germany), dissolved oxygen (Oxi340i oxygen meter, WTW, Weilheim, Germany), and pH (ph330i pH meter, WTW, Weilheim, Germany) on several dates. In addition, 1L water samples were collected and analysed for N, P, DOC and POC following methods in Tockner et al. (2002).

Site description

Springs selected for our study are all located inside the Swiss National Park in the south-east corner of the Swiss Alps. They are thus not affected by agricultural activities and tourism which are otherwise abundant in the sub-alpine zone in Switzerland. We chose four springs for their geographical proximity and difference in exposure, altitude and stream morphology. See Table 1 for physical and chemical characteristics of the studied systems.

Table 1: Physical and chemical characteristics of the studied springs. n = number of samples.

Spring	Elevat.	n	Temp.	CV	Cond.	CV	NO_2-N + NO_3-N	CV	PO_4-P	DOC	CV	POC	CV
	[m a.s.l.]		[°C]	[%]	[µS cm^{-1}]	[%]	[mg L^{-1}]	[%]	[µg L^{-1}]	[mg L^{-1}]	[%]	[mg L^{-1}]	[%]
GoFuO	1820	3	6.8	3	1967	13	<0.01		<1	0.47	57	0.1	55
Liv23b	2110	2	4.2	8	257	2	0.24	51	<1	0.49	43	0.2	17
PA1	1710	3	5.6	20	242	3	0.29	19	<1	0.70	44	3.1	50
PP11	1620	2	7.3	4	407	3	0.37	16	<5	1.04	55	0.4	61

Three of the springs – Liv23b, PA1 and PP11 – are located in Val Livigno, downstream of the Livigno hydroelectric dam. The valley is confined but generally widens above 2000 m a.s.l. The bottom of the valley is around 1600 m a.s.l. and is dominated by the highly regulated Spöl river. All springs are in sub-alpine forest dominated by Picea excelsa and Pinus mungo.

Liv23b is near Alp »La Schera« and originates at the lower edge of a formerly (>100 yr ago) grazed meadow and flows through a mainly forested slope with a southwest exposure. Bed substrata are sand/gravel/pebble with some organic matter in the form of tree branches and coniferous needles. The outflow area is a complex system of both clearly defined linear and diffuse sources. The uppermost linear spring, which provided most of the discharge, dried in August. The total discharge thus decreased from ~1 Ls^{-1} in June to <0.4 Ls^{-1} in September.

PA1 lies on the west side of the Livigno canyon and has an east exposure. The first 100 m of this system, which crosses a hiking path at about 50 m are dominated by gravel-pebble substrata and substantial amounts of tree branches and needles as well as some living roots. Several short stretches along the spring brook have a mostly sandy-silt bed. The outflow is also a complex system of mostly linear sources, some of which dried during summer. Discharge decreased from 3 Ls^{-1} in June to 1 Ls^{-1} in September.

PP11 lies at the bottom of the valley, just south of the Spöl river. Its origin is at the bottom of a large gravel field. The system is only 60 m long from its source to its outflow into the Spöl river. The spring brook has a much lower gradient (1-2%) than the other systems. The stream bed is dominated by sand and silt with some gravel in the lower half of the channel. Organic substratum is present, although non-significant. Shrubs and small trees occur along the spring brook, but most are not close to the channel to substantially influence radiation. Discharge is fairly stable at 13-16 Ls^{-1} throughout summer.

GoFuO is located outside and northeast of Val Livigno. The system lies at the bottom of a northeast-exposed slope almost completely covered by trees. The outflow of the spring consists of a pond roughly 10 m in diameter with a maximum depth of 2.5 m. This spring is clearly a special site that we chose for its unique chemical features. In the pond, there is <1 mg L^{-1} dissolved oxygen (DO) below 50 cm depth and the system is anoxic; the outflow of the pond has a DO concentration between 1 and 2 mg L^{-1}. Bed susbtrata consist mostly of silt, sand, and iron-oxide precipitates in slow flowing stretches. After 30 m, the spring brook enters a water pipe that drains into the Fuorn river about 100 m below. Summer discharge is fairly constant at 2.5-3 Ls^{-1}.

