

# Hydrological Control of Organic Carbon Support for Bacterial Growth in Boreal Headwater Streams

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**Abstract** Terrestrial organic carbon is exported to freshwater systems where it serves as substrate for bacterial growth. Temporal variations in the terrigenous organic carbon support for aquatic bacteria are not well understood. In this paper, we demonstrate how the combined influence of landscape characteristics and hydrology can shape such variations. Using a 13-day bioassay approach, the production and respiration of bacteria were measured in water samples from six small Swedish streams (64° N, 19° E), draining coniferous forests, peat mires, and mixed catchments with typical boreal proportions between forest and mire coverage. Forest drainage supported higher bacterial production and higher bacterial growth efficiency than drainage from mires. The areal export of organic carbon was several times higher from mire than from forest at low runoff, while there was no difference at high flow. As a consequence, mixed streams (catchments including both mire and forest) were dominated by mire organic carbon with low support of bacterial production at low discharge situations but dominated by forest carbon supporting higher bacterial production at high flow. The stimulation of bacterial growth during high-flow episodes was a result of higher relative export of organic carbon via forest drainage rather than increased drainage of specific “high-quality” carbon pools in mire or forest soils.

## Introduction

Terrestrial export of organic carbon to surface waters has significant impact on boreal freshwater ecosystems [15]. Due to its humic components, the allochthonous organic carbon absorbs light and decreases the intensity of light available for aquatic primary production [1]. On the other hand, organic carbon also serves as a carbon and energy source for heterotrophic bacterial production (BP) [36], thereby fueling heterotrophic food chains [16].

The question of how BP can be regulated by variations in supply and availability of allochthonous organic carbon has mainly been addressed from a spatial perspective. It has been shown that interacting landscape characteristics such as vegetation and soil type sets the prerequisites for microbial exploitation of exported organic materials [18, 23, 38] by determining both substrate quantity [40] and quality [39]. For example, boreal coniferous forests export considerably less organic carbon [11, 21] but with a higher bioavailability, compared to boreal *Sphagnum* peat mires [38]. Less is known about the temporal variations of organic carbon bioavailability.

Hydrological variations have been suggested to mediate pulses of high organic carbon loading contributing to high rates of bacterial growth [2, 6]. However, there is no complete understanding of how hydrology can affect the degree to which organic substrates support bacterial growth (e.g., BP per unit available carbon) via differences in organic carbon quality. In this paper, we make an attempt to expand the mechanistic understanding of how temporal variations in BP can be regulated by the character and the magnitude of the organic carbon that is exported from different landscape components at different hydrological situations. We studied streams in catchments with known differences in the quality and short-term bioavailability of

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organic carbon draining from the two dominating landscape components: forests and mires [3]. It has also previously been shown that forested areas in the studied catchments provide a higher share of the total landscape export of carbon during floods compared to at base flow [21, 22]. Considering that forest carbon support BP to a higher degree than mire carbon [3], we, therefore, hypothesize that BP per unit carbon is high at high flow and low at low flow in streams draining mixed catchments. Furthermore, we expect bacterial growth efficiency ( $BGE = BP/[BP + BR]$ ) to show the same pattern as BP, since BP and BGE are often correlated [10]. To test these hypotheses we used a thirteen-day bioassay approach to analyse BP and bacterial respiration (BR) in water from six small headwater streams with different catchment characteristics (forest streams, peat mire outlets, forest–mire ‘mixed’ streams), sampled at different hydrological conditions. We use BP and BGE values representing the initial state of the incubations to assess the short-term potential of the organic carbon for support of bacterial growth.

## Study Sites

The study was carried out in the Krycklan catchment at the Vindeln Experimental Forests (64°14' N, 10°46' E) in northern Sweden. Hydrological studies have been performed in this catchment for nearly three decades. We selected six of the most intensively studied first- and second-order streams of the area: two forest streams, two peat mire outlets, and two streams that drained catchments with typical (for the boreal zone) proportions between forests and mires. Forests and mires together covered 100% of the area of each catchment. Below follows a brief description of the study sites. For details regarding the methods used for determination of catchments characteristics, see Ågren et al. [40].

