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Landscape regulation of bacterial growth efficiency in boreal freshwaters

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[1] Allochthonous organic carbon in aquatic systems is metabolized by heterotrophic bacteria, with significant consequences for the biostructure and energy pathways of freshwater ecosystems. The degree to which allochthonous substrates support growth of bacteria is largely dependent on bacterial growth efficiency (BGE), i.e., bacterial production (BP) per unit of assimilated carbon. Here we show how the spatial variability of BGE in the boreal region can be mediated by the distribution of the two dominating landscape elements forest and mires. Using an 11 days bioassay approach, the production and respiration of bacteria were measured in water samples from nine small Swedish streams (64°N 19°E), representing a gradient ranging from organic carbon supplied mainly from peat mires to carbon supplied mainly from coniferous forests. BP was positively correlated to forest coverage (%) of the catchment, while bacterial respiration was similar in all streams. Consequently, BGE showed a strong positive correlation with forest coverage. Partial least square regression showed that BGE was chiefly regulated by qualitative properties of the organic material, indicated by the absorbance ratio a254/a365 plus C/N and C/P ratios. The data suggest that a share of the organic carbon pool, drained mainly from forest soils, had a potential of being incorporated into bacterial biomass with great efficiency. Its potential for supporting growth was probably nutrient regulated as indicated by inorganic nutrient enrichment experiments.

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1. Introduction

[2] Streams and lakes are recipients for terrestrial export of organic carbon; primarily in the form of dissolved humic substances. This allochthonous organic carbon favors bacterial production (BP) and bacterial respiration (BR) by providing bacteria a source of carbon and energy [*Jansson et al.*, 2000; *Jones*, 1992]. BP forms a linkage between allochthonous organic carbon and higher trophic levels [*Hessen*, 1998; *Jansson et al.*, 1999; *Jones*, 1992], as bacteria are grazed by, e.g., protists [*Jones*, 2000; *Sherr and Sherr*, 2002]. BR based on allochthonous organic carbon is of concern from a biogeochemical perspective as it represents a return of soil carbon to the atmosphere [*Cole et al.*, 1994] and may constitute an important component in the landscape carbon balance [*Algesten et al.*, 2003]. Current findings suggest that energy pathways fueled by terrestrial-derived carbon are of large importance for the function of unproductive freshwater ecosystems [*Jansson et al.*, 2007]. In humus rich lakes, up to 90% of bacterial carbon [*Hessen*, 1992; *Jansson et al.*, 1999] and 50% of zooplankton carbon [*Pace et al.*, 2004] have been reported to be of allochthonous origin. Also in clearwater [*Karlsson et al.*, 2002] and net autotrophic lakes [*Kritzberg et al.*, 2006], bacteria and higher trophic levels are largely subsidized by external inputs of organic carbon. Although the typical entrance of allochthonous carbon to the zooplankton and fish level is under debate, the pathway via bacteria and protists, together with the notion of direct utilization of particulate organic carbon [*Cole et al.*, 2006], has gained increasing support in recent literature [*Jansson et al.*, 2007].

[3] The share of assimilated carbon that is used for BP (and not for BR) is defined as the bacterial growth efficiency (BGE). BGE determines the degree to which bioavailable substrates can sustain BP and its potential use in heterotrophic food chains [*Jones*, 2000]. There is presently no clear consensus about the regulation of BGE in aquatic systems, but the availability and quality of organic carbon plus the availability of inorganic phosphorus (P) and nitrogen (N) have been suggested to be key limiting factors [*del Giorgio and Cole*, 1998]. The way these factors are expressed in aquatic systems is, in turn, dependent on the character of the catchment from which nutrients and organic carbon are imported. In this paper, we investigate the importance of the quality difference between organic matter exported by coniferous forest on one hand and peat mires on the other hand: the two dominant sources of allochthonous carbon in boreal freshwaters. Through mycorrhizal plant roots in forested soils, the dissolved organic carbon (DOC) pool is

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Table 1. Physical Characteristics of the Catchments

Site name	Forest, %	Mire, %	Lake, %	Area, km^2
Vargstugsbäcken	39.0	61.0	0.0	3.1
Stortjärnen Outlet	59.0	36.3	4.7	0.95
Kallkällsmyren	59.6	40.4	0.0	0.19
Stormyrbäcken	74.2	25.8	0.0	2.9
Övre Krycklan	83.2	14.0	1.7	20
Kallkällsbäcken	85.1	14.9	0.0	0.5
Långbäcken	89.1	9.9	0.6	7.2
Risbäcken	98.7	1.3	0.0	0.66
Västrabäcken	100.0	0.0	0.0	0.13

loaded with considerable amounts of fresh photosyntates [*Högberg and Högberg*, 2002; *Högberg et al.*, 2001]. This DOC is primarily exported to aquatic systems during episodes, when discharge is high and previously unsaturated soil horizons become activated by increased groundwater levels [*Bishop et al.*, 2004; *Laudon et al.*, 2004a]. The dynamics of mires contrast these patterns in several ways. Radiocarbon studies suggest that the export of DOC from boreal wetlands consists of relatively "young" material throughout the season [*Palmer et al.*, 2001; *Raymond and Hopkinson*, 2003; *Schiff et al.*, 1998]. Still, the organic carbon in mire litter is generally less bioavailable than in forest litter because of the vast abundance of slow-degrading bryophytic material [*Hobbie et al.*, 2000; *Turetsky*, 2004]. For example, *Sphagnum* species, which typically dominate the vegetation [*Clymo and Hayward*, 1982], have low nutrient contents [*Asada and Warner*, 2005; *Coulson and Butterfield*, 1978], comprise recalcitrant carbon compounds [*Clymo*, 1965; *Johnson and Damman*, 1991], and produce chemical species with antimicrobial properties [*Verhoeven and Toth*, 1995; *Verhoeven and Liefveld*, 1997].