Bacterial abundance

Three sediment samples per site were collected using a 60 mL syringe (sanitex tube) with the tube cut even at the 0 mL tick and then transferred to a 50 mL Greiner tube (TPP, Europe/Switzerland). Samples were stored at 4° C until analysed in the laboratory. Homogenized sediment samples were first diluted 1:10 with 10x PBS buffer (0.58M Na_2HPO_4, 0.17M $NaH_2PO_4 \bullet H_2O$, 0.68M NaCl). Following vortexing for 4 min at intensity 8 (Vortex Genie 2TM, Zurich, Switzerland), 10 mL of aliquot was further diluted 1:10 with 10x PBS buffer. Vortexing again for 2 min at intensity 8 and further diluting the aliquot 1:20 with sterile-filtered H_2O (0.4µm Millipore, MILLEX™GP, Billerica, Mass., USA), the sample was, at this stage, diluted at a ratio of 1:2000. Subsequently, 10 mL of the sample was filtered through an ethanol-cleaned suction filter (PC MB 25 mm 0.2 µm B, Sterico AG, Dietikon, Switzerland). The suction filter was carefully rinsed with 2 mL of sterile-filtered water. A microscope slide

(76x26 mm, Menzel Gläser, Switzerland) was cleaned with ethanol and then mounted with the filter. Before being covered with a cover slide (22x50 mm, Menzel Gläser, Switzerland), 50 µl of 4', 6-diamidino-2-phenylindole (DAPI) solution was added to the filter. The microscope slide was incubated in the dark at 37 ºC for 30 min, before taking photos of 20 random fields through a fluorescence microscope (Olympus BX50F, Olympus Corporation, Japan). From these photos, unfocused and otherwise unusable pictures were discarded, and 10 of the remaining clear photos were randomly selected for counting.

Hyporheic respiration

Respiration rates of hyporheic sediments and periphyton biomass on stones were determined for all sites on different dates during the summer. Five replicate samples of each site were measured. Sediment respiration was determined as the decrease in dissolved oxygen over time, after Jones et al. (1995). Sealed Plexiglas chambers, filled about halfway with sediment and topped up with stream water, were buried in the stream channel, covered with sediment to exclude light, and incubated in situ for 3–7 hours. Dissolved oxygen concentrations before and after incubation were quantified with an Oxi340i oxygen meter calibrated in the field (WTW, Weilheim, Germany). Sediments were then frozen (-25 °C) and returned to the laboratory for analysis of organic matter content.

In the laboratory, chamber sediments were analysed for particulate organic matter (POM) in four fractions: <0.063 mm, 0.063-1 mm, >1 mm, and coarse sediment. Sediments were dried (60 °C for ≥48 hours) and then weighed. POM content was determined by loss of ignition at 500 °C for 4 hours.

Nutrient uptake

We conducted nutrient uptake experiments on two occasions at each site. After taking background samples at each transect, nutrients in the form of PO_4 and NO_{3-} solutes were released near the water outflow using a 35 L Mariotte bottle at a rate of 8 mL s^{-1}. We also added NaCl as a conservative tracer to monitor the dispersion of the amended solution. After 30-50 min, samples were collected moving upstream from the farthest downstream transect. Simultaneously, we measured conductivity to account for subsurface water inflow. The 20 mL samples collected at the 4 to 5 transects were processed within 24 h using a Digital Colorimeter (AutoAnalyzer 3, Bran + Luebbe, Norderstedt, Germany). All plateau nutrient concentrations were corrected for background levels and average values (for each transect) fit to an exponential uptake model to calculate uptake parameters (STREAM SOLUTE WORKSHOP 1990).

Open system metabolism

Open system metabolism was estimated for all sites. Ecosystem respiration (ER) and gross primary production (GPP) were determined using the dual-station diel O_2 method refined by Marzolf et al. (1994). Dissolved oxygen concentrations were measured continuously over multiple days on 2-3 occasions. Stream temperature and DO were recorded at an upstream and downstream site using one Oxi340 and one Oxi340i oxygen meter (WTW, Weilheim, Germany) at 30-min intervals. Both oxygen meters were calibrated regularly to ensure accuracy both in absolute and relative measurements.