The drainage areas, Risbäcken (66 ha) and Västrabäcken (13 ha), were approximately 100% forested. Two streams drained the mires, Kallkällsmyren (19-ha catchment) and Degerö Stormyr (330-ha catchment). These mires were in part minerogenic, and thus, the drainage areas also included patches of forest. However, the mire coverage values of 69% for Degerö Stormyr catchment and of 41% for Kallkällsmyren catchment were among the highest that could be found in the region. Kallkällsbäcken (50-ha catchment) and Stormyrbäcken (294-ha catchment) were selected to represent streams with typical proportions of forests and mires in the catchment. The global mean for the boreal zone is about 20% wetland coverage [26], and the mire coverage was approximately 15% for the Kallkällsbäcken catchment and approximately 25% for the Stormyrbäcken catchment. Since mires generally export several

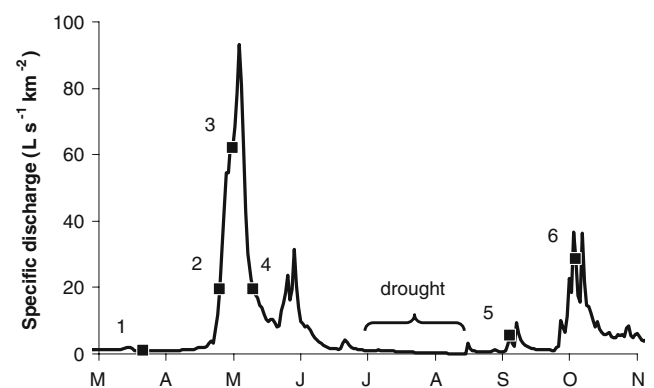
times more organic carbon per unit of area compared to forests [11, 40], it is not obvious whether the forest component or the mire component of these catchments dominated the export of organic carbon.

The forest component of the catchments was dominated by Scots Pine (*Pinus sylvestris*) in dry upslope areas and Norway Spruce (*Picea abies*) in wetter areas. Mires were dominated by peat-forming *Sphagnum* species and could be categorized as acidic, with a mixed distribution of ombrotrophic and oligotrophic minerogenic patches. Nutrient-poor peat mires like these represent the most extensive wetland type of the boreal zone [26]. Predominant soils types were peat in the mires and glacial tills in the forested areas. On average, the annual temperature of the area is 1.3°C and the annual precipitation 600 mm of which 35% falls as snow between November and April [29]. All the snow stored in winter melts during an about 6-week-long period in spring.

## Materials and Methods

### Sampling and Analyses

The six different streams were sampled for bioassays at six dates in 2006: during winter base flow, three times during the snowmelt discharge pulse and twice in association with autumn rains (Fig. 1). No summer base flow samples were obtained due to an unusual period of drought from late June to mid August, heavily reducing or totally eliminating the runoff of all catchments. Water was collected in 2.0 L acid-washed and stream water-rinsed high-density polyethylene bottles that were kept cool and in the dark until arrival at the laboratory. The samples were thereafter equilibrated with standard air (78% N<sub>2</sub>, 21% O<sub>2</sub>, and 0.03% CO<sub>2</sub>) and subsampled into 22-mL sterile glass bottles, leaving a 12-mL



**Figure 1** Daily mean values of specific discharge at the Kallkällsbäcken catchment from March to November 2006. Squares show the six sampling dates. The curve approximately represents specific discharge for all catchments in the study

headspace that was flushed with standard air and sealed with gas-tight septa. All bottles were incubated in the dark at 20°C.

We chose to work with unfiltered samples since previous studies in the same streams have found no measurable difference in the concentration of organic carbon due to filtering [40]. Particulate organic carbon concentrations are usually negligible relative to the dissolved fraction in Swedish boreal surface waters, even during high-flow episodes [13, 20]. A major motive for not filtering the samples is that we study the activity of the natural microbial community during incubations.

Triplicates of the 22-mL incubation bottles were analyzed for BP every second and BR every fourth day, during a period of 12 days starting approximately 24 h after sealing of the bottles (13 days total incubation time). We used different samples for each replicate and for each analysis so that all incubation bottles remained undisturbed until analysis. BR was measured as dissolved inorganic carbon (DIC) production using a gas chromatography–flame ionization detector (Perkin-Elmer), with a headspace autosampler that operated directly on the incubation bottles. Separation was carried out on a Haysep Q column using N<sub>2</sub> (40 mL min<sup>-1</sup>) as carrier gas. Before analysis, the samples were acidified to pH 2.5 (thus converting all HCO<sub>3</sub><sup>-</sup> and CO<sub>3</sub><sup>2-</sup> to CO<sub>2</sub> and H<sub>2</sub>CO<sub>3</sub>) and shaken vigorously to achieve equilibration between the gas phase and the water phase. It was assumed that potential respiration of protozoa and metazoa was negligible [3] due to the vast dominance of bacterial biomass in humic water during dark incubations [9]. BP was measured with the leucine incorporation method described by Smith and Azam [33], slightly modified by Karlsson et al. [19]. Portions of 1.2 mL of the samples were exposed to [<sup>3</sup>H]-leucine concentrations between 30 and 70 nmol/L during 1 h in 20°C. Blanks were pretreated with 5% w/v of trichloroacetic acid (TCA). Leucine incorporation into protein was determined by precipitation with TCA and centrifugation, followed by scintillation counting (Beckman LS 6500). The leucine incorporation was converted into carbon units according to Simon and Azam [32].

