

# Terrestrial export of highly bioavailable carbon from small boreal catchments in spring floods

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## SUMMARY

1. We assessed the terrestrial export of organic carbon, which effectively supported aquatic bacterial production (BP), from small boreal catchments during spring flood. We analysed stream runoff from nine small catchments with different proportions of peat mires and coniferous forests by monitoring the dissolved organic carbon (DOC) flux in combination with conducting bacterial bioassays.

2. Multiple linear regression analysis showed that BP during 7-day-dark bioassays (BP<sub>7</sub>;  $\mu\text{g C L}^{-1}\text{day}^{-1}$ ) was explained by both the quantity and quality (low-molecular weight fractions) of the DOC. BP<sub>7</sub> can be used as a measure of export of terrestrial organic carbon that is highly bioavailable.

3. Total export of DOC during spring flood from the different catchments ranged from 20 to 27 kg ha<sup>-1</sup> and was negatively correlated to forest cover (%). However, the export of BP<sub>7</sub> carbon was positively correlated to forest cover and varied from about 0.1 kg ha<sup>-1</sup> in mire-dominated streams to about 0.2 kg ha<sup>-1</sup> in forest-dominated streams.

4. The high bioavailability of forest carbon suggests that forests are the main contributors of BP-supporting carbon in boreal streams although mires have higher area-specific export of DOC.

*Keywords:* bacterial production, bioavailability, dissolved organic carbon, forests, mires

## Introduction

Boreal ecosystems contain approximately 50% of the soil organic carbon pool of the world (Schlesinger, 1997). Part of this pool is subject to hydrological drainage from soils to surface waters. This export and the mineralization of terrigenous organic carbon in streams and lakes can play important roles in global carbon balances (Hope, Billett & Cresser, 1997; Cole *et al.*, 2007). Moreover, recent advances in aquatic research have shown that terrigenous organic carbon make an important contribution to lacustrine food webs by supporting bacterial growth in lakes (Jansson *et al.*, 2007). This effect is particularly important in unproductive boreal lakes (Hessen & Tranvik, 1998;

Jansson *et al.*, 2000). The extent to which bacterial growth in lakes relies on imported terrigenous carbon depends both on its quantity and quality (Tranvik, 1998). The terrestrial export of dissolved organic carbon (DOC) in boreal areas can be highly variable, depending on vegetation, soil characteristics and hydrology (Tranvik & Jansson, 2002), but generally the DOC export is higher from mires than from forested areas (Hinton, Schiff & English, 1998; Raymond & Hopkinson, 2003; Ågren *et al.*, 2007). A common opinion is that the bulk of the organic carbon that enters surface water is refractory and used by bacteria at slow rates. In various batch-incubation experiments, for instance, only a few percent of the organic carbon of terrestrial origin was consumed within 10–20 days (Moran & Hodson, 1990; Tranvik, 1998). Moreover, most of this consumed organic carbon is subject to respiratory losses and does not contribute to bacterial growth (Del Giorgio & Cole,

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1998). Bacterial growth efficiency [i.e. bacterial production (BP) per unit of assimilated carbon] is dependent on DOC quality (e.g. its thermodynamic potential) and can be limited by the availability of nitrogen and phosphorus (Del Giorgio & Cole, 1998). However, the quality of the terrigenous carbon and the possible contributions of different fractions to bacterial growth are largely unknown, although low-molecular weight carbon compounds are generally considered to be better substrates than more complex organic structures (Tranvik & Jørgensen, 1995).

To explore the contributions of carbon exported from different components of the boreal landscape to bacterial metabolism in recipient freshwaters, we have previously carried out studies in the Krycklan catchment in northern Sweden (Buffam *et al.*, 2007). Carbon exported from forest soils stimulated BP and bacterial growth efficiency more than carbon from mires, which was explained by the differences in the character of the organic carbon (Berggren, Laudon & Jansson, 2007). On the other hand, areal organic carbon export was considerably higher from mires than from forested land (Ågren *et al.*, 2007).