The net oxygen production rate (ß(t)) in g O_2 m^{-2} d^{-1} was calculated using:

$ß(t) = [K_s(O_2 - O_{2sat}) + \Delta O_2/\Delta t]z$

where $K_s(T, Q)$ is the reaeration rate coefficient (h^{-1}) as a function of temperature T (ºC) and discharge Q ($m^3 s^{-1}$); z represents the mean depth (m), $\Delta O_2/\Delta t$ is the change of oxygen concentration between the upstream and downstream station, and O_{2sat} is the saturation concentration of O_2 (mg O_2 L^{-1}).

To estimate K_s, the gas exchange of a volatile tracer (sulphur hexa-fluoride, SF_6) was measured. SF_6 (gas mixture of SF_6 and N_2, 1% v/v SF_6) was continuously injected sufficiently above the upstream station to ensure complete lateral mixing when entering the study reach (Naegeli and Uehlinger 1997). Following the collection of 7 water samples per station using gas tight 50 ml glass syringes, the syringes were transferred to the laboratory where they were analysed for SF_6 on a gas chromatograph. The K_s of sulphur hexa-fluoride was calculated as

$K_s(T,Q) = \ln(c_u/c_d) \bullet (1/\tau)$

where τ is travel time of water (h) between the upstream and downstream station, and cu and cd are corresponding upstream (u) and downstream (d) steady state concentrations of SF6. Travel time was quantified by monitoring a NaCl tracer solution (1 kg NaCl per 5 L water) with a portable LF323 conductivity meter (WTW, Weilheim, Germany). The reaeration rate coefficient of oxygen was calculated by multiplying the K_s of SF_6 by 1.4 (Cirpka et al. 1993). Thyssen and Erlandsen (1987) describe temperature dependence with an exponential temperature function:

$K_s(T) = K_s(20ºC) \bullet 1.024^{(T - 20ºC)}$

where $K_s(20ºC)$ represents the reaeration rate coefficient at the reference temperature 20ºC.

Based on net O_2 production rate, ß(t), ER, GPP and the ratio of GPP to ER (P/R) were determined. To calculate ER, the average net oxygen production rate during the dark

period was extrapolated to 24 hours. GPP was calculated as the sum of ß(t) and ER. The calculation of these metabolic parameters rested upon the assumption that day respiration equals night respiration (Bott and Kaplan 1985).

Results

Bacterial abundance and organic matter in sediments

Average counts of DAPI-stained cells per mL sediment ranged from 1.14 x 10^8 in PP11 to 3.35 x 10^8 in Liv23b (Table 2). We found no significant difference (one-way ANOVA: $p > 0.05$) in bacterial abundance among sites. Ash-free dry mass (AFDM) and organic matter (OM) were lowest at PP11 and highest at GoFuO (Table 2). No significant difference existed in AFDM or OM contents among sites (one-way ANOVA: $p > 0.05$). Furthermore, no correlation between AFDM and bacterial abundance was detected.

Table 2: Bacterial abundance and ash-free dry mass.

Spring	Bacteria count [mL^{-1}]	±SD	AFDM [$g\ mL^{-1}$]	±SD	OM [%]	±SD
GoFuO	1.77 x 10^8	6.94 x 10^7	0.0178	0.0062	9.42	6.11
Liv23b	3.35 x 10^8	4.37 x 10^8	0.0190	0.0102	3.04	1.24
PA1	1.87 x 10^8	1.30 x 10^8	0.0405	0.0217	9.23	10.52
PP11	1.14 x 10^8	6.55 x 10^7	0.0178	0.0029	2.49	0.51

Hyporheic respiration

Sediment respiration rates ranged from 0.13 mg O_2 h^{-1} in PA1 to 0.46 mg O_2 h^{-1} in Liv23b. We could not assess hyporheic respiration in GoFuO due to its low (<0.3 mg O_2 L^{-1}) initial dissolved oxygen concentration. Respiration rates did not differ significantly among

springs (one-way ANOVA: $p > 0.05$). Mean coarse particulate organic matter (CPOM) per respiration chamber ranged from 0.11 g in PP11 to 1.2 g in GoFuO. Fine particulate organic matter (FPOM) ranged from 4.48 g in Liv23b to 13.6 g in PP11. Differences between sites were significant (one-way ANOVA: $p < 0.005$) for CPOM, FPOM as well as total organic matter. Respiration rates did not correlate with CPOM, FPOM or total organic matter content (one-way ANOVA: $p > 0.05$).