Unfiltered samples for analysis of total phosphorus (TP), total nitrogen (TN), and total organic carbon (TOC) were frozen directly after arrival to the laboratory. Later, TOC was measured by a Shimadzu TOC-V<sub>CPH</sub> analyzer, TN by an Antek 9000 Nitrogen Analyzer, and TP by persulfate oxidation followed by the standard molybdenum blue method [27]. Comparison between unfiltered (TOC) and filtered duplicate stream samples using 0.45-μm filters (Millipore) of dissolved organic carbon (DOC) showed no systematic difference at any time of the year, regardless of flow. Water for absorbance analysis was filtered through 0.45-μm filters (Millipore) and analyzed directly in associ-

ation with the start of the incubations. Absorbance spectra were measured between 190 and 510 nm in 1-cm quartz cuvettes with a Hewlett Packard 8452A diode array spectrophotometer.

In addition to the stream samples, we analyzed water from forest and mire soils. These samples were collected once during spring and once in the summer. The mire of the Kallkällsmyren catchment was sampled at the depths of 75, 150, 200, 250, and 350 cm, using nested wetland wells with closed bottoms, perforated at the lower 10 cm. Soil solutions in the riparian forest zone of Kallkällsbäcken were sampled 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.

Discharge was measured at the sampling site of Kallkällsbäcken using a 90-V notch weir housed in a heated shed. Daily discharge was calculated from continuous recordings of the stream water level and established height–discharge rating curves. The specific discharge at Kallkällsbäcken was used to estimate the discharge in all catchments, assuming that specific runoff was the same in all catchments. This assumption was based on a previous study from the same area [40] showing that between-stream variations in specific discharge were small and of minor importance for the export of organic carbon. In that study, the intersite differences in annual discharge (e.g., due to differences in subcatchment evapotranspiration) was calculated to be not more than ±12% (based on discrete discharge measurements at the other sites, which were compared to the continuous measurements at Kallkällsbäcken). An additional uncertainty due to intersite differences in flow regime (“flashiness”) was calculated as ±1% maximum error during the snow-free season and ±12% during the spring.

#### Calculations and Statistics

No patterns of significantly changing DIC production rates during the bioassays could be detected. We, therefore, calculated BR using the linear slope of DIC regression lines over the full incubation time. In contrast to the approximately constant BR, the average leucine uptake rate in stream samples showed a seemingly linear decline during the first incubation days, before stabilizing after about 1 week. Based on this observed pattern, previously described by Berggren et al. [3], initial values of BP were estimated as the production axis intercepts obtained using linear regression lines of BP during the first 7 days of incubation. In soil water samples, the leucine uptake rate was highly variable with no clear pattern during the incubations. Therefore, BP was averaged over the incuba-

tion time using the arithmetic mean of all data points. BGE in stream and soil water was calculated from the equation  $BGE = BP / (BP + BR)$ .

The ratio between absorbance of 254 and 365 nm was calculated and used as an index of the organic material character [3]. Absorbance spectra tend to change with increased average molecular weight of DOC. High values of the ratio between 254 and 365 nm indicates low average molecular weight of the DOC and vice versa [8, 35]. In a previous study including some of streams in this study, the  $a_{254}/a_{365}$  was positively correlated to BP [3].

Differences in measured abiotic and biotic variables between sampling dates were tested using one-way analysis of variance (ANOVA) and Bonferroni's post-hoc test. Pearson and partial correlations were used to investigate the impact of individual variables on bacterial metabolism. The partial correlations coefficients describe the linear relationship between two variables while controlling for the effects of one or more additional variables. Statistically, the partial correlation between  $X$  and  $Y$  given a control variable  $Z$  is the correlation between the residuals  $R_X$  and  $R_Y$  resulting from the linear regression of  $X$  with  $Z$  and of  $Y$  with  $Z$ , respectively. Using that method, we could control for differences in TOC concentrations between samples and, thus, expose relationships that were not due to differences in organic carbon character but rather due to organic carbon quantity. SPSS 15.0 was used for all statistical calculations.

## Results

### Patterns of Bacterial Metabolism

BR proceeded at approximately constant rates during the bioassay periods, with values of 30–151  $\mu\text{g C L}^{-1} \text{ day}^{-1}$  in the forest stream samples, 146–309  $\mu\text{g C L}^{-1} \text{ day}^{-1}$  in the mire outlet samples, and 43–243  $\mu\text{g C L}^{-1} \text{ day}^{-1}$  in the mixed catchments stream samples. The lowest BR was observed in association with winter base flow and

**Table 2** Bacterial metabolic measures correlated with log discharge, the absorbance ratio  $a_{254}/a_{365}$ , and stream water TP, TN, and TOC for six catchments sampled six times during 2006 ( $n=36$ )