[4] Our objective was to test the hypothesis that catchment characteristics influence BGE by regulating the organic matter quality. To do this, water samples were taken from nine boreal headwater streams of northern Sweden, covering a gradient ranging from catchments dominated by coniferous forest to catchments dominated by *Sphagnum* peat mires. Using a bioassay approach, the productivity and respiration of bacteria were analyzed in relation to organic carbon quality (C/N ratio, spectrophotometric properties, etc.) and physical attributes of the catchments.

2. Methods

2.1. Sampling

[5] The study was carried out at the Vindeln Experimental Forests (64°, 14′N, 19°46′E) in northern Sweden. Climatic and hydrological studies have been performed in the area for nearly three decades. We chose nine streams representing catchments along a gradient of different proportions of forest and mire coverage for this study (Table 1). All streams are located in the Krycklan catchment [*Cory et al.*, 2006] except for Vargstugsbäcken, located in the nearby Kulbäcksliden catchment. The latter stream site is almost completely dominated by organic carbon drained from a large mire (Degerö Stormyr). Norway spruce (*Picea abies*) and, in upslope areas, Scots pine (*Pinus sylvestris*) dominate all forested areas. Deciduous shrubs and trees including birch (*Betula sp.*) but also alder (*Alnus incana*) and willow (*Salix sp.*) are common only along the riparian zones of the larger streams. The climate of the region is characterized by short summers and long winters, with snow usually covering the ground from the end of October to the beginning of May. Average air temperatures are −10°C in January and 0°C over the full year. The mean annual precipitation is 600 mm, and one third comes as snow.

[6] All stream sites were sampled every second month from April to October 2005 (Figure 1). Additional sampling for nutrient enrichment experiments was carried out in June and September. Water was collected in 2.0 L acid washed and stream water rinsed HDPE bottles that were kept dark and cool until arrival at the laboratory. The samples were thereafter equilibrated with standard air (78% N_2, 21% O_2, and 0.03% CO_2) for several hours to remove supersaturation of CO_2. Water was then directly subsampled into 22 mL sterile glass bottles, leaving a 7 mL headspace that was flushed with standard air before the bottles were sealed with gas tight septa. Parallel incubations were made in 250 mL HDPE bottles with identical water: headspace ratios. Incubation was initiated at approximately 24 hours after sampling. The bottles were incubated in the dark at 20°C. Samples for measurements of water chemistry were frozen directly after arrival to the laboratory. Unfiltered samples were frozen for total phosphorus (TP), total nitrogen (TN) and total organic carbon (TOC) analyses, while water for analysis of dissolved inorganic nutrients was filtered through glass fibre filters (Whatman GF/F) and water for absorbance analysis was filtered through 0.45 μm filters (Millipore). Water for absorbance determination was also taken from the 250 mL incubation bottles at the end of the incubation.

[7] In addition to the stream samples, soil water was obtained from the two prime habitats, i.e., forest and mire. These samples were collected twice at each habitat; once during spring and once in the summer. The mire of the Kallkällsmyren catchment was sampled on 26 April and

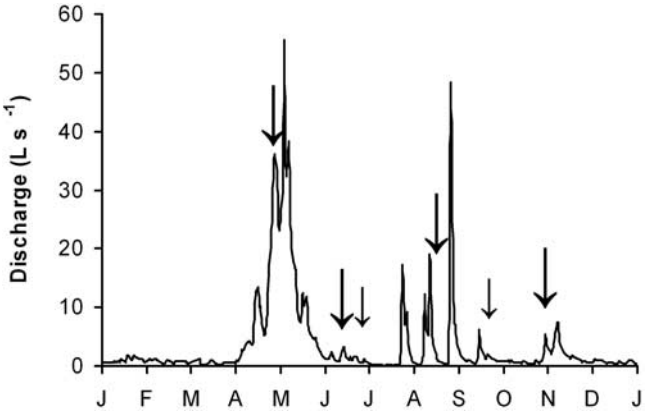

Figure 1. Discharge graph for Kallkällsbäcken throughout 2005, with arrows representing sampling dates. Small arrows indicate additional sampling efforts at Västrabäcken and Kallkällsmyren for nutrient addition experiments. The curve approximately represents relative changes in flow rates in all streams in the catchment.

4 September at the depths of 75, 150, 200, 250, and 350 cm, using nested wetland wells with closed bottoms, perforated at the lower 10 cm. In the riparian forest zone of Kallkällsbäcken, we sampled soil solutions on 2 May and 29 June at 25, 45, 55, and 65 cm depths with suction lysimeters. A 50 psi vacuum was applied to lysimeters 1 day prior to sampling, and the initial volume was discarded before collecting samples for analysis. Soil water samples were transported to the laboratory and subsampled in the same way as stream water samples.

2.2. Analyses

[8] Triplicates of the 22 mL incubation samples were analyzed for BR and BP after 1, 2, 3, 5, 8, and 11 days from the incubation start. This time frame allowed us to obtain accurate estimates of the bacterial metabolism, but also to track potential changes in rates during incubation. We used different bottles for each occasion so that no bottle was opened before analysis. BR was measured as dissolved inorganic carbon (DIC) production on a Perkin-Elmer Autosystem GC-FID, with a headspace autosampler that operated directly on the incubation bottles. Separation was carried out on a Haysep Q column using N_2 (70 ml min^{-1}) as carrier gas. Before analysis the samples were acidified to pH 2.5 (thus converting all HCO_3^- and CO_3^{2-} to CO_2 and H_2CO_3) and shaken vigorously to achieve equilibration between the gas phase and the water phase. Although it has been reported that other organisms than bacteria can constitute ~10% of total planktonic biomass in humic water during dark incubations [*Daniel et al.*, 2005], we assumed that the measured dark DIC production represented the respiration of bacteria. BP was measured by a modified version of the leucine incorporation method described by *Smith and Azam* [1992]; see *Karlsson et al.* [2002] for details. TOC was measured with a Shimadzu TOC-5000 instrument using catalytic combustion, and absorbance spectra were measured between 190 and 510 nm in 1 cm quartz cuvettes with a Hewlett Packard 8452A diode array spectrophotometer. Analyses of the N and P fractions were made with standardized methods at the Department of Ecology and Evolution, Uppsala University, Uppsala.