Table 3: Hyporheic respiration rates, coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM) content. n/a = not available.

Spring	Respiration [mg O_2 h^{-1}]	±SD	CPOM [g]	±SD	FPOM [g]	±SD
GoFuO	n/a	n/a	7.97	1.20	7.22	4.30
Liv23b	0.460	0.109	0.15	0.08	4.48	0.42
PA1	0.130	0.011	0.51	0.16	5.76	0.36
PP11	0.280	0.334	0.11	0.05	13.60	1.35

Nutrient uptake

All springs exhibited short nutrient (N and P) uptake lengths (S_w) and high phosphorus uptake rates compared to other lotic systems in the Swiss Alps (Robinson et al. 2002). We found S_w to be shortest in GoFuO (<10 m), corresponding to the highest P uptake rate (Table 4). PP11, the spring with the highest discharge in our study, showed the longest uptake lengths (33 to 60 m for P and 62 m for N) and the lowest uptake rates (0.11 to 0.48 µg P m^{-2}

h^{-1} and 57 µg N m^{-2} h^{-1}). Phosphorus uptake in this spring brook differed between July and September.

Table 4: Nutrient uptake lengths (S_w) and rates (U). n/a = not available.

Spring	Month	Discharge	S_w Phosphorus	U Phosphorus	S_w Nitrogen	U Nitrogen
		[L s^{-1}]	[m]	[µg m^{-2} h^{-1}]	[m]	[µg m^{-2} h^{-1}]
GoFuO	July	2.6	7	1.99	n/a	n/a
	September	2.6	4	4.16	n/a	n/a
Liv23b	August	0.45	n/a	n/a	11	266
	September	0.35	8	1.12	29	89
PA1	September	1.3	10	2.16	63	130
PP11	July	13	60	0.11	n/a	n/a
	September	13.5	33	0.48	62	57

Open system metabolism

Gross primary production (GPP) ranged from 0.69 g m^{-2} d^{-1} in PA1 (September) to 70.87 g m^{-2} d^{-1} in GoFuO (May). Ecosystem respiration (ER) ranged from 1.33 g m^{-2} d^{-1} in PA1 (September) to 101.79 g m^{-2} d^{-1} in GoFuO (May). The pattern of development in metabolism over the summer was similar in PA1 and PP11 (Table 5 and Figure 1). These springs displayed high levels of dissolved oxygen at the spring source. NPP generally increased during summer, whereas ER, GPP and P/R decreased.

All springs were found to be heterotrophic, production to respiration ratios (P/R) ranged from 0.48 in PP11 (August) to 0.72 in Liv23b (July). The high oxygen demand in GoFuO (Figure 2) can be explained by its low initial dissolved oxygen level and the oxygen used to oxidize iron which is abundant in this spring.

Table 5: Net primary production, ecosystem respiration and gross primary production.

Spring	Month	NPP [g O_2 m^{-2} d^{-1}]	±SD	CV [%]	ER [g O_2 m^{-2} d^{-1}]	±SD	CV [%]	GPP [g O_2 m^{-2} d^{-1}]	P/R
GoFuO	May	-30.92	0.96	3.09	101.79	0.46	0.45	70.87	0.70
	Aug	-31.99	0.69	2.15	91.13	0.66	0.73	59.14	0.65
Liv23b	July	-1.63	0.32	19.85	5.83	0.23	3.92	4.20	0.72
PA1	July	-1.84	0.45	24.44	5.94	0.41	6.83	4.10	0.69
	Sep	-0.65	0.78	120.26	1.33	0.84	63.31	0.69	0.51
PP11	June	-3.20	0.54	16.76	10.33	0.08	0.80	7.14	0.69
	Aug	-1.57	0.54	34.40	3.02	0.44	14.61	1.45	0.48