		BR ( $\mu\text{g C L}^{-1} \text{ day}^{-1}$ )	BP ( $\mu\text{g C L}^{-1} \text{ day}^{-1}$ )	BGE
Pearson	Log discharge	0.36	0.56**	n.s.
	$a_{254}/a_{365}$	n.s.	0.63**	0.80**
	TP	n.s.	n.s.	-0.34*
	TN	0.80**	0.36*	n.s.
	TOC	0.88**	0.46**	n.s.
Partial	Log discharge (control for TOC)	n.s.	0.50**	0.36*
	$a_{254}/a_{365}$ (control for TOC)	n.s.	0.71**	0.83**
	TP (control for TOC)	n.s.	n.s.	n.s.
	TN (control for TOC)	0.41*	n.s.	n.s.

Pearson correlations and partial correlations (control for TOC) are shown.

n.s. Not significant

\* $p < 0.05$ , \*\* $p < 0.01$

highest in the October high-flow samples (Table 1). Although the observed absolute values of BR varied tenfold, there was only a twofold variation in carbon-specific values (0.4–1.0%  $\text{TOC}^{-1} \text{ day}^{-1}$ ), reflected in a positive correlation between TOC and BR ( $R^2=0.78$ ,  $n=36$ ,  $p < 0.01$ ). Another variable that was significantly correlated with BR, although not as strongly, was log-specific discharge ( $R^2=0.13$ ,  $n=36$ ,  $p < 0.05$ ). However, log-specific discharge did not significantly explain any variation in BR that was not explained by TOC, as shown by an absent partial correlation between the two variables, with control for TOC (Table 2). No systematic pattern in BR  $\text{TOC}^{-1}$  was found.

Initial values of BP during the incubations were 12–94  $\mu\text{g C L}^{-1} \text{ day}^{-1}$  for the forest streams, 17–46  $\mu\text{g C L}^{-1} \text{ day}^{-1}$  for the mire outlets, and 8–74  $\mu\text{g C L}^{-1} \text{ day}^{-1}$  for the mixed streams. Differences between sampling dates were pronounced, with the lowest BP on samples from the winter base flow and the highest on water from the storm

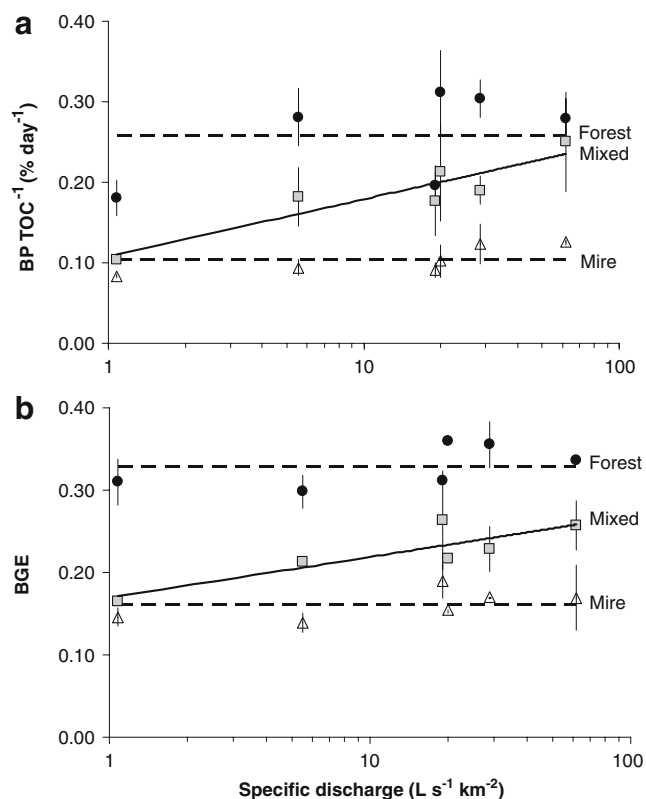
**Table 1** Mean values of bacterial respiration (BR), bacterial production (BP), and bacterial growth efficiency (BGE) plus the absorbance ratio  $a_{254}/a_{365}$  and stream concentrations of total organic carbon (TOC), total nitrogen (TN), and total phosphorus (TP)