These results raised the question of whether forests or mires, which are the dominant landscape types in boreal areas, is the major contributor of organic carbon that supports BP in freshwater systems. This question is centred around whether high-quality/low-quantity (forest) or low-quality/high-quantity (mires) sources make the largest contribution. We address the question in this study by comparing the export of BP-supporting organic carbon from catchments with different proportions of forests and mires. We define BP-supporting carbon as the amount of organic carbon used for BP during 7 days incubation of water from small streams in the Krycklan catchment, sampled during the spring flood period. The choice of the spring flood for this study was motivated by the fact that the spring flood is the major hydrological event of the year, contributing 50–70% of the annual runoff in this region (Laudon, Köhler & Buffam, 2004a), and that the spring flood replaces the entire water volume in the vast majority of Swedish boreal lakes (Lindström *et al.*, 2006). Consequently, the quantity and quality of organic carbon that is drained from terrestrial sources and flushed into lakes during spring plays a critical role for the development of lake biota at the beginning of the summer period (Drakare *et al.*, 2002).

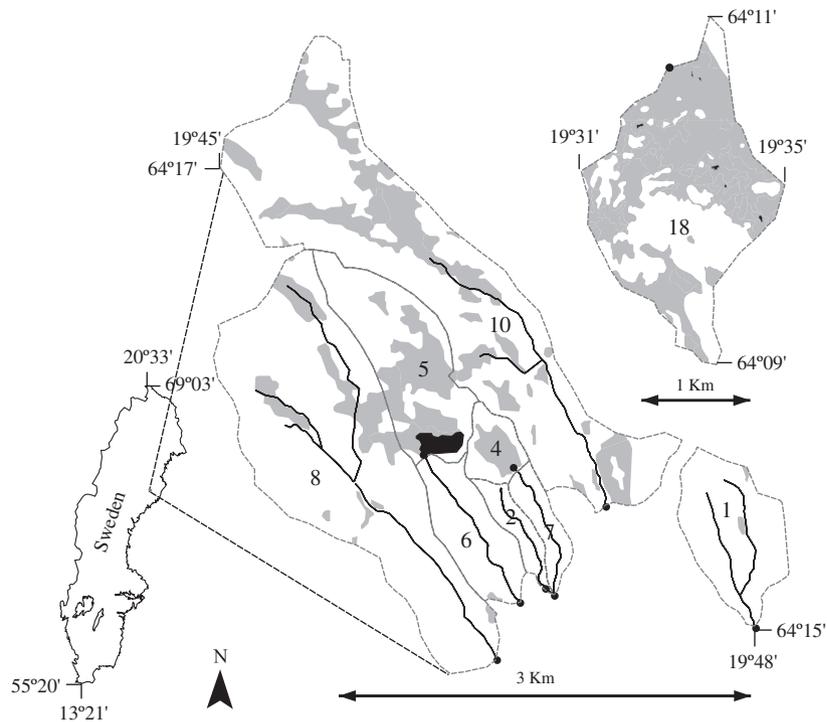
## Methods

### Study sites

Nine small streams in the Vindeln Experimental Forests were chosen: eight in the Krycklan catchment and one in the adjacent Degerö Stormyr catchment. The catchment areas range from 14 to 312 ha, and all streams are of order 1 or 2 (Table 1). Forests and peat mires collectively cover 100% of the catchment areas, except in two of the catchments where lakes cover <5% (Fig. 1). The forest proportion varies between 31% and 100%. The adjacent Degerö Stormyr catchment (C18) was included to increase the range of mire cover (from a maximum of 40% in the Krycklan sub-catchments to 69% at C18). The forests are dominated by Scots Pine [*Pinus sylvestris* (L.)] in dry upslope areas and Norway Spruce [*Picea abies* (L.)] in lower lying, wetter areas. The mires are dominated by peat-forming *Sphagnum* (L.) species and can be categorized as acid, oligotrophic and with varying proportions of ombrotrophic and minerotrophic patches (Granberg *et al.*, 1999). The dominant soil types in the study area are glacial tills (9–94%), peat (0–69%) and thin soils (6–32%). The majority of the catchments are situated above the highest post-glacial coastline (77–100%). Some catchments are interconnected (C2 and C4 drain into C7, and C5 drains into C6). Mean annual air temperature in the region is 1 °C, and the annual precipitation amounts to 600 mm, 35% of which falls as snow between November and April (Ottosson Löfvenius, Kluge & Lundmark, 2003). All snow melts during a 2-month period in spring, resulting in a distinct and annually occurring spring flood. On