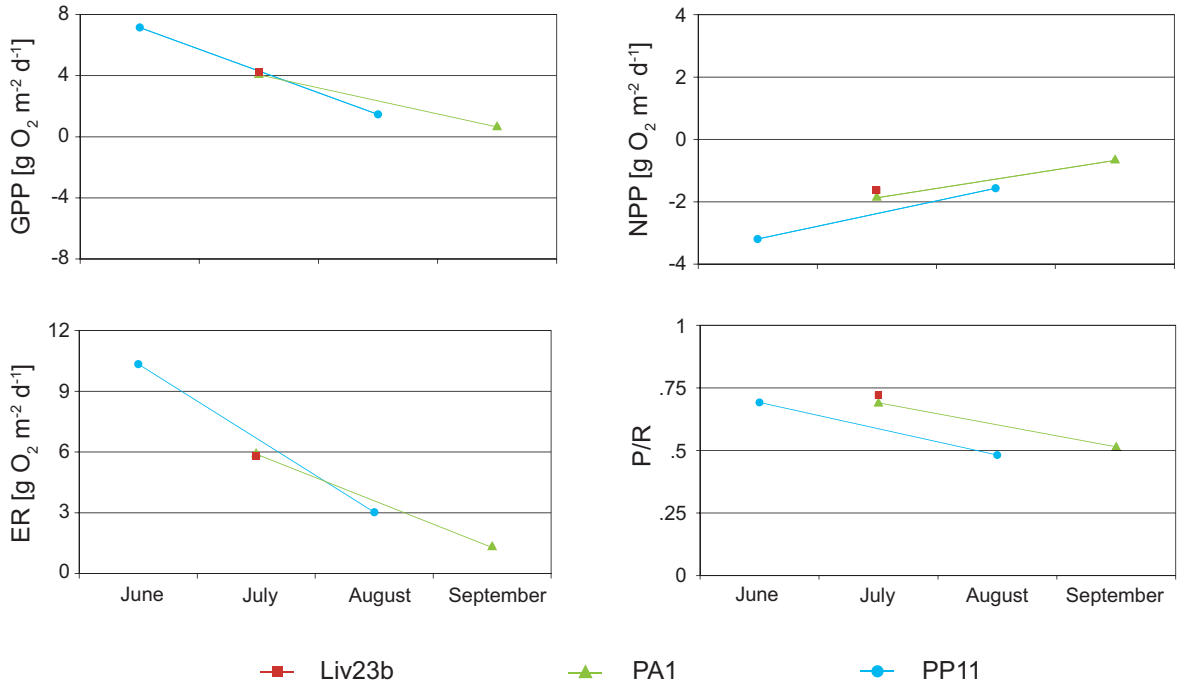

Figure 1: Gross primary production (GPP), net primary production (NPP), ecosystem respiration (ER) and production to respiration ratio (P/R) in Liv23b, PA1 and PP11.

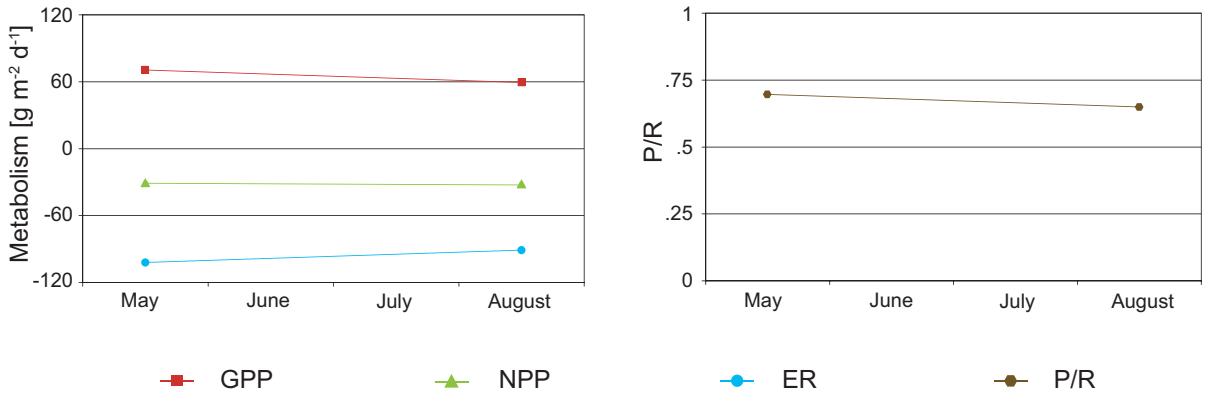

Figure 2: Metabolism (GPP, NPP, ER and P/R) in GoFuO.