[9] Nutrient enrichment experiments were performed twice with water from Västrabäcken and Kallkällsmyren. Sample preparation and analyses were the same as described above. Nutrients were added before the incubation start in the following combinations: (1) untreated controls, (2) bottles added 1 mg N L^{-1} in the form of NH_4NO_3, (3) bottles added 100 μg P L^{-1} in the form of KH_2PO_4, and (4) bottles added both 1 mg N L^{-1} and 100 μg P L^{-1}. This time, additional samples for nutrient analyses were taken from the 250 mL incubation bottles at the end of the incubations, in order to control that added nutrients were still available in excess.

2.3. Quality of Organic Matter

[10] Three indicators of organic matter quality were used. The first was the organic material C/N ratio, which is a classical general way of expressing substrate quality in both terrestrial [*Kalbitz et al.*, 2000] and aquatic [*Wetzel*, 2001] sciences. It is often assumed that a high C/N ratio reflects recalcitrance to degradation, and it has specifically been shown that C/N may be a major regulator of BGE in aquatic systems [*del Giorgio and Cole*, 1998; *Kroer*, 1993]. The second indicator was the organic material C/P ratio, which can be interpreted in a similar way as the C/N ratio. In both the dissolved [*Lennon and Pfaff*, 2005] and particulate [*Hessen*, 2006] fractions of TOC, high C/P is coupled to low degrees of biotic utilization and vice versa. Organic material C/P and C/N ratios were calculated by dividing TOC with the total organic P and N fractions which, in turn, were quantified by subtracting inorganic nutrient contents from TP and TN. Inorganic P and N were estimated as soluble reactive P and the sum of dissolved NH_4-N, NO_2-N plus NO_3-N, respectively. Finally, we used an index describing the character of the absorbance spectrum. It is well known that absorbance spectra tend to skew toward higher wavelengths as the average molecular weight of the organic matter increases [*Butler and Ladd*, 1969; *Dehaan and Deboer*, 1987]. There is, however, no standard way of accounting for this feature; ratios between different wavelengths can be used, and different spectral slopes can be calculated by fitting data points to exponential curves, covering certain ranges of wavelengths. We chose the ratio between absorbance at 254 nm and 365 nm (a254/a365) because of its simplicity and its clear negative relationships to increasing molecular weight of dissolved humic substances [*Dahlén et al.*, 1996; *Dehaan*, 1993; *Strome and Miller*, 1978]. As a control, we also calculated on spectral slopes (S) of Ln-transformed spectrograms between 250 nm and 400 nm (UV-A and UV-B region), using linear regression. Since patterns of S were the same as for a254/a365 because of a strong correlation (R^2 = 0.97), S values are not presented.

2.4. Calculations and Statistics

[11] No patterns of significantly changing DIC production rates could be detected the bioassays. We therefore approximated BR as the linear slope of DIC regression lines from start to stop of the measurements. In contrast to the approximately constant BR, the average leucine uptake dropped markedly during the first incubation days, in a seemingly linear manner, before stabilizing after about 6 days. On the basis of this observed pattern (Figure 2), start values of BP were estimated as the production axis intercepts of linear regression lines for BP during the first 7 days of incubation. Stop values were considered as the mean of the last two data points, from day 8 to day 11.

[12] All bacterial production and respiration rates were normalized to TOC for comparisons of the bioavailability of organic material between streams. Seasonal variations within streams were small, and we therefore used mean values over the sampled period when comparing the different streams. Focus was set on patterns in the bacterial utilization of organic carbon along the forest coverage gradient. Results could likewise be inversely attributed to the mire coverage gradient, as the proportions of forest and mire in the selected catchments correlate strongly (R^2 = 0.99, n = 9).

[13] Because of the relatively small number of streams studied, we experienced difficulties with evaluating the regulation of BR, BP, and BGE using multiple linear

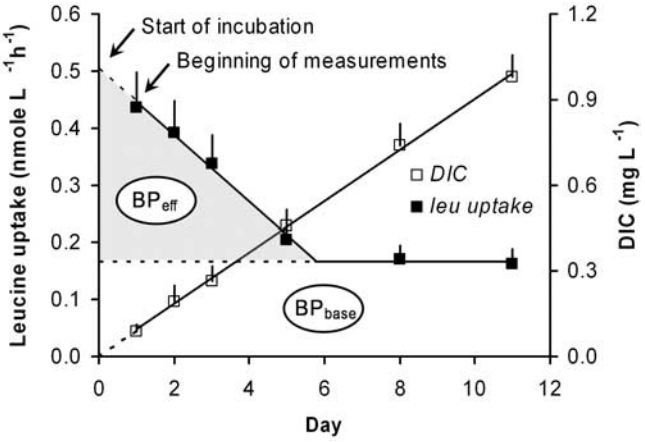

Figure 2. Mean leucine uptake and mean cumulative production of dissolved inorganic carbon (DIC) ($y = 0.089x$, $R^2 = 1.00$, $n = 9$) for the nine streams plotted over incubation time. BP_{base} represents the area below the leucine uptake baseline, and BP_{eff} represents the area of the upper left triangle, formed between the baseline and a linear regression line for the first 5 days. Error bars show 95% confidence intervals of the mean for all streams and sampling occasions ($n = 36$). Note that there was a considerable variation in BP_{eff} from case to case, although not clearly indicated by the graph.

regression methods. We therefore chose an alternative regression method that works well with short data sets, namely Partial Least Squares (PLS) regression [*Höskuldsson*, 1988; *Sobek et al.*, 2003]. Similar to multiple linear regression methods, PLS analysis aims at explaining Y data by relating it to linear combinations of X data. Instead of using X variables as direct predictors, PLS regressions extract uncorrelated latent components from the X data matrix, that maximally explain the variance in Y data. A main advantage of PLS analysis is its tolerance to dependence (correlation) among X variables. It is also believed to be less sensitive than linear multiple regression to missing data and to variables that are not normally distributed. The performance of a PLS model is evaluated in terms of explained variance (R^2Y), predictability (Q_2), and stability (background correlation in R^2Y). A robust model has high R^2Y and Q_2, but low background correlation. All PLS modeling was carried out using SIMCA-P 11.0 software (Umetrics).