**Table 1** Catchment descriptions and stream order for the nine catchments in this study

Site no.	Site name	Stream order	Area (ha)	Water (%)	Forest (%)	Mire (%)
C1	Risbäcken	1	66	0	99	1
C2	Västrabäcken	1	14	0	100	0
C4	Kallkällsmyren	1	19	0	60	40
C5	Stortjärnen Outlet	1	95	5	59	36
C6	Stortjärnbäcken	1	140	3	73	24
C7	Kallkällsbäcken	2	50	0	85	15
C8	Fulbäcken	2	248	0	89	11
C10	Stormyrbäcken	2	294	0	74	26
C18	Degerö stormyr	1	312	0	31	69



**Fig. 1** Location of the studied catchments in the Krycklan drainage basin. Forested areas are shown in white, mires in grey and lakes in black. The solid lines indicate streams, dashed grey lines catchment boundaries and black dots the sampling points. C18 is situated 10 km to the southwest of the other catchments.

average, 60% of annual runoff occurs during this period (Laudon *et al.*, 2004a).

#### *Spring melt discharge and DOC sampling*

Discharge was measured at C7 using a 90° V-notch weir housed in a heated shed. Daily discharge was calculated from continuous recordings of stream water level and established height-discharge rating curves. The specific discharge at C7 was used to estimate the discharge in all catchments, assuming that specific runoff was the same in all catchments. The uncertainty in discharge for C7 has previously been estimated to be  $\pm 5\%$  (Laudon *et al.*, 2004b). The assumption that specific runoff was the same in all catchments introduced potential errors. The inter-site differences in annual discharge (e.g. because of differences in sub-catchment evapotranspiration) has been calculated to be  $\pm 12\%$  (based on discrete discharge measurements at the other sites, which were compared with the continuous measurements at C7) (Ågren *et al.*, 2007). An additional uncertainty because of inter-site differences in flow

regime ('flashiness') has been calculated as a  $\pm 12\%$  maximum error during the spring (Ågren *et al.*, 2007).

For the export calculations, 18 stream water samples were collected from each stream during the spring flood of 2004 (15 April to 5 June) and 16 samples from each stream were collected during the spring flood of 2005 (1 April to 30 May). Samples were gathered every second-day during the peak of the spring flood and every third- to fourth-day at the end of the spring flood. Samples collected in 2004 were filtered through a 0.45- $\mu\text{m}$  mixed cellulose esters filter (Millipore Corporation, Bedford, MA, U.S.A) while those collected in 2005 were frozen without filtration. A comparison between sites covering the extremes of observed flows showed no measurable difference in the concentration of organic carbon because of filtering. Particulate organic carbon concentrations are usually negligible relative to the dissolved fraction in Swedish surface waters (Ivarsson & Jansson, 1995; Laudon & Bishop, 1999). Therefore, all of the organic carbon in the samples collected in this study is referred to as DOC.

### Bioassays

Short-term (11–13 days) bacterial bioassays were made on stream water from six streams (C1, C2, C4, C7, C10 and C18) on four occasions in 2005 and on six occasions in 2006. Although the spring-melt discharge and DOC sampling were conducted in 2004 and 2005, bioassays from 2006 were included to increase the number of laboratory observations. We found no differences between the years in terms of the regulation of bacterial metabolism as no systematic difference could be found in regression residuals (cf. Fig. 3).

Unfiltered portions of 10–15 mL of water was incubated in the dark at 20 °C in 22-mL-glass tubes sealed with gas-tight rubber septa and crimp caps. BP was followed over time using the leucine incorporation method (Smith & Azam, 1992) as modified by Karlsson, Jansson & Jonsson (2002). Subsamples (1.2 mL) from the incubation tubes were pipetted into 1.5-mL Eppendorf tubes exposed to [<sup>3</sup>H]-leucine concentrations between 30 and 70 nmol L<sup>-1</sup> during 1 h in 20 °C. Blanks were pre-treated with 5% w/v of TCA (trichloroacetic acid). 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 & Azam (1989).

Subsamples for BP analyses were taken immediately before the analysis and the rest of the water in the incubation tube was discarded. Every analysis of BP was, in this way, carried out with water from a tube which was undisturbed by previous sampling. During 2005, BP was measured after 1, 2, 3, 5, 8 and 11 days of incubation. In 2006, BP was measured after 1, 3, 5, 7, 9, 11 and 13 days of incubation. As a result of equilibration with a standard air gas mixture before the start of the incubations, the initial concentration of O<sub>2</sub> was 9 mg L<sup>-1</sup> in all samples. Oxygen consumption, calculated from dissolved inorganic carbon production assuming a respiratory quotient of 1, was always less than that value. Considering that an additional 100–300 mg of oxygen per liter of sample water was available in the headspace of the incubation vials, there should not have been any oxygen deficiency during incubations.