Date	BR ( $\mu\text{g C L}^{-1} \text{ day}^{-1}$ )	BP ( $\mu\text{g C L}^{-1} \text{ day}^{-1}$ )	BGE (%)	$a_{254}/a_{365}$	TOC (mg C $\text{L}^{-1}$ )	TN (mg N $\text{L}^{-1}$ )	TP ( $\mu\text{g P L}^{-1}$ )
3/22	69 <sup>a</sup> [42]	15 <sup>abc</sup> [5]	21 [7]	4.12 [0.34]	14 <sup>a</sup> [8]	0.52 [0.27]	20 <sup>a</sup> [11]
4/26	138 [37]	43 <sup>a</sup> [16]	24 [7]	4.47 [0.28]	22 [3]	0.71 [0.16]	21 [5]
5/2	128 [15]	44 <sup>b</sup> [16]	26 [7]	4.56 [0.24]	20 [2]	0.48 [0.07]	14 [1]
5/11	80 <sup>b</sup> [11]	27 <sup>d</sup> [7]	25 [6]	4.35 [0.25]	18 [2]	0.45 [0.09]	11 [2]
9/5	146 [78]	35 <sup>c</sup> [8]	22 [7]	4.50 [0.34]	24 [14]	0.90 [0.44]	26 [7]
10/5	191 <sup>ab</sup> [40]	63 <sup>cde</sup> [19]	25 [8]	4.58 [0.32]	32 <sup>a</sup> [8]	0.81 [0.17]	14 <sup>a</sup> [3]

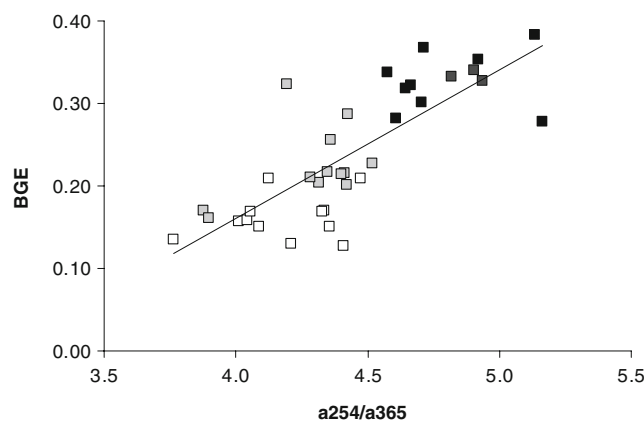
Data are shown for six dates in 2006 (see Fig. 1), and SD of six streams is in brackets. Shared index letters within columns identify variables statistically different from each other ( $p < 0.05$ ) as determined by one-way ANOVA and Bonferroni's post-hoc test

discharge peak in early October (Table 1). BP was positively correlated to stream TOC concentration ( $R^2=0.21$ ,  $n=36$ ,  $p<0.05$ ) and to the absorbance ratio  $a_{254}/a_{365}$  ( $R^2=0.39$ ,  $n=36$ ,  $p<0.01$ ). According to the partial correlation between BP and  $a_{254}/a_{365}$  with control for TOC (Table 2), the absorbance ratio  $a_{254}/a_{365}$  explained a significant share of the variation in BP not explained by TOC.

Combining the three stream categories, BP increased linearly with rising log-specific discharge ( $R^2=0.31$ ,  $n=36$ ,  $p<0.01$ ). This relationship was not dependent on patterns in TOC quantity, as shown by the partial correlation with control for TOC (Table 2). Patterns in carbon-specific BP were not the same for the different stream types. When averaging the catchments within each category, neither mire outlets nor forest streams showed a significant correlation between BP  $\text{TOC}^{-1}$  and log-specific discharge. However, the relationship was strong for mixed streams samples (Fig. 2a).



**Figure 2** Initial incubation values of BGE (a) and  $\text{BP TOC}^{-1}$  (b) over a gradient of specific discharge. Shown for forest streams (black circles), mire outlets (white triangles), and streams with mixed catchments (gray squares). Error bars denote  $\pm 1$  SD of two streams. Significant correlations for BGE ( $y=0.02\ln(x)+0.17$ ,  $R^2=0.76$ ,  $n=6$ ,  $p<0.05$ ) and  $\text{BP TOC}^{-1}$  ( $y=0.03\ln(x)+0.11$ ,  $R^2=0.85$ ,  $n=6$ ,  $p<0.05$ ) in the mixed streams are shown by regression lines. In the absence of significant correlations, dotted lines represent mean values



**Figure 3** The relationship between BGE and  $a_{254}/a_{365}$  ( $y=0.18x-0.56$ ,  $R^2=0.63$ ,  $n=36$ ,  $p<0.01$ ) for all streams and sampling dates during 2006. Black markers denote forest streams, white markers peat mire outlets, and gray markers streams with a mix of forests and mires in the catchments

Initial values of BGE during the incubations were 0.28–0.38 for the forest catchments, 0.13–0.21 for the mire catchments, and 0.16–0.32 for the mixed catchments. Combining the three stream categories, BGE was correlated to  $a_{254}/a_{365}$  ( $R^2=0.63$ ,  $n=36$ ,  $p<0.01$ ; Fig. 3). Although BGE was similar between sampling dates (Table 1), there was a significant partial correlation between log-specific discharge and BGE, with control for TOC (Table 2).