3. Results

[14] Bacterial respiration (BR) proceeded at approximately constant rates during the 11-day periods of DIC measurements (Figure 2), with mean values of 66–98 μg C L^{-1} d^{-1} for the different streams (Figure 3a). No relationship was observed between absolute or carbon-specific BR and forest coverage. Contrary to BR, the rates of bacterial production (BP) were not constant during the bioassays. At the incubation start, BP ranged from 16 to 52 μg C L^{-1} d^{-1}, and absolute as well as carbon-specific BP were positively correlated to catchment forest coverage (Figures 3a and 3b). No such correlations were found by the end of the incubation, where BP had decreased to 9–17 μg C L^{-1} d^{-1}. Mean initial BGE of the sites ranged from 0.17 to 0.41, and BGE was positively correlated with forest coverage (Figure 3c). At the end of the incubations, BGE of all

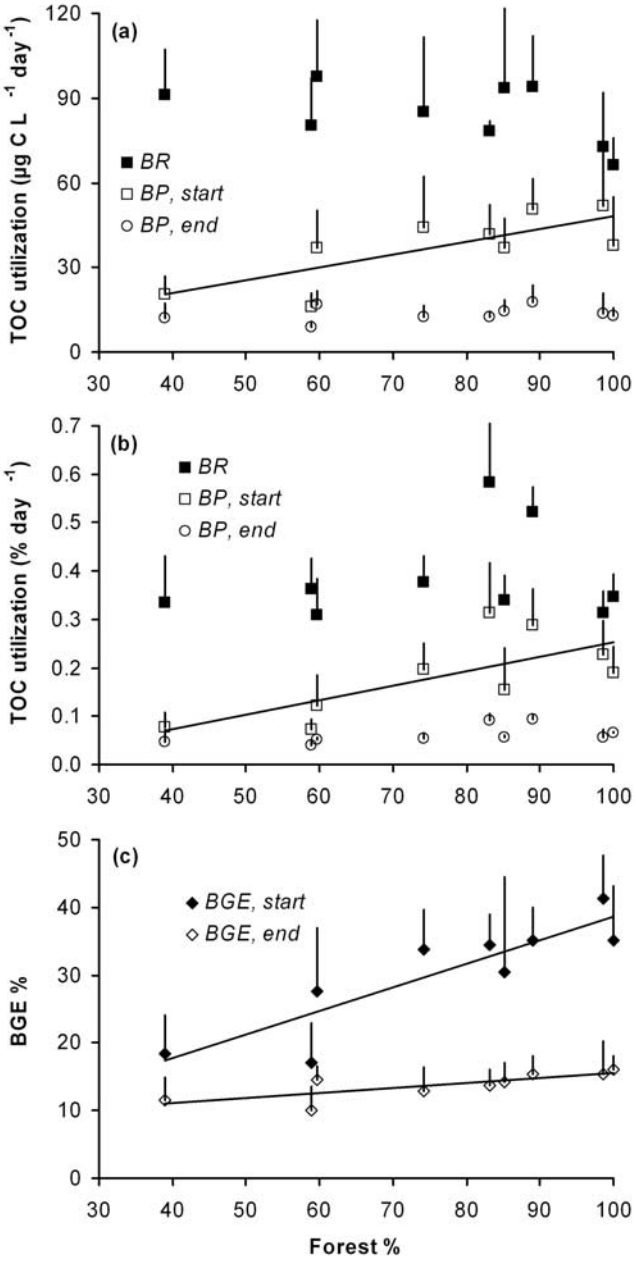

Figure 3. (a) Bacterial respiration (BR) and bacterial production (BP) in relation to forest coverage of the catchment. BP is shown for the incubation start ($y = 0.45x + 2.61$, $R^2 = 0.58$, $n = 9$) and stop. (b). Same as Figure 3a but normalized to total organic carbon (TOC) ($y = 0.0030x - 0.05$, $R^2 = 0.51$, $n = 9$). (c) Bacterial growth efficiency (BGE) in relation to forest coverage at the incubation start ($y = 0.35x + 3.77$, $R^2 = 0.78$, $n = 9$) and stop ($0.075x + 8.06$, $R^2 = 0.61$, $n = 9$). Symbols represent the mean of four sampling dates during the season, and error bars denote SD.

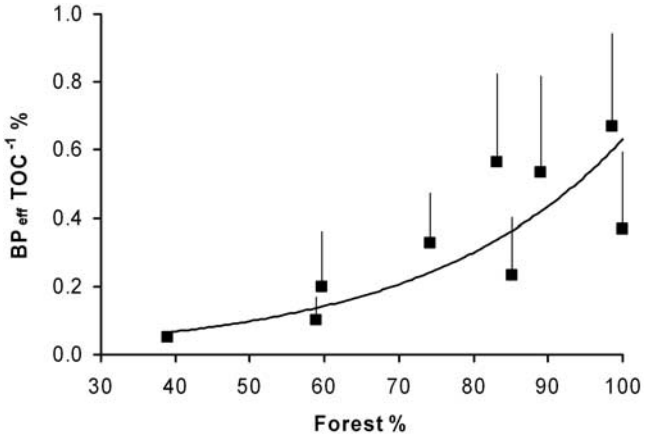

Figure 4. Relationship between BP_{eff} TOC^{-1} (estimated from case to case) and forest coverage of the catchment ($y = 0.015e^{0.037x}$, $R^2 = 0.80$, $n = 9$). Error bars show SD of four sampling dates.