Under these conditions BP decreased dramatically during the first 7–8 days of incubation, before continuing at a low level [Fig. 2, see also Berggren *et al.* (2007)]. We denote BP during the first 7 days as BP<sub>7</sub>

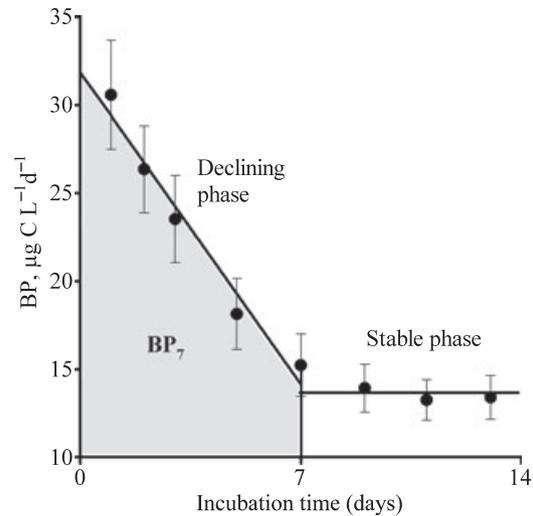


Fig. 2 The definition of bacterial production during 7-day-dark bioassays, BP<sub>7</sub> (shown as the grey area in the graph).

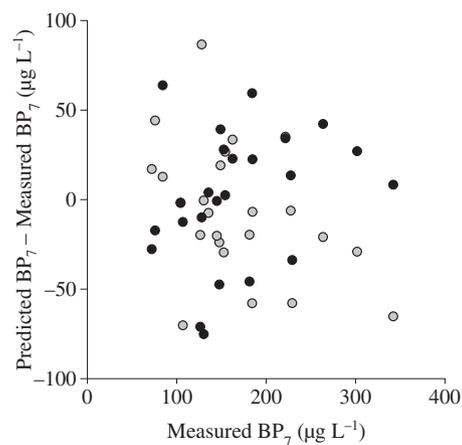


Fig. 3 Residuals from eqn (1) versus measured BP<sub>7</sub> values. The grey dots denote measurements from 2005 and the black dots denote measurements from 2006.

( $\mu\text{g C L}^{-1}\text{day}^{-1}$ ). BP<sub>7</sub> represent the total BP during the first 7 days of incubation but also the amount of organic carbon substrates that supports this BP. In this study, we use BP<sub>7</sub> as a measure of the amount of carbon that supports BP<sub>7</sub> in the different streams; in other words, BP<sub>7</sub> is used as an index of catchment carbon export.

### N, P and DOC analyses

Samples for analyses of N and P fractions were frozen for later analysis. Total nitrogen (TN) and total

phosphorus (TP) were measured on unfiltered water using an Antek 9000 Nitrogen Analyzer (ANTEK instruments L.P., Houston, TX, U.S.A.) and persulphate oxidation. Dissolved inorganic nutrients were measured on filtered water (Whatman GF/F; Whatman International Ltd, Kent, UK);  $\text{NO}_2 + \text{NO}_3$  using an Alpkem RFA 300 autoanalyzer (Astoria-Pacifi.c, Intl. Clackamas, OR, U.S.A.),  $\text{NH}_4$  by the indophenol method and inorganic P as soluble reactive phosphorus (SRP). Dissolved inorganic nitrogen (DIN) was calculated as the sum of  $\text{NO}_2$ ,  $\text{NO}_3$  and  $\text{NH}_4$ . Water samples for DOC analysis were collected in acid-washed, 250 mL high-density-polyethylene bottles, after multiple rinses with stream water. The samples were stored frozen until analysis. The DOC concentrations were analysed using a Shimadzu TOC- $V_{\text{CPH}}$  analyzer (Shimadzu, Kyoto, Japan), after acidifying and sparging the water to remove inorganic carbon. Within 24 h of sampling, absorbance spectra of room temperature samples were analysed in 1-cm quartz cuvettes using a Hewlett Packard 8452A diode array spectrophotometer (Hewlett Packard Corp., Palo Alto, CA, U.S.A.) and portions of purified (ultra) water as blank.