Discussion

Bacterial abundance and organic matter in sediments

With our results, we could not attest to the positive relationship between microbial abundance and the amount of organic matter found in other studies (e.g. Bott and Kaplan 1985, Logue et al. 2004). Reasons thereof could be the strong influence of other environmental factors – temperature, conductivity, quantity and quality of organic matter, etc. – on bacterial abundance. Lack of significant differences in bacterial abundance and organic matter content among streams suggests ecological proximity of their hyporheos.

Analyzing cell density in running waters is challenging. Bacterial abundance was estimated counting DAPI-stained cells using a microscope. Different sample preparation and processing can lead to different results in direct cell counting (Zarda et al. 1997, Gough and Stahl 2003, Proctor and Souza 2001). In the applied direct cell counting protocol, no fixation buffer such as ethanol or paraformaldehyde (Zarda et al. 1997) was used, taking into account that bacteria were insufficiently separated from the sediment matrix. In addition, no anti-fading agent was used, resulting in a rapid processing of samples. Cell numbers can, therefore, only be looked upon as relative values.

Nutrient uptake

Differences in uptake length between springs are minor compared to differences to other stream ecosystems (Robinson et al. 2002, Davis and Minshall 1999, Minshall et al. 1983, Hall and Tank 2003). Overall, our results confirm the assumption that uptake lengths are relatively short in spring brooks. High spatial heterogeneity and high macrophyte density are probably the major determinants of nutrient uptake in the studied spring brooks. Phosphorus

and nitrogen uptake rates however were found to be low compared to other stream studies (Robinson et al. 2002, Davis and Minshall 1999).

The nutrient concentrations used in the solution for the injection experiments were calculated using directives from the STREAM SOLUTE WORKSHOP (1990). Webster and Ehrman (1996) note that in-stream concentrations should be increased 5- to 10-fold over background levels. The calculated concentrations of the amended solution turned out to be too low for uptake detection in several cases. Notably N concentrations used in GoFuO, PA1 and PP11 in July were not sufficiently high. We thus increased nutrient levels in the solution by 45-115% (Phosphorus) and 100-450% (Nitrogen). This increase still did not produce results for N uptake in GoFuO. This spring brook features a section with a relatively wide wetted channel and low transport velocity containing extended moss coverage. The moss might account for high uptake rates and the slow flowing stretch is in violation of the presupposition of uniform channel and flow characteristics as proposed in the STREAM SOLUTE WORKSHOP (1990).

Open system metabolism

The high levels in oxygen demand in GoFuO show the tight integration of stream metabolism with its chemical characteristics. Biological turnover probably plays a minor role in this system's metabolism. Purely biological metabolism is thus very difficult to measure, the results presented in this study just reflect the overall oxygen demand.
Our results endorsed the assumption that all springs in our study were heterotrophic. Low background nutrient concentrations coupled with relatively abundant organic matter in the streambed led us to this assumption.

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Appendix

Appendix A
Survey dates, physical and chemical measurements

Spring	Date	Time	Cond [µS/cm]	Temp [°C]	DO [mg/l]	DO Sat [%]	pH	Q [l/s]
GoFuO	25.5.04	12:10	2120	6.9			7.7	3.07
GoFuO	1.7.04	10:00	1682	6.6	1.74	18.5	6.3	
GoFuO	20.7.04	14:00	2140	7.9			6.3	2.6
GoFuO	27.7.04	12:45	2190	8				2.4
GoFuO	10.8.04	16:00	2100	7	1.8	18	7.6	
GoFuO	7.9.04	15:00	1677	6.2			7.5	
GoFuO	15.9.04	9:00	1665					2.6
Liv23b	4.8.04	16:20	238	9.8	8.3	95	8.1	
Liv23b	11.8.04	11:30		10.1	8.8	99		
Liv23b	18.8.04	14:30	286	11				0.45
Liv23b	26.8.04	10:00	245	7	9.4	100	8.2	
Liv23b	3.9.04	10:00	246	7.2	9.4			0.4
Liv23b	6.9.04	14:00	211	12.1	9.9	117	8.2	
Liv23b	21.9.04	13:30	247	9.9				0.35
PA1	9.7.04	12:00	244	4.5	10.2	98	8.3	2.3
PA1	21.7.04	10:00	224	7.7				1.6
PA1	4.8.04	10:00	228	5.9	10	99	8.2	
PA1	18.8.04	11:30		7.1	9.2	93		
PA1	26.8.04	12:00	260	6	10	100	8.3	
PA1	2.9.04	12:30	273	8.6				1
PA1	6.9.04	16:30	202	5.6			8.2	
PA1	21.9.04	16:30	287	4.9				
PP11	9.7.04	10:00	417	7.1	9.6	97	8.0	16
PP11	21.7.04	14:00	421	7.5				13
PP11	4.8.04	11:15	425	7.4	11.6	117	7.8	
PP11	26.8.04	14:00	428	7.5	9.5	97	8.0	
PP11	2.9.04	14:30	417	8.2				13.5
PP11	7.9.04	10:30	332	7.5	9.6	96	8.0	
PP11	15.9.04	13:00	425	8.1				