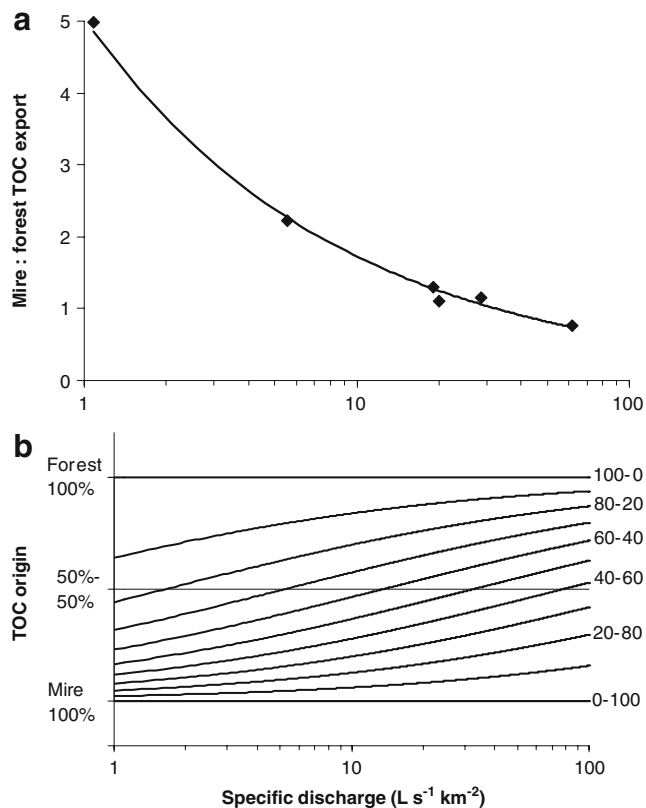
There were significant relationships between bacterial metabolic measures and nutrient variables, but these largely reflected covariations with TOC. Neither BP nor BGE showed any partial correlations with TP or TN, when controlling for TOC (Table 2). The exception was a positive and significant relationship both in terms of direct and partial correlations between BR and TN.

#### Patterns of TOC Export

Sample concentrations of TOC ranged from 7 to 29  $\text{mg L}^{-1}$  in the forest streams, 18 to 53  $\text{mg L}^{-1}$  in the mire outlets, and 8 to 36  $\text{mg L}^{-1}$  in the streams with mixed catchments. The lowest values were observed at winter base flow and the highest at the October storm rise (Table 1). At winter base flows, there was a strong positive correlation between percentage of mire in the catchment and stream TOC ( $R^2=0.76$ ,  $n=6$ ,  $p<0.05$ ). Extrapolating this relationship to 0% mire (=100% forest) and to 100% mire (=0% forest), the data suggest that there was a mire/forest TOC export ratio of about five (assuming the same specific runoff in all catchments). However, during spring flood and other high discharge events, this mire/forest TOC export ratio was close to one, as TOC concentrations were similar in all streams. Hence, there was a temporal variation in relative magnitude of TOC export from the two catchment types.

The variation in the mire/forest TOC export ratio could be well explained by a power relationship with specific discharge (Fig. 4a). Thus, by multiplying mire/forest TOC export ratios with mire/forest catchment coverage proportions, we could calculate the shares of the stream TOC pool coming from the two sources at different flow situations and in streams draining catchments with different proportions between forest and mire coverage. The calculation (Fig. 4b) showed that as little as 20% mire coverage was sufficient for resulting in a mire-dominated TOC pool at low flow ( $1 \text{ L s}^{-1} \text{ km}^{-2}$ ), while more than 60% mire coverage was needed for mire dominance at high flow ( $100 \text{ L s}^{-1} \text{ km}^{-2}$ ).

Organic carbon quality depended on hydrology as indicated by a weak but significant overall correlation between log-specific discharge and  $a_{254}/a_{365}$  ( $R^2=0.15$ ,  $n=36$ ,  $p<0.05$ ). At winter base flow, the mean value of  $a_{254}/a_{365}$  was 4.1, whereas it was 4.6 at spring or autumn



**Figure 4** **a** Relationship between the mire/forest TOC export and discharge ( $y=5.03x^{0.46}$ ,  $R^2=0.98$ ,  $n=6$ ,  $p<0.05$ ). The figure is based on six sampling dates in 2006. **b** The relative contribution of TOC from the two sources forests and mires (calculated from **a**) at different specific discharge and in streams draining catchments with different proportions between forests and mires (the different curves). The uppermost curve represents a catchment with 100% forest and 0% mire (proportion “100–0”) and the lowest curve a catchment with 0% forest and 100% mire (proportion “0–100”), while the intermediate curves show mixed catchments with varying proportions of the two landscape components

peak flows (Table 1). However, again, patterns were not the same for the different catchments types. Looking at the average stream within each category, log-specific discharge explained a great portion of the variation in  $a_{254}/a_{365}$  in the mixed streams ( $R^2=0.81$ ,  $n=6$ ,  $p<0.05$ ) but a smaller share in the peat mire outlets ( $R^2=0.68$ ,  $n=6$ ,  $p<0.05$ ). For the forest streams, there was no significant correlation. While the forest streams had stable values around 4.8 (mean=4.81, SD=0.19,  $n=12$ ) and the mire streams values around 4.2 (mean=4.18, SD=0.20,  $n=12$ ),  $a_{254}/a_{365}$  values in the mixed streams were close to the mire signal at low to moderate flows but approached the forest signal at high flow.