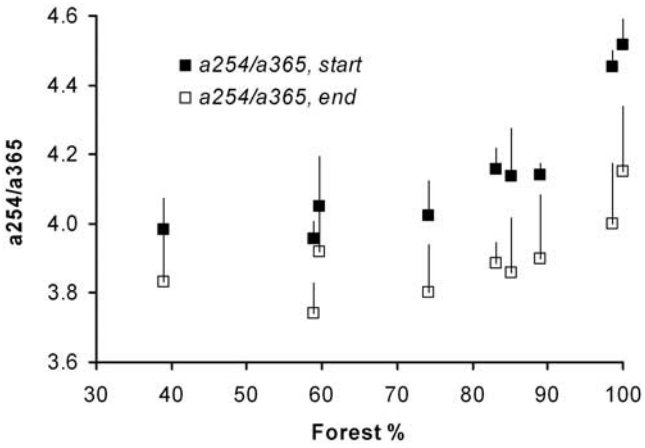

Figure 5. Relationship between forest coverage of the catchment and the average a254/a365 ratio at the incubation start ($y = -0.14\text{Ln}(101 - x) + 4.53$, $R^2 = 0.96$, $n = 9$) and stop ($y = -0.076\text{Ln}(101 - x) + 4.10$, $R^2 = 0.78$, $n = 9$). Error bars stand for SD of four sampling dates.

sites had dropped to about 0.14, and the association with forest had weakened (Figure 3c). Thus during the 11-day incubation period, steady respiration rates coupled to decreased production rates shaped a general decline in BGE. The clear pattern of linearly decreasing BP, which then stabilized on seemingly constant rates after about 6 days (see section 2), made it possible to separate bacterial production into two categories: BP_{base} for baseline production and BP_{eff} for the initial efficient production (see definitions in Figure 2). Through case to case estimates of BP_{eff}, it was shown that, besides BP_{base}, up to 1% of TOC was readily incorporated into bacterial biomass during an initial high-efficiency phase. It was also found that BP_{eff} was exponentially related to the forest coverage (Figure 4).

[15] Differences in organic carbon quality along the catchment forest coverage gradient were indicated by successive changes in absorbance ratios as well as by changes in the nutritional status of the organic matter. The average C/P ratio of the organic material was negatively correlated with forest coverage ($R^2 = 0.54$, $n = 9$, $p < 0.05$), and the corresponding relationship for C/N was close to significant ($R^2 = 0.40$, $n = 9$, $p < 0.08$; data from Tables 1 and 2). The absorbance ratio a254/a365 peaked in the forest streams and declined in a logarithmic manner with lower forest coverage (Figure 5). Concurrently with the drop in BGE, differences in a254/a365 ratios were observed between start and stop of the incubation (Figure 5). We further found that ΔBGE ($BGE_{stop} - BGE_{start}$) was positively related to Δa254/a365 ($a254/a365_{stop} - a254/a365_{start}$; Figure 6). Corresponding correlation was also significant ($p < 0.05$) between ΔBGE and ΔS, where S is the spectral slope for 250–400 nm (data not shown). Stream concentrations of TP, soluble reactive P (SRP), TN, and dissolved inorganic N (DIN) are shown in Table 2. No relations between any of these four nutrient variables and physical attributes of the catchments were found. Nor were any of them directly correlated to BGE or rates of BP and BR (normalized or not normalized to TOC).

[16] The PLS models for BR TOC^{-1} and start values of BP TOC^{-1} extracted one significant component each from the data matrix that explain 85% and 90% of the variations in respiration and production, respectively ($R^2Y = 0.85$ and 0.90). Predictability is high for both models ($Q_2 = 0.70$ for BR model; $Q_2 = 0.73$ for BP model), and permutation tests showed that they were stable (background correlations in $R^2Y = 0.17$ and 0.14). The component loadings (Table 3) show that pH was a positive regulator in the two models. Forest coverage and a254/a365 showed stronger loadings in the production model compared to the respiration model,

Table 2. Concentrations of Total Organic Carbon (TOC), Total Phosphorus (TP), Soluble Reactive Phosphorus (SRP), Total Nitrogen (TN), Dissolved Inorganic Nitrogen (DIN), pH Plus C/P and C/N Ratios (by Moles) of the Organic Matter, Calculated as TOC/(TP-SRP) and TOC/(TN-DIN)[a]

Site Name	TOC, mg C L^{-1}	TP, μg P L^{-1}	SRP, μg P L^{-1}	TN, mg N L^{-1}	DIN, μg N L^{-1}	pH	C/P, by moles	C/N, by moles
Vargstugsbäcken	28 [4]	12 [1]	5 [3]	0.41 [0.05]	30 [23]	4.4 [0.1]	1635 [545]	63 [2]
Stortjärnen Outlet	22 [4]	12 [2]	4 [2]	0.36 [0.05]	15 [8]	4.9 [0.3]	1161 [321]	56 [3]
Kallkällsmyren	34 [13]	12 [5]	4 [3]	0.48 [0.21]	27 [17]	4.3 [0.2]	1518 [304]	65 [5]
Stormyrbäcken	23 [7]	13 [5]	5 [3]	0.37 [0.10]	16 [15]	5.1 [0.4]	1073 [290]	56 [7]
Övre Krycklan	14 [3]	14 [4]	2 [1]	0.30 [0.05]	13 [9]	6.5 [0.1]	433 [64]	42 [2]
Kallkällsbäcken	27 [9]	18 [5]	8 [2]	0.43 [0.13]	19 [13]	4.9 [0.3]	1102 [269]	57 [6]
Långbäcken	18 [5]	24 [11]	2 [1]	0.33 [0.10]	10 [10]	5.8 [0.2]	360 [120]	49 [3]
Risbäcken	23 [6]	13 [4]	3 [1]	0.42 [0.08]	26 [13]	5.4 [0.3]	934 [141]	51 [4]
Västrabäcken	19 [4]	11 [2]	2 [2]	0.32 [0.09]	12 [10]	5.0 [0.1]	866 [163]	55 [4]

[a]SD of four sampling dates is in brackets.