Appendix B

Nutrien uptake regression and calculation

GoFuO, 20.07.04				
a (wetted channel width) [m]	0.5			
Q (discharge) [m3 min-1]	0.156			
Phosphorus				
	Coefficients	Standard Error	t Stat	P-value
Intercept	0.9060	0.1385	6.5395	0.0966
X Variable 1	-0.1517	0.0089	-16.9598	0.0375
k (regr. slope)		-0.1517		
Sw (uptake length)		6.59	m	
Vf (uptake velocity)		0.0473	m min-1	
U (uptake rate)		0.0331	µg m-2 min-1	
Nitrogen				
	Coefficients	Standard Error	t Stat	P-value
Intercept	-8.6404	0.8106	-10.6588	0.0018
X Variable 1	0.0743	0.0396	1.8747	0.1575
k (regr. slope)		0.0743		
Sw (uptake length)		13.4548	m	
Vf (uptake velocity)		0.0232	m min-1	
U (uptake rate)		0.0337	µg m-2 min-1	

GoFuO, 15.09.04				
a (wetted channel width) [m]	0.5			
Q (discharge) [m3 min-1]	0.156			
Phosphorus				
	Coefficients	Standard Error	t Stat	P-value
Intercept	3.8861	0.8855	4.3885	0.0482
X Variable 1	-0.2571	0.0482	-5.3337	0.0334
k (regr. slope)		-0.2571		
Sw (uptake length)		3.89	m	
Vf (uptake velocity)		0.0802	m min-1	
U (uptake rate)		0.0694	µg m-2 min-1	
Nitrogen				
	Coefficients	Standard Error	t Stat	P-value
Intercept	-4.9025	1.3064	-3.7528	0.1658
X Variable 1	-0.0278	0.0675	-0.4116	0.7514
k (regr. slope)		-0.0278		
Sw (uptake length)		36.0169	m	
Vf (uptake velocity)		0.0087	m min-1	
U (uptake rate)		n/a	µg m-2 min-1	

Liv23b, 19.08.04				
a (wetted channel width) [m]	0.1			
Q (discharge) [m3 min-1]	0.027			
Phosphorus				
	Coefficients	Standard Error	t Stat	P-value
Intercept	-0.0734	3.2695	-0.0225	0.9857
X Variable 1	-0.0056	0.0622	-0.0900	0.9429
k (regr. slope)		-0.0056		
Sw (uptake length)		178.82	m	
Vf (uptake velocity)		0.0015	m min-1	
U (uptake rate)		0.0003	µg m-2 min-1	
Nitrogen				
	Coefficients	Standard Error	t Stat	P-value
Intercept	-1.5273	0.4214	-3.6240	0.1714
X Variable 1	-0.0870	0.0136	-6.4219	0.0983
k (regr. slope)		-0.0870		
Sw (uptake length)		11.49	m	
Vf (uptake velocity)		0.0235	m min-1	
U (uptake rate)		4.4479	µg m-2 min-1	