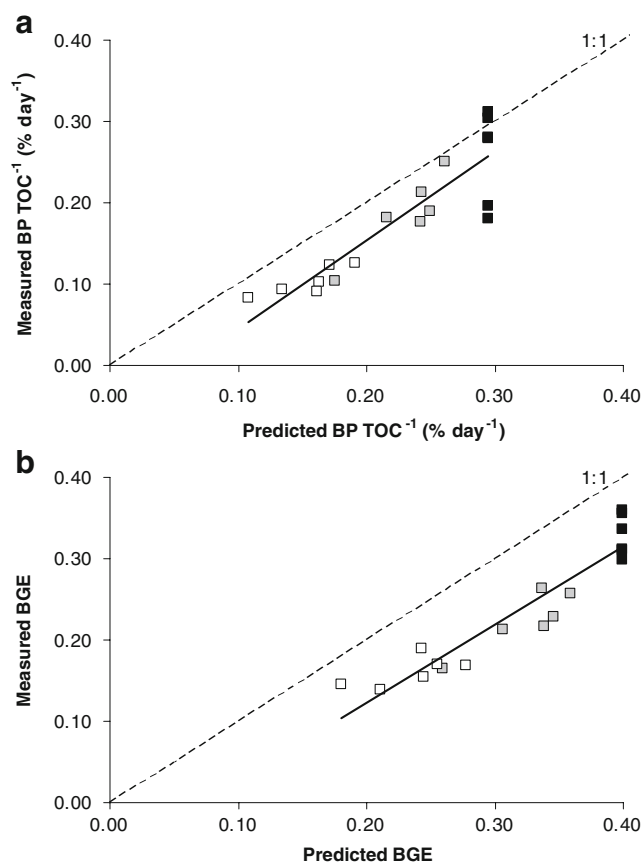
#### Modeling Bacterial Metabolism from Patterns of TOC Export

In the riparian forest soil of Kallkällsbäcken, mean BP  $\text{TOC}^{-1}$  (%  $\text{day}^{-1}$ ) and mean BGE for the different depths were 0.30 (SD=0.07) and 0.39 (SD=0.07), respectively. Corresponding values for the Kallkällsmyren catchment were 0.07 (SD=0.03) and 0.14 (SD=0.05). There were no consistent differences between soil depths. Applying these values as forest and mire end members in a linear two-source mixing model (Fig. 5), stream values of BP  $\text{TOC}^{-1}$  and BGE (see Fig. 2) could be estimated based on the known mixing of TOC from forest and mire sources (see Fig. 4). This mixing model analysis explained more than 80% of the variation in both BP  $\text{TOC}^{-1}$  (Fig. 5a) and BGE (Fig. 5b). However, in both cases, values were consistently overestimated (Fig. 5).

#### Discussion

This study demonstrates how the combined influence of landscape characteristics and hydrology can shape seasonal patterns in stream TOC support of bacterial metabolism. We argue that streams with a mix of forests and mires in the catchment can be dominated by forest TOC supporting high BP when discharge is high and by mire TOC supporting less BP at low flow.

Previous studies from the Krycklan catchment show that most of the water (and TOC) in forest streams comes from groundwater with low TOC concentration at winter base flow, while TOC in the mire streams originate from the organic-rich riparian peat soils in winter [21]. During snow melt, the groundwater levels in forested areas rise and activate new soil TOC sources, thus increasing forest stream TOC concentrations [5]. In contrast, no new sources are activated in the mires, where instead increases in overland runoff dilute stream TOC concentrations [30]. Consequently, the contribution of forest TOC to total



**Figure 5** Relation between measured and predicted **a** BP TOC<sup>-1</sup> ( $y = 1.09x - 0.06$ ,  $R^2 = 0.80$ ,  $n = 18$ ) and **b** BGE ( $y = 0.96x - 0.68$ ,  $R^2 = 0.88$ ,  $n = 18$ ), showing the performance of the linear mixing model. Data are shown for three stream categories and for six sampling dates in 2006. Each point represents the mean of two streams within its category. Marker color denotes stream category: black for forest streams (0% mire), white for peat mire outlets (55% mire), and gray for streams with a typical mix of forests and mires in the catchments (20% mire)

stream TOC increases during snow melt. These winter–spring dynamics are similar from year to year at many different sites in the Krycklan catchment [7, 40].