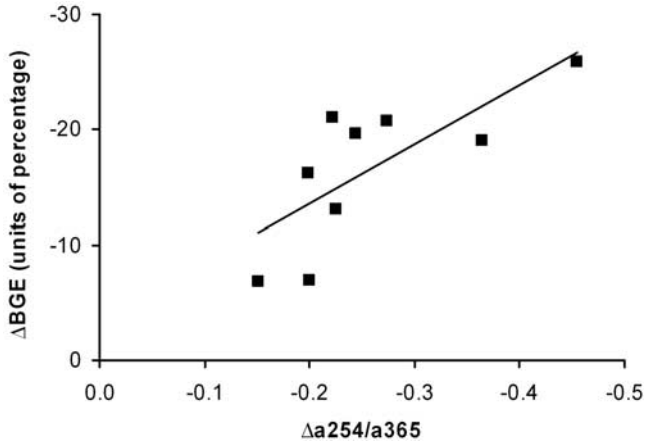

Figure 6. Relationship between ΔBGE (assuming constant respiration) and Δa254/a365 ($y = 51.74x - 3.18$, $R^2 = 0.56$, $n = 9$). The term "Δ" denotes incubation stop values minus incubation start values.

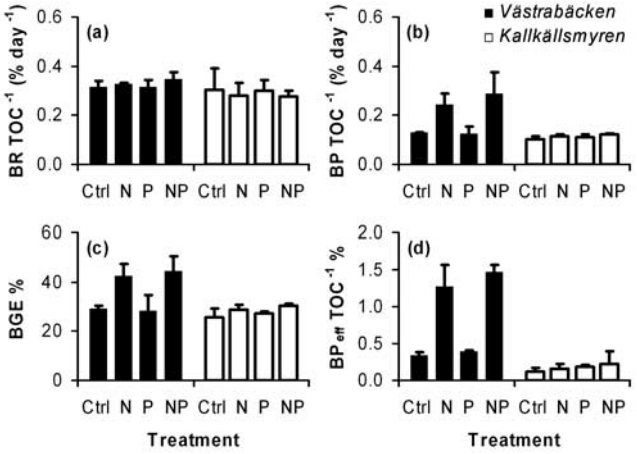

Figure 7. Nutrient addition experiments on batch cultures of water from Västrabäcken and Kallkällsmyren. Data are shown for estimated start values of (a) BR TOC^{-1}, (b) BP TOC^{-1}, and (c) BGE, plus (d) BP_{eff} TOC^{-1}. Error bars represent SD of two measures during 2005.

while the opposite was true for log transformed catchment area. Continuing to the model for BGE, the PLS procedure extracted two significant components that collectively explain 88% of the variance in start values of growth efficiency ($R^2Y = 0.88$, $Q_2 = 0.71$). Most of the explained variation (79%) can be attributed to the first component, while the second component accounts for a minor share (9%). Background correlation in R^2Y is low for the first component (0.13) and reasonably low for the full model including both components (0.28). The loading chart (Table 3) shows that forest coverage was a strong positive regulator of BGE and that lake coverage of the catchment plus C/P ratio had negative influences. The absorbance ratio a254/a365 was an additional variable of large importance, with loadings similar to both BGE and forest coverage. Parameters of moderate importance were pH and the C/N ratio of the organic material. Area was a weak regulator of BGE that showed no association with the dominant PLS component, i.e., axis 1. Stop values of BP TOC^{-1} and BGE showed small variations and could not be modeled with high predictability ($Q_2 < 0.55$) using PLS regression. The nutrient variables TP, SRP, TN, and DIN were not included in any of the PLS models as they did not contribute to explaining Y data, but rather to introduce increased background correlation in R^2Y.

Table 3. PLS Loading Chart of the One Component Models for Bacterial Respiration (BR) TOC^{-1} and Start Values of Bacterial Production (BP) TOC^{-1}, Plus the Two Component Model for Start Values of Bacterial Growth Efficiency (BGE)[a]

	BR TOC^{-1} Model	BP TOC^{-1} Model	BGE Model Axis 1 | 2
	X Loadings		
C/P of total organic matter	N/A	N/A	−0.39 | 0.21
C/N of total organic matter	N/A	N/A	−0.35 | 0.28
Log catchment area	0.66	0.38	0.02 | −0.33
A254/a365 nm (start value)	−0.07	0.33	0.45 | 0.26
pH	0.70	0.66	0.35 | −0.22
Forest coverage of the catchment, %	0.19	0.53	0.54 | 0.27
Lake coverage of the catchment, %	0.19	−0.16	−0.32 | −0.81
	Y Loadings		
BP, BR, or BGE	0.68	0.67	0.49 | 0.21

[a]Nonapplicable (N/A) variables, where X and Y have TOC as a common element, are excluded.

[17] The nutrient enrichment experiments displayed N limitation of BP and BGE, but not BR, in batch cultures from Västrabäcken (Figures 7a–7c). Kallkällsmyren did not show any clear response to nutrient treatment. Similarly, N addition enhanced BP_{eff} for Västrabäcken, but not Kallkällsmyren (Figure 7d). When both N and P were added in excess, the Västrabäcken BP_{eff} value reached 1.48%, which can be compared to corresponding control value of 0.35% (Figure 7d) or the value of 0.37% obtained by the regular survey (Figure 4, marker to the far right). This increase in BP_{eff} was partly due to elevated initial BP rates and partly due to delayed convergence with the control baseline. Two-way factorial analyses of variance confirmed that N was a significant factor regulating the Västrabäcken BP ($F_{1,4} = 14.44$, $p = 0.02$), BGE ($F_{1,4} = 18.07$, $p = 0.01$), and BP_{eff} ($F_{1,4} = 70.26$, $p < 0.01$). In all nutrient-treated samples, ~50% or more of added concentrations of inorganic nutrients remained in solution by the end of the incubations.