#### Characterization of DOC

The following indices of DOC character were calculated. Organic material C/P and C/N ratios were calculated by dividing DOC by the organic P and N fractions which, in turn, were quantified by subtracting SRP and DIN from TP and TN respectively. The C : N ratio is a significant parameter because organic matter with a high C : N ratio is generally recalcitrant to degradation and aquatic microbes tend to grow inefficiently on it (Kroer, 1993; Del Giorgio & Cole, 1998). The C : P ratio can be interpreted in a similar way, since high C : P is coupled to low-bacterial growth efficiency and BP and vice versa (Lennon & Pfaff, 2005). Further, the ratio between absorbance at 254 nm and 365 nm ( $A_{254}/A_{365}$ ) was calculated. This ratio is negatively correlated with the average molecular weight of DOC (Strome & Miller, 1978; De Haan, 1993; Dahlén, Bertilsson & Pettersson, 1996). Carbon-specific UV absorbance ( $\text{SUVA}_{254}$ ), which is positively correlated with the aromaticity of DOC (Weishaar *et al.*, 2003; Hood, Gooseff & Johnson, 2006), was calculated as the absorbance at 254 nm divided by DOC concentration.

#### Statistical analyses and calculations

We used stepwise multiple linear regression [SPSS 15.0 (SPSS Inc., Chicago, IL, U.S.A.)] to test possible relationships between  $\text{BP}_7$  ( $\text{mg L}^{-1}$ ) and abiotic properties of the stream water. Before the regression analysis all the variables were tested and, where necessary, transformed to fit normal distributions. The organic material parameters (C : N, C : P,  $A_{254}/A_{365}$  and  $\text{SUVA}_{254}$ ) and other measures of water chemistry (TN, TP, DIN, SRP and pH) were used as independent variables. The independent variables were entered into the equation in order of their predictive power for  $\text{BP}_7$ . The process was repeated until adding or removing variables did not significantly improve the explanation of  $\text{BP}_7$ . As stepping method criteria, we used a <0.05 probability of *F* for variable entry and <0.10 probability for removal. The residuals were tested for heteroskedasticity with Whites test (Gupta, 1999).

#### Export calculations

Daily DOC concentrations and absorbance ratios ( $A_{254}/A_{365}$ ) were calculated by linear interpolation between measured values during the spring flood of 2004 and 2005. The daily export of DOC was calculated from daily DOC concentrations, and daily discharge from C7. With these data and using a linear regression model which was used to estimate  $\text{BP}_7$  from absorbance ratio and DOC concentration, we calculated the export of  $\text{BP}_7$  from all nine study catchments during the spring flood periods of 2004 and 2005. Total export of DOC and  $\text{BP}_7$  during the spring flood was obtained as the sum of the daily exports. The uncertainty in calculating  $\text{BP}_7$  from the multiple regression model was calculated as the standard deviation of the residuals in the regression. The uncertainties in  $\text{BP}_7$  export were calculated using Monte Carlo simulations. The combined error from the discharge measurements and  $\text{BP}_7$  estimates from the multiple regression was calculated using 10 000 realizations with random parameters generated from the distributions above.

#### Results

Both the character and the quantity of organic carbon were of importance in explaining the amount of  $\text{BP}_7$

carbon exported from forests and mire soils. The stepwise multiple linear regression procedure resulted in a model with the two variables  $A_{254}/A_{365}$  (organic carbon quality) and DOC-concentration (organic carbon quantity) as the best combination of independent variables for explaining variation in  $BP_7$  (eqn 1). A linear regression between DOC and  $A_{254}/A_{365}$  showed no significant relationship between the variables ( $r^2 = 0.04$ ,  $P = 0.13$ ,  $n = 60$ ); hence they showed a low degree of collinearity and can both be included in the model. Neither graphical inspection of the residuals (Fig. 3) or White's test indicated heteroskedasticity in the residuals.

$$BP_7(\mu\text{g L}^{-1}) = 147.5 A_{254}/A_{365}(\text{unitless}) + 4.9 \text{ DOC (mg L}^{-1}) - 581.6$$