Liv23b, 21.09.04				
a (wetted channel width) [m]	0.1			
Q (discharge) [m3 min-1]	0.027			
Phosphorus				
	Coefficients	Standard Error	t Stat	P-value
Intercept	4.1836	1.9271	2.1709	0.1621
X Variable 1	-0.1267	0.0680	-1.8635	0.2034
k (regr. slope)		-0.1267		
Sw (uptake length)		7.90	m	
Vf (uptake velocity)		0.0266	m min-1	
U (uptake rate)		0.0186	µg m-2 min-1	
Nitrogen				
	Coefficients	Standard Error	t Stat	P-value
Intercept	-2.0605	0.1982	-10.3954	0.0019
X Variable 1	-0.0344	0.0072	-4.7854	0.0174
k (regr. slope)		-0.0344		
Sw (uptake length)		29.03	m	
Vf (uptake velocity)		0.0072	m min-1	
U (uptake rate)		1.4832	µg m-2 min-1	

PA1, 21.07.04				
a (wetted channel width) [m]	0.2			
Q (discharge) [m3 min-1]	0.096			
Phosphorus				
	Coefficients	Standard Error	t Stat	P-value
Intercept	0.3057	n/a	n/a	n/a
X Variable 1	-0.0528	n/a	n/a	n/a
k (regr. slope)		-0.0528		
Sw (uptake length)		18.93	m	
Vf (uptake velocity)		0.0254	m min-1	
U (uptake rate)		0.0242	µg m-2 min-1	
Nitrogen				
	Coefficients	Standard Error	t Stat	P-value
Intercept	-4.4883	1.6770	-2.6764	0.2276
X Variable 1	0.0004	0.0204	0.0187	0.9881
k (regr. slope)		0.0004		
Sw (uptake length)		2620.72	m	
Vf (uptake velocity)		0.0002	m min-1	
U (uptake rate)		0.042	µg m-2 min-1	

PA1, 21.09.04				
a (wetted channel width) [m]	0.2			
Q (discharge) [m3 min-1]	0.078			
Phosphorus				
	Coefficients	Standard Error	t Stat	P-value
Intercept	4.0737	0.4023	10.1254	0.0021
X Variable 1	-0.1034	0.0135	-7.6681	0.0046
k (regr. slope)		-0.1034		
Sw (uptake length)		9.68	m	
Vf (uptake velocity)		0.0403	m min-1	
U (uptake rate)		0.0361	µg m-2 min-1	
Nitrogen				
	Coefficients	Standard Error	t Stat	P-value
Intercept	-2.9981	0.1947	-15.3991	0.0006
X Variable 1	-0.0160	0.0065	-2.4486	0.0918
k (regr. slope)		-0.0160		
Sw (uptake length)		62.61	m	
Vf (uptake velocity)		0.0062	m min-1	
U (uptake rate)		2.1741	µg m-2 min-1	

PP11, 21.07.04				
a (wetted channel width) [m]	1.5			
Q (discharge) [m3 min-1]	0.78			
Phosphorus				
	Coefficients	Standard Error	t Stat	P-value
Intercept	1.1570	0.3181	3.6370	0.0358
X Variable 1	-0.0168	0.0076	-2.2070	0.1144
k (regr. slope)				
Sw (uptake length)			m	
Vf (uptake velocity)			m min-1	
U (uptake rate)			µg m-2 min-1	
Nitrogen				
	Coefficients	Standard Error	t Stat	P-value
Intercept	-4.0037	n/a	n/a	n/a
X Variable 1	-0.0573	n/a	n/a	n/a
k (regr. slope)		-0.0573		
Sw (uptake length)		17.45	m	
Vf (uptake velocity)		0.0298	m min-1	
U (uptake rate)		3.2703	µg m-2 min-1	

PP11, 21.09.04				
a (wetted channel width) [m]	1.5			
Q (discharge) [m3 min-1]	0.81			
Phosphorus				
	Coefficients	Standard Error	t Stat	P-value
Intercept	2.5278	0.3937	6.4207	0.0077
X Variable 1	-0.0308	0.0093	-3.3149	0.0452
k (regr. slope)		-0.0308		
Sw (uptake length)		32.51	m	
Vf (uptake velocity)		0.0166	m min-1	
U (uptake rate)		0.0080	µg m-2 min-1	
Nitrogen				
	Coefficients	Standard Error	t Stat	P-value
Intercept	-3.9434	0.6638	-5.9405	0.0095
X Variable 1	-0.0162	0.0156	-1.0369	0.3760
k (regr. slope)		-0.0162		
Sw (uptake length)		61.64	m	
Vf (uptake velocity)		0.0088	m min-1	
U (uptake rate)		0.9538	µg m-2 min-1	