[18] In the soil water, there were no systematic changes in the rates of either BR or BP during incubation. Therefore soil water BR was accounted for in the same way as stream water BR and soil water BP could be averaged over the incubation time using the arithmetic mean of all data points. Mean BGE was 36–50% in the riparian forest soil of Kallkällsbäcken and 6–21% in the mire soil of the Kallkällsmyren catchment (Table 4). Carbon-specific respiration was about 0.4% of TOC d^{-1} in both systems, while BP TOC^{-1} demonstrated higher values in the forest soil (~0.3% d^{-1}) than in the mire soil (~0.1% d^{-1}). The

Table 4. Soil Water Measurements of BR TOC^{-1}, BP TOC^{-1}, BGE and the Absorbance Ratio a254/a365[a]

Soil Depth	BR TOC^{-1}, % d^{-1}	BP TOC^{-1}, % d^{-1}	BGE, %	a254/a365
		Forest Soil		
25 cm	0.49 [0.17]	0.28 [0.11]	36.3 [1.3]	5.05 [0.08]
45 cm	0.46 [0.08]	0.28 [0.04]	37.7 [1.1]	3.37 [0.23]
55 cm	0.41 [0.09]	0.41 [0.02]	49.8 [4.0]	3.26 [0.11]
65 cm	0.38 [0.05]	0.21 [0.03]	35.8 [6.0]	3.73 [0.11]
		Mire Soil		
75 cm	0.31 [0.12]	0.02 [>0.01]	5.8 [1.9]	4.23 [0.07]
150 cm	0.55 [0.36]	0.09 [0.09]	11.3 [6.7]	4.13 [0.06]
200 cm	0.39 [0.30]	0.12 [0.11]	21.4 [3.8]	4.08 [0.03]
250 cm	0.26 [0.19]	0.06 [0.06]	16.8 [6.1]	4.04 [0.08]
350 cm	0.39 [0.16]	0.09 [0.08]	16.4 [7.8]	3.51 [0.04]

[a]SD of two sampling dates is in brackets. Only the start value of a254/a365 is presented, as changes during incubation time were small.

absorbance ratio a254/a365 showed its highest value in the most superficial layer of the forest soil (>5), but a decline with soil depth was pronounced. In the mire samples, a254/a365 was more stable, with values about 4 in most layers (Table 4).

4. Discussion

[19] The bacterial consumption of TOC, measured as the sum of BP and BR, during the 11 days of incubation in this study amounted to 4–8% of TOC, which is similar to what is mostly reported for bacterial degradation of natural humic substances in short-term (weeks) degradation experiments [*Tranvik*, 1998]. Differences in BR and BP between sampling occasions were small within all streams. The combined results from each individual stream can hence be considered as replicates for comparing TOC bioavailability between the different streams.

[20] Bacterial respiration was similar in all streams and proceeded at constant rates throughout the incubation (Figures 2 and 3). Bacterial use of stream TOC as an energy source was therefore independent of catchment character and by aging of the substrate pool during incubation. Bacterial production, in contrast to BR, showed distinct dynamics over time during incubation, and differences between streams were evident (Figures 2 and 3). The variation in BGE was therefore entirely dependent on BP variations.

[21] Bacterial production, and hence also BGE, decreased from initial high values and levelled out at seemingly constant rates after ~6 days in most samples (Figure 2). The decrease in BP and BGE over time was simultaneous with qualitative changes of the TOC pool as shown by the parallel decline in BGE and the absorbance ratio a254/a365 (Figure 6). Lowered values of the absorbance ratio probably reflected a shift in molecular weight distribution toward a stronger dominance of larger molecules [*Dehaan*, 1993; *Strome and Miller*, 1978] indicating exhaustion of a pool of low molecular weight material during incubation or, alternatively, that high molecular weight material was formed during incubation. We consider consumption of low molecular weight material as a more likely interpretation in line with bacterial depletion of the TOC pool during incubation; especially since high BGE has been shown to be coupled to small molecular size classes [*Amon and Benner*, 1996]. Our interpretation in this respect is also analogous to observations from UV-light exposure experiments where gradual increases in a254/a365 ratios were coupled to enhancement of bacterial growth [*Lindell et al.*, 1995; *Obernosterer and Herndl*, 2000]. In those experiments the absorbance ratio responded quickly even to small effects of photo-bleaching. Also in dark incubations, a254/a365 has been reported to be a significant predictor of BP and a sensitive indicator of changes in the character of organic carbon [*Tadonleke*, 2007]. These findings support the plausibility in that the bacterial use of organic carbon in this study was large enough to affect a243/a365a.

[22] An alternative explanation to decreasing BP and BGE is that available inorganic nutrients were expended as they were used for BP, introducing nutrient limitation over time. However, this possibility was not supported by data. Start values of BP and BGE were nutrient limited for the forest stream Västrabäcken (Figure 7) but nutrient-enriched samples showed a gradual convergence with the control baseline during incubation. Consequently, BP and BGE were more nutrient limited at the start than at the end of the experiments. We therefore suggest that inorganic nutrients restricted the initial rates of BP and the initial BGE, before depletion of low molecular weight (''high quality'') substrates. BP and BGE in the mire stream Kallkällsmyren were not nutrient limited at any time during incubation (Figure 7). The result is logical if the kind of substrates that supported BP_{eff} were lacking in mire streams. This interpretation is offered substantial support by the fact that streams draining catchments with high shares of mires lacked the characteristics of labile carbon. The a254/a365 ratio, BP, and BGE were low already at the start of the incubation, and the change over time of these variables was small, especially when compared with forest streams (Figures 3–6). In contrast to the stream water samples, there were no clear declining trends of BP or BGE during incubation in the soil water. We suggest that the lack of temporal dynamics here was due to absence of carbon supporting BP_{eff} in the mire soil samples and due to excess of that carbon in the forest soils, so that the incubation time was too short for diminishing BP_{eff}.