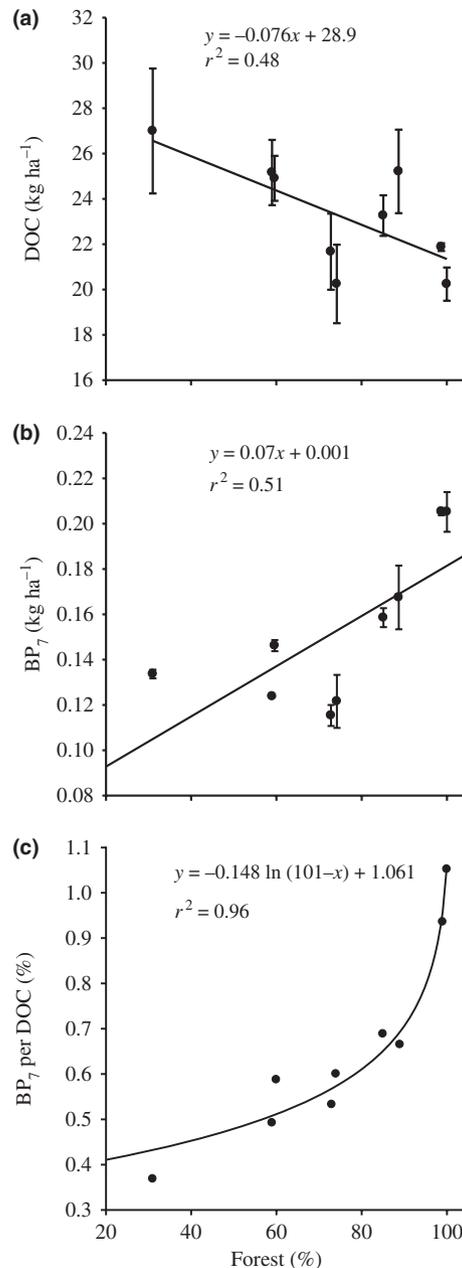
$$(r^2 = 0.54, P < 0.001, n = 60) \quad (1)$$

This result raised the possibility of using eqn (1) as a model for estimating  $BP_7$  carbon for sites or occasions where we did not measure  $BP_7$  but have data on  $A_{254}/A_{365}$  and DOC concentrations. In this way, we could increase the number of observations to be used for assessing the differences between forest and mires with respect to their export of  $BP_7$  carbon.

Approximately 32 000 kg of DOC were exported from the nine catchments during snowmelt (average of the 2 years). The corresponding export of  $BP_7$  carbon was 190 kg. Area-specific export of DOC during snowmelt ranged, on average, from 20 to 27 kg ha<sup>-1</sup> between the catchments and was negatively correlated with forest cover (%) of the catchment (Fig. 4A). The calculated export of  $BP_7$ , on the other hand, was positively correlated with forest cover, with values between 0.12 and 0.21 kg ha<sup>-1</sup> (Fig. 4B). The relationship in Fig. 4B suggests that forests exported about 0.2 kg ha<sup>-1</sup> of  $BP_7$  carbon while mires exported <0.1 kg ha<sup>-1</sup>. Consequently, the percentage of DOC export that supports  $BP_7$  was positively correlated to forest cover (Fig. 4C) and increased logarithmically with increasing forest cover. The Monte Carlo analysis showed that the uncertainty in the calculation of  $BP_7$  export ranged from  $\pm 31$  to  $\pm 33\%$  among the nine sites.

## Discussion

As reported in many previous studies of DOC export from terrestrial systems (Hinton *et al.*, 1998; Schiff



**Fig. 4** (a) Average amounts of dissolved organic carbon (DOC; kg ha<sup>-1</sup>) and (b) calculated [from eqn (1)] spring flood export of  $BP_7$  carbon from nine catchments with differing forest cover. Error bars show  $\pm 1$  SD from the mean of 2004 and 2005 spring export. Both regressions are significant at the 0.05 probability level. Panel c shows  $BP_7$ -carbon expressed as a percentage of total DOC export; this regression is significant at the 0.001 probability level.

*et al.*, 1998; Creed *et al.*, 2003), our study showed that mires export more DOC per unit area to aquatic systems than forested areas. The comparison of the nine catchments included in this study indicated that

mires could export about 1.5 times more DOC, per unit area, than forests during spring flood. Thus, it might be assumed that mires provided disproportionately high amounts of aquatic BP-supporting organic carbon relative to the areas they cover in the catchments. However, this was not the case, since the higher availability of the forest DOC for BP compensated for the lower areal export of forest DOC. The areal export of BP<sub>7</sub> carbon was approximately twice as high from forested land than from mires during the spring flood. In turn, this means that in catchments with the average proportion of forests and mires in the boreal area [75% forest, 20% mire (Nilsson, 2007)] almost 90% of the BP<sub>7</sub> carbon may come from forests.