Based on the power relationship between specific discharge and mire/forest TOC export ratio (Fig. 4a), we estimated the relative TOC contribution from the two sources, forests and mires (Fig. 4b), and showed how this contribution was dependent on the proportions between mire and forest and of discharge. The proportion between TOC exported by mire and forest soils was related to discharge in a similar way in all seasons (Fig. 4).

The role of the different soil types as sources of TOC was further stressed by the linear two-source mixing model based on the observed TOC mixing pattern (Fig. 4b). In this paper, we explained the variation in BP and BGE, using values from soil water at different soil depths in forest and mire catchments as end members (Fig. 5). The model predicted changes in BP and BGE well, but both BP and BGE were systematically overestimated by the model. This

suggests that bacteria grew on soil water organic carbon at higher rates and efficiencies than they were able to do on the TOC in streams. Possibly, the potential to support BP decreases with transit time of the water from soil to stream, which is consistent with reports of rapid bacterial turnover of the most labile organic carbon fractions in both soils and streams [3, 37]. Alternatively, the change in BP may be mediated by a parallel change in bacterial community composition, since the soil water bacterial community can be more specialized on degrading the TOC source compared to bacterial communities of streams and lakes [17]. Nevertheless, the model supports our interpretation of how discharge variations affect the export of TOC from forest and mire soils which, in turn, affects aquatic bacterial metabolism.

The hydrology-dependent variations in the dominance of forest and mire TOC sources had pronounced effects on the TOC support for BP in receiving streams. These effects were mediated by TOC quality characteristics and not by the availability of inorganic nutrients, indicated by absent partial correlations (control for TOC) between nutrient variables and BP or BGE (Table 2). Instead, both BP and BGE were strongly correlated to the absorbance ratio  $a_{254}/a_{365}$  (Table 2; Fig. 3) showing that short-term support of bacterial growth was connected to characteristics of TOC reflected by the absorbance ratio. High absorbance ratio probably indicated a high share of low molecular weight compounds in the TOC pool [35], which has been shown to stimulate bacterial growth [24, 28]. In a previous study in the Krycklan catchment [3], we also showed that TOC drained from forests had higher absorbance ratio and promoted BP and BGE to a higher degree than TOC from mires. Consequently, we interpret the results of this study so that increased discharge, during all seasons, activates forest soil layers containing high TOC concentrations, while no corresponding effect occurs in mires. As a result, the influence of forest TOC increases the bacterial substrate availability in the stream, partly because of the high concentrations of TOC in the forest drainage but mainly because forest TOC has a higher substrate quality. Our results (Fig. 2) showed that increased discharge did not increase or decrease the substrate quality of the TOC exported from forest or from mires. Therefore, the stimulation of BP and BGE observed in the streams draining catchments with both forest and mire was an effect of an increased proportion of forest TOC and not of a changing substrate quality of the TOC exported from forest (or mire).

While a clear hydrological control of organic carbon character and support for BP was identified, BR was seemingly independent of the character of the organic carbon (Table 2). This result fits the general picture of BP being more variable and resource dependent than BR [10,

25]. A wide range of natural compounds can be used by aquatic bacteria for respiration, but only substrates of high energy potential can support efficient bacterial growth and only when essential inorganic nutrients are accessible [10, 31]. In addition, while the minimum BR of a bacterium must meet the energy requirements for cell maintenance, BP can proceed at highly variable rates among cells and taxa depending on variations under the conditions controlling growth [25, 34].

The quality differences addressed in this study, which promote BP at high-flow situations, add to the effects of increased concentrations of TOC observed during high-flow episodes in boreal streams, caused by different flow pathways in forest soils [11, 12, 20]. Overall stimulation of BP is an effect of water of higher TOC concentration of higher substrate quality entering the aquatic system. One aspect of this result concerns the effects of high-flow episodes on BP in lakes, where high discharge can cause rapid replenishment of water and TOC resources. Our results can help to explain previous observations of increased BP in boreal lakes during and shortly after high-flow episodes [4, 14].

To conclude, our study demonstrates how patterns in TOC export from different sources can control temporal variations of bacterial growth in receiving freshwaters. Forest drainage supported higher BP and higher BGE than drainage from mires. The relative export of organic carbon from forests was several times larger at high runoff than at low runoff. Consequently, streams, with typical boreal proportions between forest and mire in their catchments, primarily received mire carbon with less support for BP at low flow and forest carbon with higher support for BP at high flow. Stimulation of bacterial growth during high-flow episodes was a result of higher relative export of “high-quality” organic carbon via forest drainage rather than of generally increased drainage of “high-quality” carbon from any specific terrestrial source.

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