[23] Thus our results demonstrate that BR was independent of observed organic substrate quality changes and inorganic nutrient limitation in all streams but that BP was boosted by a fraction of ''high quality'', probably low molecular weight substrates, in several of the streams. We interpret our results so that BP and BGE in most streams were controlled mainly by organic substrates limitation in combination with inorganic nutrients availability which agrees with major conclusions in the review of *del Giorgio and Cole* [1998]. The substrate pool which supported BP_{eff} in our streams made up a minor share of TOC (typically <1%) and was rapidly exhausted during our incubations. This is consistent in comparison with boreal forest soil water, which has a similar sized pool of rapidly metabolized low molecular weight DOC [*van Hees et al.*, 2005]. It should be noted, though, that the carbon with potential of supporting BP_{eff} might have been somewhat underestimated

in our incubations (e.g., in Figure 4). As illustrated by the nutrient enrichment experiment on water from Västrabäcken (Figure 7), BP_{eff} increased considerably when the bacteria were relieved from nutrient deficiency.

[24] The initially high values of BP and BGE were expressed differently in different streams in patterns which were predicted by forest coverage of the catchment. Organic carbon drained from forests supported considerably higher BP TOC^{-1} and BGE than carbon drained from mires (Figure 3), and BP_{eff} was more or less exclusively based on carbon from forested areas (Figure 4). High values of the absorbance ratio a254/a365 were associated with large degrees of forest coverage (Figure 5), and the PLS analysis (Table 3) showed that initial BGE values were strongly related to the absorbance ratio. We therefore conclude that TOC in drainage water from forest soils supported bacterial growth in streams more than drainage water from mires. Further support for this view was acquired by the soil water analyses (Table 4). We suggest that this difference between forest and mire streams was an effect mainly due to differences in organic carbon quality. In the forests, relatively young detritus with high nutritional qualities is drained from surface soil horizons [*Laudon et al.*, 2004b; *Stepanauskas et al.*, 2000]. Peat mires lack similar dynamics [*Laudon et al.*, 2004a] and may also lack the kind of labile leachates that forest soils gain from tree roots with mycorrhizal fungi [*Högberg and Högberg*, 2002].

[25] The time delay for water and TOC between entering the small study streams and sampling was less than a few hours in most cases. Considering that BP decreased rapidly during incubation, especially in the forest streams, the effect of soil drainage on BP in receiving streams and lakes is strongly linked to water residence times. Stimulation of BP by BP_{eff} persisted for ~6 days in our incubations (20°C and in the dark). Depletion of BP during natural conditions can be expected to be slower considering the temperature difference between our incubations (20°C) and the ambient stream temperature which seldom exceeded 10°C during the study. If we assume a Q10 value of 2–3 for BP_{eff}, the effect of BP_{eff} should persist for about 2–3.5 weeks in natural streams. Forest soil drainage should then be sufficient to support BP_{eff} more or less all the time in streams which are continuously receiving water and TOC from adjacent soils. Consequently, depletion of the carbon fraction that supports BP_{eff} can be expected to take place mainly in lakes where water renewal times usually are from weeks to years. The use of this substrate should depends on catchment characteristics, transit time of TOC from soils via streams to lakes, and the water renewal time of the lakes. Our results in this respect are consistent with previous investigations in the River Öre catchment close to the Krycklan catchment [*Bergström and Jansson*, 2000] which demonstrated that BP was higher in the inlet to the lake than in the lake itself and that transition times in stream water dictated by runoff had considerable influence on BP in the lake. Additional support for the proposal that lakes are major sites for a decline of BP_{eff} was offered by this study. The lowest initial BGE and the poorest fit to the linear prediction model based on forest coverage (Figure 3) was the station at the outlet of the lake, Stortjärnen. This site is different from the other sites in our study in the sense that water is drained directly from the lake. Moreover, the PLS model (Table 3) shows a potential negative association between lake prevalence in the catchment and BGE. We therefore suggest that drainage water from forest soils can be a considerable stimulation to bacterial growth in boreal lakes.

[26] The fact that BR was constant over time in our incubations also largely fit the picture on lake respiration of allochthonous organic carbon. Boreal unproductive lakes are generally net heterotrophic [*del Giorgio et al.*, 1997] and supersaturated with respect to CO_2 due to bacterial respiration of allochthonous organic carbon. Supersaturation of boreal lakes is correlated mainly with DOC (or TOC) concentrations [*Algesten et al.*, 2003; *Sobek et al.*, 2003], and temporal variation appears to be rather small [*Jonsson et al.*, 2001].

[27] In summary, our study demonstrates how the spatial variability of BGE in the boreal region may be mediated by the distribution of the two dominating landscape elements forest and mires. Our results show that drainage water from forest soils contains organic substrates, possibly of low molecular weight, which efficiently support BP and stimulate BGE in receiving waters. We suggest that depletion of this pool, unless not replenished, occurs within weeks in natural systems, is nutrient limited and mainly takes place in lakes. Drainage water from mire systems may have higher TOC concentrations, but is void of a similar pool of "high quality" substrates and thus supports BP at lower relative rates than forest drainage water. After depletion of this pool there is no difference between forest and mire drainage TOC in its support of BP. There was no difference between forest and mire drainage with respect to bacterial respiration, and respiration rates were not affected by substrate aging, nutrient limitation, or variations in BP and BGE during our incubations.

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