We have insufficient data for explaining why DOC from mires and forested land differ in the level of support provided to BP. However, we attribute this difference to differences in the composition of their DOC rather than to their contents of inorganic nutrients, since (i) BP<sub>7</sub> was strongly correlated with the measured DOC properties (eqn 1), (ii) no correlations were found between BP<sub>7</sub> and concentrations of organic or inorganic nitrogen and phosphorus fractions or organic C : N and C : P ratio and (iii) nutrient-enrichment experiments have indicated that BP is more nutrient limited in streams draining forests than in streams draining mires (Berggren *et al.*, 2007). The correlation of BP<sub>7</sub> with the  $A_{254}/A_{365}$  ratio (eqn 1) suggests that BP<sub>7</sub> is dependent on low-molecular fractions of bulk DOC. This interpretation is supported by UV-light exposure experiments, where increases in  $A_{254}/A_{365}$  ratios have been coupled to decreasing molecular weight of substrates and to enhancements of bacterial growth (Lindell, Graneli & Tranvik, 1995; Obernosterer & Herndl, 2000). Fractions of low-molecular weight DOC can originate (*inter alia*) from the exudation of simple organic carbon compounds by roots and mycorrhizal fungi and the leaching of low-molecular weight organic acids from dead roots and recently deposited litter (Van Hees, Rosling & Finlay, 2006). These compounds should be produced at faster rates and to greater extents in forest systems, where production and degradation of organic material can be expected to occur at significantly higher rates than in oligotrophic mires.

It should be stressed here that our measure of BP<sub>7</sub> carbon is not identical to the total amount of carbon

supporting BP that is supplied by spring flood DOC. As can be seen in Fig. 2, the DOC also stimulated BP over a longer term, but at much lower levels, presumably because of its content of recalcitrant, but slowly exploited substances. This fraction appears to be less important for BP than the readily available fraction (BP<sub>7</sub>), at least during high-flow episodes like the spring flood when input to aquatic systems exceeds biological exhaustion rates. It should also be noted that the BP<sub>7</sub> assays were carried out at 20 °C, which is considerably higher than the temperatures (usually well below 10 °C) in streams and lakes during spring flood period. Thus, the use of the BP<sub>7</sub> carbon is likely to be considerably slower in nature than in our laboratory incubations. Since the transit time for water between entering a stream and reaching a lake during the spring flood is short (ranging from minutes to a few days at most), most of the BP<sub>7</sub> supporting DOC is likely to be metabolized in lakes, where the retention times are weeks, or longer, even during high flow. It is, therefore, interesting to compare our results with those of previous studies of the humic Lake Öträsket, which is close to the Krycklan catchment. The spring flood replaced all the water in this lake, and BP was high throughout the spring flood period but markedly declined during the summer (Bergström & Jansson, 2000). It was suggested that the high BP after the spring flood was because of inputs of highly bioavailable DOC. Other studies in the same lake showed that high BP after the spring flood was a regular phenomenon that substantially affected the productivity and composition of the planktonic community (Drakare *et al.*, 2002). The present study of the Krycklan catchment suggests that high-lake BP during and some time after the spring flood are driven by DOC exported from the soils of the coniferous forests, and that even though BP<sub>7</sub> is supported by a small sub-pool of total DOC, this pool can be a major contributor to lake BP. Further corroboration of the importance of a small, readily available carbon fraction, is provided by a recent study of a slightly humic lake in northern Sweden, in which import of amino acids and monosaccharides (accounting for at most a few percent of inlet DOC) appeared to be sufficient to support about 30% of the BP during summer (Jonsson, Ström & Åberg, 2007).

We conclude that forest soils can export DOC with a higher potential to support aquatic BP than mire soils

in boreal catchments, and that BP in surface waters of typical boreal catchments is supported mainly by drainage from forested land during the spring flood period. We suggest that most of the BP<sub>7</sub> carbon is metabolized and used for BP in lake ecosystems and supports high BP values in boreal lakes during and shortly after the spring flood period.

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